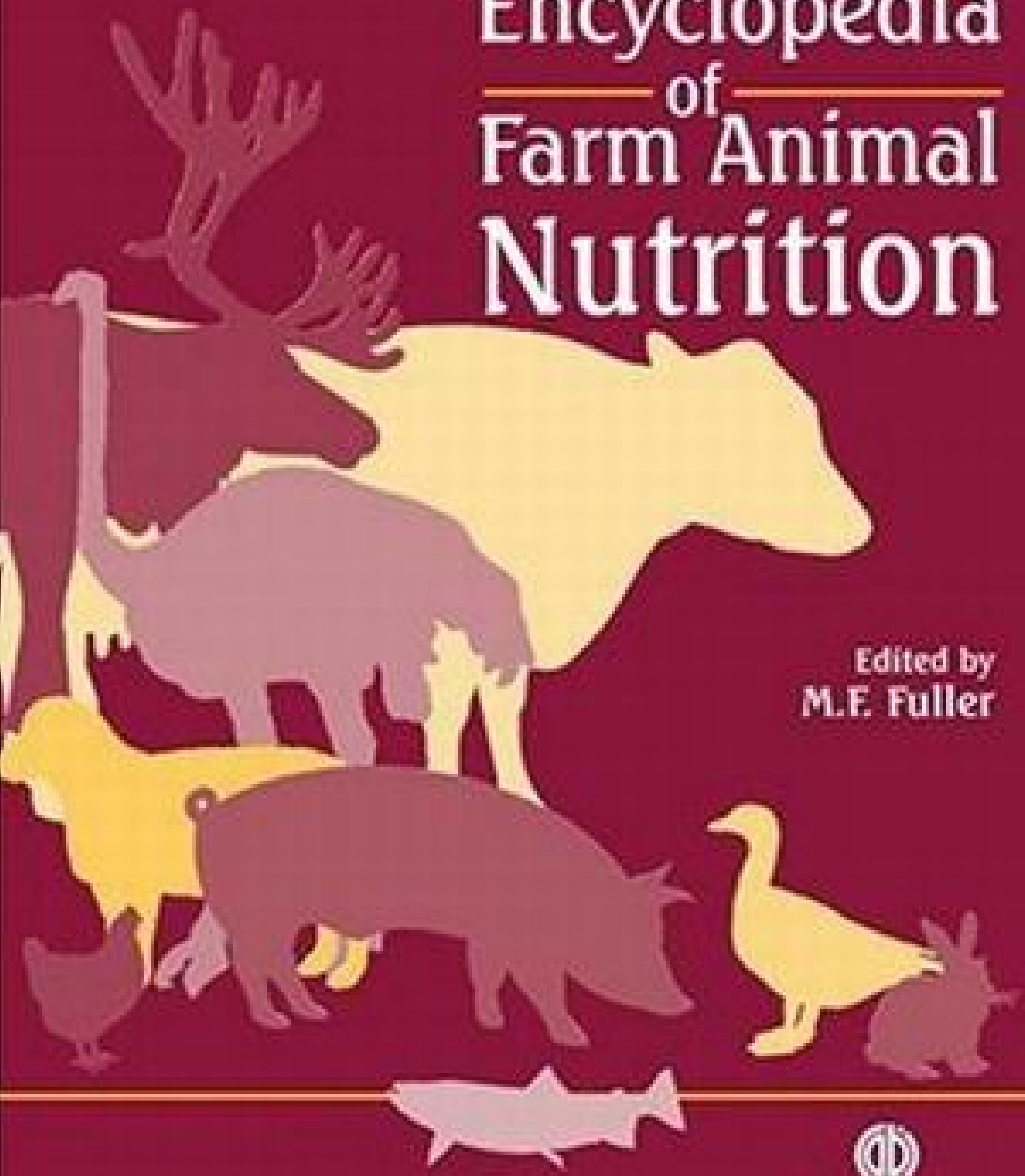
The Encyclopedia of Farm Animal Nutrition



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Preface

An encyclopedia should properly encompass the totality of human knowledge, or at least of some particular sector of it. Not so many years ago it would have been possible to contain all that was known of animal nutrition in a book the size of this, for the science of nutrition is young, but such has been the pace of its growth that that is no longer possible. The nutrition of farm animals is a complex subject, reaching into biochemistry, physiology, pathology, veterinary medicine, animal husbandry and agriculture and even, as evidenced in the following pages, beyond those disciplines. The subject matter of farm animal nutrition is covered in a large number of text books – most are referred to in the entries of this encyclopedia – but their arrangement does not lend itself to the rapid recovery of specific pieces of factual information and it was with that object in view that this encyclopedia was devised and written. Its aims are completeness, accuracy, succinctness and ease of access. The aim of completeness – to include as much factual information as possible – was addressed by embracing all the ramifications of nutrition just mentioned. Yet, no doubt there are omissions. To achieve a high degree of accuracy authors were chosen for their expertise in specialized areas of nutrition. But mistakes there surely are and for those that I have failed to spot I would plead, as that pioneer lexicographer Dr Johnson famously pleaded, when asked by a lady why he had defined 'pastern' as 'the knee of a horse', 'Ignorance, Madam, pure ignorance'. To encompass the whole of farm animal nutrition in this space obviously requires succinctness and all the contributors were enjoined to be as brief as possible – though some found it harder than others. Finally, ease of access is ensured by the alphabetical arrangement of the entries and the system of cross-references. There is more on this in the note that follows.

Although there have been other encyclopedias of nutrition they have been more in the nature of collections of review articles, valuable certainly, but not providing the ready access to specific facts and figures that is the essence of this work. This is the first encyclopedia to be devoted exclusively to the nutrition of farmed animals, including birds and fish. It contains some 2000 entries, written by about 100 specialists and reviewed by an international editorial panel. The entries range from short definitions of terms to extended descriptions of subjects of major importance. The entries are illustrated by figures (e.g. chemical structure, anatomy, graphs), tables (e.g. families of nutrients, feed composition) and photographs (of things that can best be appreciated visually). Entries are supported by references to important original papers and reviews, with suggestions for further reading. The encyclopedia includes definitions of terms commonly used in nutrition; chemical structures and functions of nutrients, important metabolites, toxins, etc.; explanations of nutritional processes; their physiological and metabolic bases; descriptions of the major farmed species, their metabolism and practical feeding; composition and nutritional value of important crops and feedstuffs; feed processing; feeding systems. It is intended as a book that users will regularly refer to for information because they know it will be there.

Because this is the first time that such an encyclopedia has been published, it must also be seen as a work in evolution, not yet complete. To further its evolution, so that future editions can be more nearly complete, more accurate and more informative, readers are invited, and requested, to submit their suggestions for amendments. Just as the first editor of the *Oxford English Dictionary* relied upon a host of contributors to submit material, it seems appropriate to ask the readers of this volume, some of whom undoubtedly have specialized knowledge, to contribute, if they will be so kind. Suggested amendments should be addressed to the Editor-in-chief, care of the publisher.

This book represents the combined efforts of many people and I would like to thank, first, the authors, who have distilled their many years of learning into a very few words. I owe a great debt of gratitude to my fellow editors who have not only secured the services of the many contributors but helped me to edit the resulting writing so as to achieve some kind of uniformity of presentation. In addition to the editors whose names are on the title page, I am most grateful to those who, for various reasons, were unable to complete their roles; to the late Dr John Topps, to Dr Angus Russell, Dr Colin Fisher and Dr Julian Wiseman.

I wish to express particular appreciation to Rebecca Stubbs, Development Editor (Books and Reference Works) at CAB International. Her patience in the face of numerous delays and her helpfulness have made an enjoyable experience of what could have been an irksome chore. I am also most grateful to Sarah Williams for her careful work on the manuscript and to Rachel Robinson for production. Finally, I thank my wife Margaret for her tolerance of all the hours in which I have neglected her, the house and the garden.

Malcolm Fuller
Stony Brook, New York
September 2003

Notes on Using the Encyclopedia

The entries are in alphabetical order, using English, not American, spelling. Where there are two or more names for the same subject, the entry appears under the most common name, alternative names appearing as blind entries, directing the reader to the common name under which the entry appears. For example '**Gossypose:** *see* Raffinose'.

Within an entry, a bold typeface highlights a word that is an entry in its own right. For example, in the entry 'calorimetry' the passage 'Distinction must be made between **direct calorimetry**, which is the physical measurement of heat given off by the animal, and **indirect calorimetry**, in which the measurements are of the chemical quantities involved in metabolism … ' indicates that there are also entries on direct calorimetry and indirect calorimetry.

Where information related to the content of an entry is to be found elsewhere, but where the cross-reference is not indicated by a highlighted word in the text, there may be a footnote beginning '*See also*' to direct the reader to that other material. For example, the entry 'absorption' does not contain the word 'digestion' but the entry 'digestion' nevertheless includes information on absorption.

A

Abalone A large marine snail or gastropod of the family of molluscs Haliotidae. More than 50 species have been identified. Abalone have a hard shell and a muscular foot. They inhabit rocky shorelines, from shallow water up to depths of approximately 40 m. Their shells are rounded or oval with a large dome towards one end. The shell has a row of respiratory pores. The muscular foot has strong suction power, permitting the abalone to clamp tightly to rocky surfaces.

Abalones have succulent meaty bodies with a delicious flavour, placing them in high demand in Japan, China and other Asian countries. With their capture fisheries in serious decline, abalone farming is expanding in Taiwan, Chile, Iceland, Mexico, USA, Australia, Thailand and several countries in South-east Asia; however, South Africa is the world's largest producer of cultured abalone. In the natural environment abalone graze on benthic (bottom-growing) algae, but formulated diets from a combination of animal and plant protein sources have been developed for feeding farmed abalone. (SPL)

Abdominal fat In most domesticated species, deposits of abdominal fat can be divided between peritoneal and inguinal regions; the exception is the duck, in which subcutaneous fat deposits, required for thermal insulation, comprise the largest single depot and are a special development in this species. The fat of the peritoneum is located within the abdominal cavity and extends ventrally over the visceral mass, being attached to the peritoneal membranes lining the abdominal wall. Inguinal fat lies along the interior femoral and tibiotarsal region and extends from the sartorious muscle to approximately two-thirds the length of the tibiotarsus. Consistency and appearance of fat in terms of its chemical and physical nature can vary between species, reflecting not only genetic traits but also diet. For example, abdominal deposits of fat in horses and certain Channel Island breeds of cattle are yellow while those of sheep are hard and white and those of pigs soft and greyish in colour. Body temperature is important, with fat being almost semi-fluid compared with that at cooler temperatures. Brown adipose tissue is not found in abdominal fat stores. (MMax)

Abomasum The fourth compartment of the ruminant stomach. It communicates anteriorly with the omasum through the omaso-abomasal opening, and posteriorly with the duodenum via the pyloric orifice. Like the stomach of non-ruminants, it is lined with a glandular epithelium that secretes mucus, hydrochloric acid and proteolytic enzymes. (RNBK)

Abortion Abortion is defined relative to the stage of pregnancy when the embryo or fetus is lost. In cattle, early embryonic death refers to deaths occurring from the day of conception until about 42 days of gestation (the end of the embryonic period), which coincides with the end of differentiation. Embryos lost during this period may be either resorbed or aborted. A normal rate of early embryo resorption (0–45 days) is 9–12% and abortion or resorption after 45–60 days is usually rare (1–2%). Higher rates are attributed to disease. Bovine fetuses discharged from day 42 until approximately 260 days are generally called abortions, and from day 260 until normal term (281 ± 3 days), premature births.

Dietary causes of embryonic death, abortion or premature birth include poisonous plants, fungi and synthetic toxicants. Plants associated with abortion or premature birth include *Pinus* species (*P. ponderosa*, *P. radiata*, *P. taeda*, *P. cubensis*), *Juniperus communis*, cypress (*Cupressus macrocarpa*), snakeweeds (*Gutierrezia sarothrae* and *G. microcephala*), locoweeds (*Astragalus* spp. and *Oxytropis* spp. containing swainsonine), hairy vetch (*Vicia villosa*), darling pea in Australia (*Swainsona* spp.) and leucaena (*Leucaena leucocephala*). Mycotoxins include ergot alkaloids from grains and grasses infected with *Claviceps* and *Balansia* spp., loline alkaloids from endophyte-infected tall fescue, trichothecenes from *Fusarium* spp., grains and maize silage infected with *Aspergillus* and *Penicillium* spp. and hay and straw and mouldy sweet clover (dicoumarol) contaminated with *Stachybotrys* spp. Xenobiotics believed to contribute to embryo or fetal loss include nitrates and nitrites, high-protein diets (excess urea), carbon monoxide, oestrogenic compounds, glucocorticoids, lead, phenothiazines, oxytocin, chlorinated pesticides (DDT, dieldrin, heptachlor) and warfarin (coumarins). (KEP)

Absorption The process by which nutrients are transported from the lumen of the gastrointestinal tract to the blood or lymphatic system. Absorption of most nutrients occurs predominantly in the **jejunum**. Absorption of intact macromolecules is very limited. Most are degraded into their constituents by digestive enzymes in the intestinal lumen: proteins to amino acids and small oligopeptides; glycogen to maltose, isomaltose and small oligosaccharides; triglycerides to fatty acids, 2-monoglycerides and glycerol. Further degradation of proteins and carbohydrates occurs at the brush border surface under the influence of a large number of specific enzymes for degradation to their monoconstituents, amino acids (small amounts of peptides may pass to the blood) and the hexoses glucose, fructose and galactose (fructose is converted to glucose in the intestinal cells before being transferred to the blood). Degradation products from lipids are emulsified by bile salts and lecithin and organized in micelles which diffuse through the unstirred water layer to the membrane of the brush border, where the components are absorbed except the bile salts.

Absorption of macromolecules can occur in specific instances; for example, absorption of immunoglobulins from colostrum in newborn mammals is performed by pinocytosis, mainly in the ileum.

Absorption of some minerals and of degradation products from microbial fermentation, such as short-chain fatty acids (SCFA), also takes place in the large intestine. In the horse, up to 70% of the absorbed energy is absorbed as SCFA in the colon. In ruminants, absorption of these products mainly takes place in the fore-stomach.

Little water is absorbed from the stomach, but it moves freely across the mucosa in both directions in the small intestine and large intestine and generally the osmolality in the intestinal lumen is close to that of plasma. In the colon, sodium is pumped out and water moves passively with it. (SB)

See also: Digestion; Intestinal absorption

Acceptability: *see* Palatability

Acetaldehyde An aldehyde, $CH_3 \cdot CHO$. It can be produced chemically by oxidation of ethanol $CH_3 \cdot CH_2OH$. In cellular metabolism, acetaldehyde is an intermediate produced in the conversion of ethanol to acetic acid. After activation in the cell, acetic acid can be used as a source of energy. Acetaldehyde can be toxic. (NJB)

Acetate $CH_3 \cdot COO^-$. Acetic acid, $CH_3 \cdot COOH$, is one of the three (acetic, propionic, butyric) common short-chain volatile fatty acids found in intestinal contents. This fatty acid accounts for a major proportion (more than half) of the short-chain fatty acids produced by anaerobic fermentation in the rumen or in the large intestine. In cellular metabolism, acetate is converted to acetyl-coenzyme A (CoA) prior to being used in catabolic or anabolic processes. Acetyl-CoA is a major metabolic intermediate in the catabolism of fatty acids and carbohydrates to carbon dioxide and water and of amino acids to carbon dioxide, water and nitrogen end products in the production of the cellular energy in the form of ATP. In cellular biosynthetic activities, acetate as acetyl-CoA is the precursor for all of the carbon in long-chain fatty acids (16–18 carbons), ketones and cholesterol. (NJB)

Acetic acid: *see* Acetate

Acetoacetate $CH_3 \cdot CO \cdot CH_2 \cdot COO^-$, one of the three ketone bodies (acetoacetate, β-hydroxybutyrate and acetone) produced in the incomplete oxidation of fatty acids. In the liver, fatty acids, via their metabolism to acetyl-coenzyme A, can produce acetoacetyl-coenzyme A which in turn can be converted to the other two ketone bodies. Acetoacetate and β-hydroxybutyrate can be taken up by other tissues and used for energy. (NJB)

Acetone $CH_3 \cdot CO \cdot CH_3$, one of the three ketone bodies (acetoacetate, β-hydroxybutyrate and acetone) produced in the incomplete oxidation of fatty acids. Because acetone is volatile and has a unique sweet odour, it can sometimes be detected in the breath of ketotic animals. Acetone is not further metabolized and is lost from the animal. (NJB)

Acetyl-CoA Acetyl coenzyme A, $CH_3 \cdot CO \cdot SCoA$, is the metabolically active form of acetate. It is produced in the metabolism of carbohydrates, fatty acids and some amino acids. Free acetate is converted to acetyl-CoA in the cytoplasm of cells and utilizes coenzyme A and ATP in its production. (NJB)

Acetylcholine A neurotransmitter, $(CH_3)_3N^+ \cdot CH_2 \cdot CH_2OOC \cdot CH_3$. It is formed in nerve endings by combining acetyl-CoA with choline and is found in synaptic vesicles. These vesicles are released into the synapse in response to nerve impulses and initiate a response in another nerve or muscle. (NJB)

Acid–base equilibrium The balance between acids (elements or compounds that increase H^+ concentration) and bases (elements or compounds that decrease H^+ concentration). Neutrality (equal balance of acid and base) is at a pH of 7.0 (H^+ concentration $= 1 \times 10^{-7}$ mol l^{-1}). However, homeostatic mechanisms in living organisms tend to maintain an extracellular fluid pH between 7.35 and 7.45. Survival of the organism is not possible outside of the range of a pH between 7.0 and 7.7. Acidosis is defined as a blood pH < 7.35 and occurs with prolonged starvation, severe diarrhoea, asphyxia, ketosis and lactic acidosis. Alkalosis is defined as a blood pH > 7.45 and is associated with hyperventilation, vomiting of gastric acid and diuresis. Three systems within the body are primarily responsible for maintenance and regulation of acid–base equilibrium. These are the physiological buffers, the respiratory system and the renal system. These systems are interrelated and provide relatively rapid responses to shifts in acid–base equilibrium. The gastrointestinal tract also plays important roles in acid–base equilibrium but the responses are of greater consequence to long-term regulation and involve shifts in absorption and excretion of mineral ions.

Major physiological buffers include bicarbonate, phosphate and proteins. Bicarbonate ions (HCO_3^-) and hydrogen ions (H^+) are in equilibrium with carbonic acid (H_2CO_3), a weak acid. Carbonic acid is produced by enzymatic action of carbonic anhydrase from CO_2 and H_2O. The formation and end-products of bicarbonate can be easily eliminated via respiratory or renal systems without an effect on pH. Since mechanisms exist to maintain a constant extracellular concentration of bicarbonate ions (which are an excellent buffer for physiological fluids), the bicarbonate buffer does not provide a means for net elimination of acidic or basic loads imposed on the body. In terms of acid–base equilibrium, the bicarbonate buffer is considered a futile cycle since net elimination of bicarbonate as CO_2 via the lungs is eventually compensated for by renal synthesis of bicarbonate by the kidneys with no net change in H^+. Phosphate ions buffer H^+ in physiological fluids and contribute to the net equilibrium of acids and bases in the body. Within physiological pH ranges the concentration of dibasic (HPO_4^-) phosphate ions is approximately four times the concentration of monobasic ($H_2PO_4^-$), but the kidneys can concentrate H^+ in urine to a pH as low as 4.5. As urine pH decreases, the dibasic phosphate ions provide a buffer by accepting H^+ to form monobasic phosphate, thus providing net elimination of H^+ from the body.

Another major route for a net elimination of H^+ from the body involves renal production and secretion of ammonium ions from glutamine catabolism. Under acid loads a transporter in renal mitochondria is inhibited, resulting in additional degradation of glutamine and excretion of H^+ as ammonium (NH_4^+).

The strong ion difference (SID), which is the sum of all strong cations (mol l^{-1}) minus the sum of all strong anions (mol l^{-1}), also impacts on the regulation of acid–base equilibrium. The SID affects the partial pressure of blood CO_2 and renal electrolyte excretion. Shifts in SID impact renal compensation by changes in the relative amounts of ammonium and phosphate ion excretion. (TDC)

Acid-detergent fibre (ADF) The detergent fibre analysis scheme was introduced to overcome inadequacies in the use of the traditional acid–alkali crude fibre estimation when applied to fibrous forage feeds for ruminants (Van Soest, 1970; see table).

The determination of ADF involves the extraction of food (1 g) by boiling (1 h) in acid-detergent solution (100 ml; 2% cetyltrimethylammonium bromide (CTAB) in 0.5 M H_2SO_4). The insoluble residue is filtered, washed with acetone, dried (8 h, 100°C) and weighed. This residue, which includes cellulose, lignin and some inorganic elements such as silica, is described as ADF. The residue can be used for subsequent measurement of cellulose after oxidation of lignin by saturated potassium permanganate solution and removal of manganese dioxide by oxalic acid (Van Soest and Wine, 1968). (IM)

References and further reading

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Acid-detergent fibre nitrogen (ADFN) The amount of nitrogen retained in the acid-detergent fibre residue. Also called acid-detergent insoluble nitrogen (ADIN), it has been used to determine heat damage to proteins in feedstuffs. Excessive heating of foods containing protein and carbohydrate leads to Maillard reactions which cause the formation of covalent bonds between aldehyde groups in carbohydrate and free amino group residues on protein, especially lysine. ADFN is an indicator of these heating effects, which decrease the digestibility of the protein. (IM)

Classification of forage fractions using the detergent fibre methods of Van Soest (1967).

Fraction	Components
Cell contents (soluble in neutral detergent	Lipids
	Sugars, organic acids and water-soluble matter
	Pectin, starch
	Non-protein N
	Soluble protein
Cell wall constituents (fibre insoluble in neutral detergent)	
1. Soluble in acid detergent	Hemicelluloses
	Fibre-bound protein
2. Acid-detergent fibre	Cellulose
	Lignin
	Lignified N
	Silica

Acid treatment Acids are generally applied to forages either to improve the degradability of poor quality cereal crop residues or to enhance pH reduction during ensiling. They are also used as dietary supplements to help maintain blood pH. The addition of either hydrochloric or sulphuric acid to cereal straws reduces hemicellulose content but has little effect on either cellulose or lignin. However, digestibility and intake improve and so, like alkali treatment, acid treatment may hydrolyse the ester bonds between lignin and the other cell wall polysaccharides. Again like alkali treatment, acid treatment improves degradability, but sufficient dietary protein must be supplied to ensure that this potential can be realized. Animals consuming cereal straw treated with acid and urea have been shown to have both an enhanced flow of microbial protein to the small intestine and increased nitrogen retention. An additional benefit identified with this combined treatment is that acidification appears to enhance the degree of ammoniation of straw by the urea. When sulphuric acid is used, the sulphur content of the treated material increases, which may be beneficial as sulphur is a vital element in the production of microbial protein. It is generally recommended that where additional nitrogen is supplied, sulphur should be provided at a ratio of S:N of about 1:12. Short-term treatment of cereal straw with organic acids such as formic acid have no effect on either digestibility or intake, with the acids being degraded in the rumen to methane and carbon dioxide.

The most common use of acids is their incorporation into the herbage mass to enhance the rate of pH reduction during ensiling. Successful preservation of plant material as silage depends on rapidly achieving a controlled fermentation under anaerobic conditions and the conversion of water-soluble carbohydrates to lactic acid. At pH 3.8 to 4.3, microbial activity is inhibited, resulting in well-preserved, stable silage. When the crop and conditions within the silo permit, no additives are needed; but where either these are inadequate or to minimize losses in fermentation, the desired pH can be partly achieved by direct acidification. This promotes a lactic acid fermentation and lowers the energy cost of fermentation. A.I. Virtanen of Finland first developed the use of acids in this way in the 1930s. In what became known as the AIV method, combinations of sulphuric and hydrochloric acids were added to forages at ensiling to encourage the rapid reduction of pH (< 4) so as to suppress proteolytic activity. A number of acid-based silage additives are now available. For safety and to limit their corrosive effect, weaker organic acids such as formic acid are used, either alone or in combination with fermentation inhibitors such as formalin. The application of acids has been shown to increase animal performance, due to reduced losses of nutrients as well as improved protein quality, palatability and intake. (FLM)

Acidification Acids are sometimes added to animal feed ingredients or diets to protect the material against microbial deterioration or to reduce the pH in the animal's stomach. Propionic acid can be added to hay or cereal grains to prevent the growth of moulds and the formation of mycotoxins. This allows such feed materials to be stored safely with a higher moisture content than is normally recommended. Short-chain organic acids (e.g. formic, propionic, fumaric and citric) can be added to diets for newly weaned piglets to reduce digestive upsets. The young piglet has an immature gut, where enzymatic activity and hydrochloric acid secretion are not sufficiently developed; piglet feeds often have a high acid-binding capacity and are fed in relatively large meals. Organic acids reduce the incidence of diarrhoea in piglets by their antimicrobial action on the feed itself, by reducing stomach pH and by acting as energy sources. Lactic acid can be added to dried milk powder for artificial rearing of calves. Lactic acid preserves reconstituted milk, allowing *ad libitum* feeding of cold milk; it also reduces the pH of the calf's abomasum, thereby assisting clot formation. (PCG)

Acidity of the gastrointestinal tract The quality of being acid describes a solution with a pH less than 7.0. The contents of the stomach or abomasum are normally acid because of the secretion of 0.15 M hydrochloric acid by the parietal cells in the gastric mucosa. This acid is bacteriocidal for many ingested organisms; it also provides the necessary pH for the conversion of pepsinogen to pepsin and for the latter to start the digestion of dietary protein. The gastric mucosa is protected from self-digestion by an unstirred layer of mucus, made alkaline with bicarbonate.

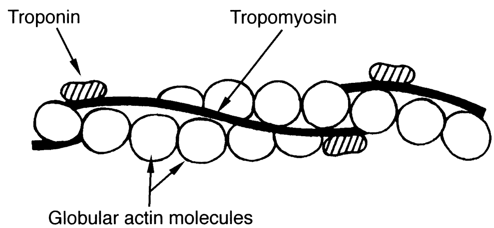
Because of its high content of bicarbonate, the pancreatic juice secreted into the duodenum is alkaline, e.g. pH 8.0. In addition, bile and intestinal juice both tend to be alkaline and so these three secretions soon neutralize the gastric contents entering the duodenum and raise the pH of the duodenal contents to 6.0–7.0. By the time the chyme reaches the jejunum, its reaction is neutral or may become alkaline, depending on the species. This has an important bearing on the solubility of calcium phosphate and the absorption of calcium ions from the upper part of the small intestine (*see* **Hyperparathyroidism**).

The pH of the contents of the large intestine is close to neutrality; however, in the horse, and other species in which there is a good deal of cellulose fermentation in the caecum and colon with the production of volatile fatty acids, the pH of the gut contents in these regions is nearer 6.0 than 7.0. (ADC)

Acidosis: *see* Lactic acidosis

Acorn The fruit of the oak tree (*Quercus* spp.). Acorns can be dehulled but are more frequently fed whole as, for example, to Iberian pigs in southern Europe to produce highly prized hams. These hams are considered to have special flavour due to the tannins and fatty acids in the acorns. The tissues of pigs fed acorns have high concentrations of α-tocopherol, which reduces oxidative damage to the tissue. The crude protein of acorns is low (about 60 g kg^{-1}) and their digestible energy for pigs is 11–12 MJ kg^{-1}. Acorns contain hydrolysable tannins which degrade to produce pyrogallol. The consumption of acorns has been responsible for pyrogallol toxicity in cattle. (TA)

Actin A water-soluble protein (molecular weight 43,000) containing 376 amino acids. It is found in muscle and other tissues with motile function. It provides the thin filament backbone and combines with myosin to produce muscle contraction in the presence of adenosine triphosphate (ATP). Actin is the second most abundant protein in muscle, making up 10% of the total protein. (NJB)



The arrangement of actin, tropomyosin and troponin in the thin filament.

Activity, of enzymes: *see* Enzyme activity

Activity, physical Activity is brought about by muscular contractions in which chemical energy stores are converted into mechanical energy, which in turn is converted into heat as the work is performed. In this sense it is wasted energy but some activity is essential – for example, foraging by free-range animals, which involves further energy expenditure. This has led to the development of intensive production systems for egg layers and for growing chickens, pigs and calves, where activity is minimized.

Although chemical energy can be mobilized very quickly for vigorous work, this may not be reflected immediately in the animal's oxygen consumption, but the delay is only of short duration and the so-called oxygen debt is usually made up in a few minutes by increased respiration. Changes in **oxygen consumption** of an animal thus provide a good indication of the heat produced by activity. Even mild exercise can cause a considerable increase in oxygen consumption, and therefore in **heat production**, and at higher levels of activity increases of up to ten times the resting oxygen consumption can be sustained for prolonged periods, e.g. in draft animals, sheep being herded, racehorses and animals in flight from predators.

There have been few direct measurements of the metabolic cost of activity in farm animals. Most estimates take the form of comparisons of heat produced under different conditions, such as standing vs. lying, walking vs. standing still, walking uphill vs. walking on the level. These comparisons are surprisingly consistent, even between species. When cattle and sheep stand up, the effort involved in getting up causes increased oxygen consumption of some 30% over a few minutes, after which the standing:lying ratio is of the order of 1.12–1.20:1. The metabolic cost of continued standing over lying has been estimated as 0.07 to 0.14 watts kg^{-1} body weight (6–12 kJ kg^{-1} day^{-1}). In horses, which have the ability to sleep whilst standing, there is little difference in oxygen consumption between standing and lying.

The cost of movement on treadmills has been measured for animals and humans. The results for horses, cattle and sheep may be very crudely summarized as the increase in heat production per kg body weight in moving a distance of 1 m; it is 1.5–3 J kg^{-1} m^{-1} for horizontal movement and 25–35 J kg^{-1} m^{-1} for vertical upward movement. Speed of the movement has little effect on these estimates of total energy cost, because the effort of rapid movement has to be sustained for less time to cover the same distance. All these treadmill measurements may seriously underestimate the practical energy cost to animals of moving over soft or otherwise difficult ground. Experiments on animals dragging loads suggest that the mechanical work performed (i.e. force × distance) multiplied by three provides an approximate estimate of the extra heat produced by the animal. The metabolic cost of activities of humans, who are cooperative subjects, has been extensively studied and may provide a guide as to what may be expected in animals. (JAMcL)

Further reading

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Acylglycerol A form of lipid made up of one glycerol molecule combined with three individual (not necessarily identical) fatty acid molecules attached to the glycerol by ester bonds. Acylglycerols form part of the neutral lipid fraction. (NJB)

***Ad libitum* feeding** Feeding at will. Unlimited access to feed allows animals to satisfy their appetites at all times. Synonymous with full feeding. Their intake when feeding *ad libitum* is termed **voluntary food intake**. (MFF)

Adaptation The term adaptation implies that there is some sort of norm from which the body or system deviates in response to changes in the normal environment. Within the normal population a range of values is seen for any particular criterion that is examined, whether it be, say, activity of an enzyme, a blood parameter or body weight. Thus there is the statistical concept of the normal distribution. Adaptation implies a shift in the normal distribution or in the values for a particular individual. The former may be a long-term phenomenon in response to, e.g., climatic change where those animals best suited genetically to the change will survive. Short-term adaptation implies that the physiological systems can respond to changes in external factors. These factors include **environmental temperature**, light cycle or intensity, stocking density, the physical environment and nutrition (particularly in relation to energy or protein intake). In general, the term can relate to a modification that lessens the negative impact of imposed change or takes advantage of an opportunity afforded.

One major aspect relates to changes in environmental temperature. Homeothermic animals tend to have a defined range of temperature – the thermoneutral zone – within which core body temperature remains constant without any change in heat production. The thermoneutral zone varies for different species and stages of development and may also be modified by adaptation of an animal to prolonged exposure to an environment that falls outside the thermoneutral zone. However, within the zone, different species have a wide range of mechanisms by which they can adapt to maintain homeostasis. For example, poultry can increase heat loss in warm environments by increasing blood flow to the comb, wattles and shanks and, conversely, can reduce heat loss by reducing blood flow, changing posture and piloerection, thus improving body insulation. Pigs, individually housed, alter posture to increase or decrease heat loss and, in groups, can significantly reduce heat loss by huddling together. Environmental temperatures below the thermoneutral zone result in shivering, which is a rapid noradrenaline-induced mechanism for increasing heat production. Prolonged exposure to low temperature results in an increase in basal metabolic rate, due to non-shivering thermogenesis. This adaptation takes several weeks to complete in response to a permanent reduction in environmental temperature.

Feed intake is increased at low temperatures and reduced at temperatures close to or above the upper limit of the thermoneutral zone. In the case of domestic fowl, food intake declines linearly across the normal range of environmental temperature (15–30°C). Stocking density and availability of trough space can also lead to marked changes in food intake. In pigs, for example, it has been observed that intakes are 10–15% higher with individually housed animals compared with those in groups. It is unclear whether this is a behavioural adaptation to boredom on the part of individual pigs or depression of intake due to competition in groups. However, there is a wide range of behavioural adaptations associated with changes in the physical environment etc. For example, stereotypic behaviours such as bar-biting by sows tethered in stalls and reductions in tail-biting and aggression by pigs provided with the opportunity to root are negative and positive examples of such adaptations.

Of particular importance is the ability of the body systems to respond to changes in nutrition, especially in relation to energy and protein. One of the most extreme examples of response to undernutrition relates to studies by McCance and Mount (1960) on young pigs. These pigs were maintained for long periods on just sufficient quantities of a normal diet to maintain body weight. Whereas the **maintenance** requirement (MR) of normal piglets would be around 550 kJ kg^{-1} metabolic body weight ($W^{0.75}$), these undernourished pigs showed an MR of 250 kJ kg^{-1} $W^{0.75}$. The speed with which such changes occur in response to energy or protein deprivation was demonstrated by McCracken and McAllister (1984), who observed a reduction of approximately 25% in calculated maintenance requirement over a 3-week period. Changes in organ size relative to body weight have been observed during **undernutrition** of a wide variety of species, including poultry, pigs, cattle and sheep, and can be considered as contributing to the improved economy of the system. Conversely, increases in energy intake during lactation are associated with increased digestive organ capacity and increased metabolic rate. Similarly, offering a high-fibre (less digestible) diet to non-ruminants results in increased digestive organ size and weight, particularly in the hindgut, and increased energy supply from microbial fermentation.

In summary, the human or animal body has a wide range of mechanisms for coping with external stressors and a multitude of short-term and long-term adaptations have been reported, of which only a few examples have been discussed above. (KJMcC)

See also: Energy intake; Thermoregulation; Voluntary food intake

Key references

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Additive, feed Any substance that is regularly added to feeding stuffs to alter their characteristics or nutritive value. Within the European Community the term has been assigned a particular meaning, primarily for clarity in feeding stuffs legislation (The Feeding Stuffs Regulations 2000 [SI 2000 No. 2481]) as follows.

A substance or preparation used in animal nutrition to

(a) affect favourably the characteristics of feed materials, compound feeding stuffs or animal products,
(b) satisfy the nutritional needs of animals or improve animal production, in particular by affecting the gastro-intestinal flora or the digestibility of feeding stuffs,
(c) introduce into nutrition elements conducive to obtaining particular objectives or to meeting the nutritional needs of animals at a particular time or,
(d) prevent or reduce the harmful effects caused by animal excretions or improve animal environment.

This excludes everything not covered by EU Council Directive 70/524/EE concerning additives in feeding stuffs.

Recognized and permitted additives are listed in the pertinent directive by different groups under their allocated EU reference numbers and name or description together with qualifying information where appropriate. The qualifying information includes specific additive name, chemical formula, kind of animal for which it may be used, maximum or minimum quantity permitted and any special conditions of use. The various categories of additives are as follows.

Permitted antioxidants, added to feeding stuffs to help prevent oxidative deterioration. For example: E304, 6-palmitoyl-L-ascorbic acid, $C_{22}H_{38}O_7$, permitted for use in any feeding stuff.

Permitted colourants, included in feeding stuffs to modify the colour of animal products used as human food, such as eggs (yolk colour) or salmon and trout (flesh colour). For example: E161I, citranaxanthin, $C_{33}H_{44}O$, permitted in the nutrition of laying hens so long as the content in a complete feeding stuff does not exceed 80 mg kg^{-1} alone or with other carotenoids and xanthophylls.

Permitted emulsifiers, thickeners and gelling agents, used to manipulate the viscosity of liquids or the 'set' of feed blocks or buckets. This category of additive is more often used in the preparation of feeding stuffs for companion animals rather than farmed livestock. The category is subdivided into those permitted for use in any feeding stuff, such as E415, xantham gum, most often used in the manipulation of viscosity of liquid feeding stuffs, and those with more specific uses such as E488, polyoxyethylated glycerides of tallow fatty acids, permitted for calves at no more than 5000 mg kg^{-1} in milk replacer feeds only.

Vitamins A, D_2 and D_3 are permitted for the supplementation of a variety of feeding stuffs but mainly in milk replacer feeds. The simultaneous use of E670, vitamin D_2 and E671, vitamin D_3, is frequently prohibited. An example of more general use is E671, vitamin D_3, which can be used for cattle up to a maximum of 4000 IU kg^{-1} of a complete feeding stuff.

Trace elements, in the forms listed, can be added to animal feeding stuffs. Their conditions of use are subject to close control. For example, E4, copper, can be added in various forms, including basic cupric carbonate, monohydrate ($Cu(CH_3.COO)_2.H_2O$) and cupric sulphate, pentahydrate ($CuSO_4.5H_2O$), to the diets of fattening pigs up to 16 weeks of age, provided that the total (added plus background level) does not exceed 175 mg Cu kg^{-1} of the complete feeding stuff. For other species and categories of farm animals, the total (added and background) level of copper in the complete diet must not exceed 35 mg kg^{-1} but for ovines the permitted upper limit is 15mg Cu kg^{-1} of complete feeding stuff.

Aromatics and appetizing substances include natural substances and corresponding synthetic products as well as artificial substances such as E954ii, sodium saccharin, $C_7H_4NNaO_3S$, which is permitted for piglets up to 4 months of age to a maximum inclusion of 150 mg kg^{-1} of a complete feeding stuff.

Preservatives are divided into two groups. The first includes substances used mainly in the feeding of farm livestock such as E280, propionic acid, $C_3H_5O_2Na$. Within this group hydrochloric acid (HCl) and E513, sulphuric acid (H_2SO_4), can only be used in the preparation of silage. Most of the preservatives in the second group are permitted only in feeding stuffs for dogs and cats or other companion animals. For example, E217, sodium propyl 4-hydroxybenzoate, $C_{10}H_{11}O_3Na$, is permitted in any feeding stuff for companion animals. E285, methylpropionic acid, $C_4H_8O_2$, may be used in feeding stuffs for ruminants at the beginning of rumination at levels between a maximum of 4000 mg kg^{-1} and minimum of 1000 mg kg^{-1} in complete feeding stuffs

Acidity regulators are permitted primarily in feeding stuffs for dogs and cats. An example is E500I, sodium carbonate.

Permitted binders, anti-caking agents and coagulants are used to improve the physical characteristics of feeding stuffs as in the production of stable, durable pelleted feeding stuffs or the maintenance of meals in a free-flowing form. For example E565, lignosulphonates, can be used as binding agents in the production of pelleted feeding stuffs.

Permitted enzymes form a relatively large category including substances used to improve the digestibility of feeding stuffs or the efficiency of the animal's digestive process to make better use of feeding stuffs or reduce the level of undesirable excretions. For example: EC 3.2.1.1, α-amylase, produced by *Bacillus amyloliquefaciens* (CBS 360.94) with minimum levels of activity of 45,000 RAU g^{-1} in solid preparations and 20,000 RAU ml^{-1} in liquid preparations can be used for fattening pigs up to 1800 RAU kg^{-1} of complete feeding stuff, provided that the directions for use of the additive or premixture indicate the storage temperature, storage life and stability to pelleting. A dose rate of 1800 RAU kg^{-1} complete feeding stuff is recommended and it is used exclusively in compound feeding stuffs destined for liquid feeding systems containing starch-rich feed materials (e.g. < 35% wheat).

Selected microorganisms can be added to feeding stuffs to assist or enhance digestion or digestive efficiency, particularly in feeding stuffs for ruminants in which organisms such as yeast (*Saccharomyces cerevisiae*) may beneficially modify rumen fermentation. For example: *Saccharomyces cerevisiae*, CNCM 1-1077, in a preparation containing a minimum of 2×10^6 colony-forming units (CFU) g^{-1}, is permitted in feeding stuffs for dairy cows at concentrations between 5.5×10^8 and 1.5×10^9 CFU kg^{-1} of complete feeding stuff provided that the directions for use indicate storage temperature, storage life and stability to pelleting. The quantity of *S. cerevisiae* in a daily ration must not exceed 8.4×10^9 CFU for 100 kg body weight and 1.8×10^9 CFU for each additional 100 kg body weight.

Zootechnical additives are substances such as antibiotics, coccidiostats, other medicinal substances or growth promoters which are listed in one or more of the groups specified in Part I of Annex C to Council Directive 70/524/EEC concerning additives in feeding stuffs. They are listed linked to either a person responsible for their marketing, species or category of animal and other constraints of use. For example: the antibiotic Avilamycin 200 g kg^{-1} (MaxusG200, Maxus 200; Eli Lilly and Company Ltd) is permitted for turkeys when used between 5 mg and 10 mg active substance kg^{-1}. Others are known by their generic names, such as Antibiotic E714, monensin sodium, and Coccidiostat E750, amprolium.

All additives permitted for use in animal feeding stuffs within the EU are continually under review, and from time to time regulations controlling their use may be changed or modified and entries added or removed.

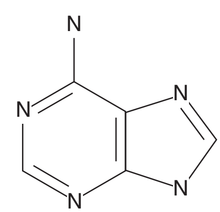
(CRL)

Further reading

European Community (1970) Council Directive 70/524 EEC (JO No L270, 14.12.70, p.1 OJ/SE Vol. 18, p.4) concerning additives in feeding stuffs.

Williams, D.R. (2000) *Feed Legislation*, 4th edn. HGM Publications, Bakewell, UK, 192 pp.

Adenine 6-Aminopurine $C_5H_5N_5$, one of the two purine (adenine, guanine) nucleic acid bases found in DNA and RNA. It is also part of molecules that are essential cofactors in metabolism, including ATP (adenosine triphosphate), ADP (adenosine diphosphate), NAD (nicotinamide adenine dinucleotide), NADP (nicotinamide adenine dinucleotide phosphate), FAD (flavine adenine dinucleotide) and CoA (coenzyme A).



(NJB)

Adenosine diphosphate (ADP): *see* Adenosinetriphosphate

Adenosine monophosphate (AMP): *see* Adenosinetriphosphate

Adenosine triphosphate (ATP) A water-soluble compound critical to cellular metabolism. It can store chemical energy for a short time (seconds to minutes) and then release that energy to support cellular processes (ATP → ADP + work + heat). The energy is derived from the electrons removed during the cellular catabolism of carbohydrate, fatty acids and amino acids. These electrons are used to reduce oxygen to water in the mitochondrial electron transport chain. In this process energy is stored in the terminal phosphate bond when adenosine diphosphate (ADP) is reconverted to ATP. (NJB)

Adenylate cyclase A cytoplasmic enzyme involved in the production of the second messenger cyclic AMP (cAMP) from ATP. The cellular concentration of cAMP is increased or decreased by the action of hormones on adenylate cyclase activity. Cellular responses are modified by changes in the concentration of cAMP. (NJB)

Adhesion receptors Receptors (which may have other functions) by which bacteria adhere to epithelial cells in the gastrointestinal tract. Adhesion is mediated by a specific **lectin** on either the receptor or the bacterium. (SB)
See also: Chemical probiosis; Gastrointestinal microflora; Probiotics

Adipocyte A fat cell, a specialized cell in particular regions of the body in which neutral fats (triacylglycerols) are stored. Adipocyte diameter can vary over threefold depending on lipid content, which varies between the adipose tissue sites in the body. (NJB)

Adipose tissue There are two types of adipose tissue: white and brown. White adipose tissue (WAT) is the main site of fat deposition in the animal body. Its main function is as an energy store, which accumulates in times of positive energy balance and is mobilized in times of negative energy balance. In addition, it protects certain internal organs against physical damage and provides thermal insulation.

The main WAT depots are subcutaneous, perinephric (perirenal), pericardial, abdominal (mesenteric and omental, sometimes also called gut and channel fat), intermuscular and intramuscular. In newborn animals there is very little WAT. It is a late-developing tissue that accumulates as animals approach their mature body size.

The main cell type found in adipose tissue is the adipocyte. Adipocytes range in size from 20–200 μm. The size and number of adipocytes vary between adipose tissue depots. Intermuscular adipose tissue contains a large number of small adipocytes whereas perinephric adipose tissue contains a small number of large adipocytes.

The main metabolic processes in adipose tissue are: (i) fatty acid synthesis and (ii) triacylglycerol synthesis, jointly known as lipogenesis; and (iii) lipolysis, the breakdown of triacylglycerols to yield glycerol and non-esterified fatty acids (NEFA). Adipose tissue is the major site of *de novo* fatty acid synthesis in ruminant species. In non-ruminant mammals, fatty acid synthesis occurs in both adipose tissue and liver; whereas in avian species, adipose tissue is not an important site of fatty acid synthesis and triacylglycerols are synthesized from fatty acids of dietary origin or synthesized in the liver. In ruminant adipose tissue, acetate is the primary substrate for fatty acid synthesis. In non-ruminant mammals and birds, glucose is the major substrate.

Brown adipose tissue (BAT) is a specialized form of adipose tissue. Its function is the generation of heat by the oxidation of fatty acids by the process of non-shivering thermogenesis. It is particularly important in neonatal animals. In some species (e.g. lambs) the ability to generate heat by non-shivering thermogenesis is lost within 2–3 days of birth; in others (e.g. rats) this property persists into adult life. Some species, such as the pig, do not have BAT and are particularly susceptible to cold immediately after birth. BAT is pale brown in appearance, due to the well-developed blood supply and to the presence of numerous mitochondria in adipocytes. It is found in a number of anatomical locations, e.g. in interscapular, axillary and perinephric regions. Its ability to generate heat is due to the ‘uncoupling’ from ATP synthesis of mitochondrial electron transport by uncoupling proteins (UCPs). These proteins cause the disruption of the proton gradient across the inner mitochondrial membrane. (JRS)

Adrenal The adrenal gland is located above the anterior portion of the kidney. It is made up of two distinct anatomical and functional parts, the cortex and medulla. The cortex secretes three types of hormones: glucocorticoids, mineralocorticoids and androgens. The medulla produces and releases the catecholamine hormones, **dopamine**, **norepinephrine** and **epinephrine**. (NJB)

Adrenaline: *see* Epinephrine

Adverse effects of food constituents Any of the major food constituents (protein, carbohydrate, fat, mineral, vitamin, fibre, water) can induce adverse effects if they are not balanced for the requirements of the consumer. If the constituents are not balanced, the food may be avoided or, if it is the sole food available, intake will be low. One example is fibre which, being indigestible or only slowly digested (by microbes in the digestive tract), imposes physical work on the digestive tract as well as limiting the capacity to eat food. Other examples are specific plant toxins that interfere with metabolism, reducing the overall satisfaction the animal derives from each unit of food eaten. Many plants have evolved these to avoid being eaten. Another way in which food can have adverse effects is by the heat produced by its ingestion, digestion and metabolism, especially in a hot environment in which this extra heat is difficult to lose. A diet excessively high in protein can have such adverse effects due to the heat produced in the deamination of the excess amino acids. Excessive concentrations of individual minerals, particularly in plants that accumulate the minerals as a means of protection, can induce specific toxicity symptoms or adverse effects by disturbing the mineral balance. Plants with a high water content, such as young herbage, may adversely effect the intake of dry matter, particularly if requirements are high and intake capacity is limited. (JMF)

Aflatoxins A family of bisfuranocoumarin metabolites of toxigenic strains of *Aspergillus flavus* and *A. parasiticus*.

The name derives from *Aspergillus* (a-), *flavus* (-fla-) and toxin. The major aflatoxins (AFs) are AFB1, B2, G1 and G2. The AFs are bioactivated by hepatic enzymes to toxic metabolites including AFB1-8,9-epoxide, and AFM1 (in milk). The AFs occur in the field in seeds (maize, cottonseed, groundnuts) and in storage of grains (maize, soybeans).

Biological effects are liver damage (acute and chronic) and liver cancer (chronic), reduced growth, impaired lipid absorption, with induced deficiencies of vitamins A, D and K, causing impaired blood coagulation, haemorrhage and bruises (poultry), and adverse reproductive effects. Differences in susceptibility between species of animals relate to the activity of hepatic cytochrome P450 enzymes, which bioactivate AF to the toxic metabolites. Rabbits, ducks and turkeys are highly susceptible to AF toxicity, while rats and sheep are less sensitive. Chronic AF intoxication is caused by 0.25 ppm (dietary) in ducks and turkeys, 1.5 ppm in broilers, 0.4 ppm in swine and 7–10 ppm in cattle. AF metabolites in liver cross-link DNA strands, impairing cell division and protein synthesis. AFB1 metabolites form DNA adducts, causing liver cancer. AF has immunosuppressive effects, impairing cell-mediated immunity. (PC)

Age at first egg The age, usually expressed in days, at which an individual bird lays its first egg. The mean age at first egg for a flock of birds approximates to the age at which the flock reaches a 50% rate of egg production (see table).

Typical mean ages at first egg for domesticated birds fed *ad libitum*, with conventional lighting.

Species	Mean age at first egg
Domestic fowl	19–21 weeks
Duck	16–18 weeks
Turkey[a]	32–34 weeks
Quail	6–7 weeks

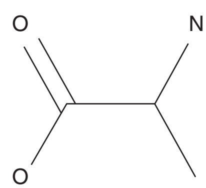
[a] When photostimulated at about 30 weeks and following at least 8 weeks of exposure to short days.

(PDL)

Age at weaning The age, often expressed in days, at which a young mammal ceases to receive its mother's milk. It is also used, as in calf rearing, to denote the age at which any natural or artificial milk is withdrawn from the ration. (PJHB)

Agglutinins: *see* Haemagglutinins

Alanine An amino acid (CH_3·CH·NH_2·COOH, molecular weight 89.1) found in protein. It can be synthesized in the body from pyruvate and an amino donor such as glutamic acid. Substantial quantities of alanine are synthesized in gut mucosa and muscle, and the alanine not used for protein synthesis is transported to the liver where the enzyme alanine aminotransferase converts alanine to pyruvate. Mitochondrial pyruvate in the liver can either be used in the **TCA cycle**, or it can be converted (carboxylated) to oxaloacetate, some of which is subsequently reduced to malate, some transaminated to aspartate, and some decarboxylated to phosphoenolpyruvate. All three of these compounds can escape the mitochondrion and enter the cytosol to be used for gluconeogenesis. Integration of these processes involving muscle and liver tissue is often referred to as the glucose–alanine cycle.



(DHB)

See also: Gluconeogenesis; Pyruvate

Albumin Albumins were originally classified as proteins that were soluble in a 50% saturated solution of ammonium sulphate. Albumins (five separable proteins) account for approximately half of the protein in blood plasma. Plasma albumin plays an important role in regulation of osmotic pressure. Bilirubin, free long-chain fatty acids and a number of steroid hormones are found bound to albumin. (NJB)

Alcohols Alcohols have a functional ·COH group. The group includes primary, secondary and tertiary alcohols, with one, two and three ·COH groups. Long-chain alcohols (up to 30 carbons) are found as esters with palmitic acid. Glycerol and cholesterol are alcohols. Ethanol, CH_3·CH_2OH, is an alcohol produced by fermentation and can be used as a source of metabolic energy. It has a caloric value of 29.7 kJ g^{-1} or 23.4 kJ ml^{-1}. (NJB)

Aldehydes Aldehydes have a functional ·CHO group. Many six-carbon (e.g. glucose), five-carbon (e.g. ribose) or four-carbon sugars (e.g. erythrose) have a functional aldehydic carbon. Aldehydes are intermediates when a functional alcohol carbon is converted to an acid carbon. Aldehydes such as formaldehyde and acetaldehyde are highly toxic and react with tissues. (NJB)

Aldosterone A 21-carbon steroid hormone synthesized in the adrenal cortex and classified as a mineralocorticoid. It plays a role in sodium retention and potassium excretion by the kidney. (NJB)

Aleurone The single outer layer of living cells surrounding the endosperm of cereal grains. Rich in protein, these cells synthesize the enzyme α-amylase, which is responsible for the breakdown of the stored starch in the endosperm into maltose and glucose during germination. The aleurone layer remains attached to the bran during milling. (ED)

See also: Cereal grains

Alfalfa: *see* Lucerne

Algae Plant-like organisms that possess chlorophyll *a* in combination with other chlorophylls or accessory photosynthetic pigments, and have minimal differentiation into defined tissues or organs. They range from single microscopic cells to among the tallest organisms known (giant kelps, *c.* 40 m) and are mainly aquatic, with some tolerating periodic or prolonged exposure to air. (CB)

See also: Marine plants; Seaweed

Further reading

Hoek, C. van den, Mann, D.G. and Jahns, H.M. (1995) *Algae: an Introduction to Phycology* (1997 reprint). Cambridge University Press, Cambridge, 627 pp.

Algal toxins Toxins of algal origin (also called phycotoxins) are most often produced by unicellular marine flagellates, particularly dinoflagellates, but also by members of other major flagellate algal groups, such as raphidophytes, haptophytes and pelagophytes. A few species of the diatom genus *Pseudo-nitzschia* synthesize a potent neurotoxin, domoic acid. In fresh and brackish waters, cyanobacteria ('blue-green algae') are often implicated as toxic algal contaminants in drinking-water supplies for humans and livestock. In the marine environment, cyanobacterial toxins are responsible for 'netpen liver disease' in caged salmonids. When present in high abundance or during periods of rapid growth ('blooms'), algae can cause water discolorations known as 'red tides', usually in fresh or coastal waters – these phenomena are not always associated with toxicity. Toxic events associated with algae may be divided into two types: (i) those caused by the production of specific toxic metabolites; and (ii) those resulting from secondary effects, such as post-bloom hypoxia, ammonia release, or other artefacts of decomposition on marine flora and fauna. Phycotoxins and their causative organisms are globally distributed in marine coastal environments, from the tropics to polar latitudes, and few areas are exempt from their effects, which may be expanding in geographical extent, severity and frequency on a global basis. In a few cases, this may be linked to eutrophication, but there is no general hypothesis to explain all such events.

Among the thousands of extant species of marine microalgae, only several dozen produce highly potent biotoxins that profoundly affect the health of marine ecosystems, as well as human and other animal consumers of seafood products. As an operational category, certain toxic microalgae are often called 'fish-killers' because of their potent direct effects on fish, particularly in aquaculture systems. Such toxins are poorly characterized and the mechanism of action is often not well understood, although the toxic effects are typically mediated through the gills. In contrast, the toxins associated with human illnesses by consumption of contaminated finfish (e.g. ciguatera fish poisoning, clupeotoxicity) and paralytic, amnesic, neurotoxic and diarrhoeic shellfish poisoning (PSP, ASP, NSP and DSP, respectively) caused by ingestion of shellfish are much better known. The phycotoxins responsible for these syndromes constitute a heterogeneous group of compounds, affecting a variety of receptors and metabolic processes, acting as Na^{+}-channel blockers, Ca^{2+}-channel activators, glutamate agonists, phosphatase inhibitors etc. These pharmacologically active compounds also include the emerging problems associated with 'fast-acting toxins' of poorly defined human health significance, such as gymnodimine and spirolides. Many of the phycotoxins can be propagated within marine food webs from phytoplankton through zooplankton (copepods, krill), then from ichthyoplankton to large carnivorous fish, and even marine birds and mammals. Toxin accumulation within fish stocks (e.g. anchovies) harvested for fish-meal production may even be a risk for aquaculture of certain species. Except in bivalve shellfish, where oxidative and reductive transformations mediated by both enzymatic and non-enzymatic processes have been determined, and in the case of biotransformation within fish tissues of ciguatoxin precursors from dinoflagellates, metabolism of phycotoxins is poorly understood. (AC)

See also: Marine environment; Marine toxins

Reference and further reading

Anderson, D.M., Cembella, A.D. and Hallegraeff, G.M. (eds) (1998) *Physiological Ecology of Harmful Algal Blooms.* NATO Advanced Study Institute Series, Vol. 41. Springer-Verlag, Heidelberg, Germany, 662 pp.

Botana, L.M. (ed.) (2000) *Seafood and Freshwater Toxins: Pharmacology, Physiology, Detection*. Marcel Dekker, New York, 798 pp.

Hallegraeff, G.M., Anderson, D.M. and Cembella, A.D. (eds) (2002) *Manual on Harmful Marine Microalgae.* Monographs on Oceanographic Methodology, Vol. 11. Intergovernmental Oceanographic Commission, UNESCO, Paris.

Acute toxicity (LD_{50}) of selected phycotoxins after intraperitoneal injection into mice. Only major toxin analogues found in shellfish or finfish, and/or the corresponding toxigenic microalgae, for which the pathology in mammals is known or highly suspected are included. Note that multiple derivatives of varying toxicity are common for most toxin groups. Data summarized from citations in Hallegraeff *et al.* (2002).

Toxin group	Analogue	Toxicity ($\mu g\ kg^{-1}$)	Primary pathology
Azaspiracid	AZA	200	Gastrointestinal
	AZA2	110	Gastrointestinal
	AZA3	140	Gastrointestinal
	AZA4	470	Gastrointestinal
	AZA5	1000	Gastrointestinal
Brevetoxin	BTX-B1	50	Neurological
	BTX-B2	300	Neurological
	BTX-B3	> 300	Neurological
Ciguatoxin	CTX1	0.25	Neurological
	CTX2	2.3	Neurological
	CTX3	0.9	Neurological
Gambiertoxin	GTX-4B	4.0	Neurological
Maitotoxin	MTX1	0.05	Neurological
	MTX1	0.05	Neurological
	MTX2	0.08	Neurological
	MTX3	0.1	Neurological
Okadaic acid	OA	200	Gastrointestinal; tumour promotion
Dinophysistoxin	DTX1	160	Gastrointestinal
	DTX3	500	Gastrointestinal
Gymnodimine		96	Neurological(?)
Pectenotoxin	PTX1	250	Hepatotoxic
	PTX2	230	Hepatotoxic; gastrointestinal
Saxitoxin	STX	11	Neurological
	NeoSTX	12	Neurological
Gonyautoxin	GTX1	11	Neurological
	GTX2	32	Neurological
	GTX3	16	Neurological
	GTX4	13	Neurological
Spirolide	B	200	Neurological (?)
	des-methyl-C	40	Neurological (?)
Yessotoxin	YTX	100	Cardiotoxic

Alimentary tract: *see* Gastrointestinal tract

Alkali disease A chronic form of selenosis, which occurs in cattle and horses after prolonged consumption of plants with high selenium concentrations. It is characterized by alopecia, hoof dystrophy, lack of vitality, emaciation, poor quality hair, sloughing of the hooves and stiff joints. Although not widespread, it is of major importance in some localized areas, such as parts of the Great Plains of North America.

(CJCP)

Alkali treatment The principle behind the treatment of cellulosic substrates with alkali is that it hydrolyses ester bonds between the cell wall polysaccharides (cellulose and hemicellulose) and lignin, rendering the material more susceptible to rumen microbial degradation. Early techniques in the late 19th century were industrial processes requiring both heat and pressure. However, in the Beckmann process, the first on-farm methodology, cereal straw was soaked for up to 2 days in a dilute (1.5%) sodium hydroxide solution, then washed to remove any excess alkali. This technique improved degradability but considerable soluble (i.e. potentially degradable) material was lost during the washing process. The use of more concentrated solutions, either sprayed on to chopped or shredded straw, or applied by dipping baled straw into vats which was then allowed to 'mature' for up to a week prior to feeding, reduced these losses. The delay ensured that residual sodium hydroxide had reacted with carbon dioxide, to form sodium carbonate. Because alkali treatment raises the ash content, the apparent digestibility of organic matter improves less than that of dry matter.

The response to treatment varies inversely with the quality of the untreated straw. To realize the potential improvement in degradability, sufficient dietary nitrogen and sulphur must also be provided. Sodium hydroxide is the most commonly applied alkali, though potassium hydroxide (often as wood ash), calcium hydroxide, alkali hydrogen peroxide and calcium oxide (lime) have all been used. A disadvantage of the technique is that water consumption is increased (a potential drawback in arid regions), leading to increased urine output, which generates a problem with quantity and disposal of bedding. The high urinary output of sodium may damage soil structure.

The technique has also been used to treat cereal grain. The action disrupts the integrity of the seed coat, increasing the accessibility of the starch to the rumen microorganisms without the requirement for physical processing. Conventionally harvested grain is blended with sodium hydroxide, water is then added and the material mixed. This reaction produces considerable heat, following which the grain should be remixed prior to storage. The amount of sodium hydroxide required for optimum digestibility varies with the fibre content of the grain husk. About 25 kg t^{-1} is used with wheat and 40–45 kg t^{-1} for oats. Treated grain can be fed direct or after mixing with water, which causes the seed coat to swell and rupture. The slower release of starch relative to that from ground or rolled grain interferes less with fibre degradation, allowing higher intakes of roughage to be maintained. Residual alkali helps to maintain rumen pH, reducing the incidence of acidosis when high levels of grain are offered. An additional benefit is that sodium hydroxide treatment has a preservative effect on high-moisture grain, reducing both bacterial and fungal growth. Offered to cattle, treated grain maintains a higher rumen pH, tends to increase the acetic:propionic acid ratio, and reduces the incidence of rumenitis in comparison with cattle fed conventionally processed material. Similarly, when high levels are offered to dairy cows, depressions in milk fat content are minimized and roughage intake is maintained.

The requirement for supplemental dietary nitrogen, and the observation that other alkalis also improved digestibility, led to the development of systems using either gaseous (NH_3) or aqueous (NH_4OH) ammonia. Ammonia is injected into straw stacks sealed with plastic sheeting or film, or into large bales, as either gas (straw must contain at least 10% moisture) or solution (100 l of 300 g NH_3 l^{-1}). Under temperate summer temperatures the process is generally complete in 4–6 weeks and results in organic matter digestibility increasing from 45% to 55% and intake by anything up to 30%. Nitrogen content is also enhanced (1.4 vs. 0.8% in dry matter), thereby increasing rumen microbial activity and yield. It is recommended that, as nitrogen retention is directly proportional to the straw moisture content, treatment should occur as soon as possible after combining. Treatment with gas can also be undertaken in 'ovens'. Oven treatment takes only 24 h and enables straw to be treated during periods of cold weather or under winter conditions. An added advantage is that ammonia treatment inhibits spoilage organisms, especially moulds, thereby increasing the storage properties of damp straw.

In tropical environments the high ambient temperatures mean that the treatment of rice, maize or sorghum straws is achieved in 2–3 weeks. Urea, or even urine, can be used as the ammonia source, as the higher temperatures speed the conversion of urea to ammonia by urease enzymes present in straw. Urease levels have been enhanced by the addition of jackbeans to the straw prior to treatment.

Toxic symptoms may arise if high quality forages (e.g. grass or lucerne hay) are ammoniated and offered to ruminants. This takes the form of a hyper-excitability, commonly referred to as 'crazy cow syndrome', which is totally unconnected with bovine spongiform encephalopathy (BSE). Roughages with a high carbohydrate content prior to ammoniation are particularly implicated, with the compound generally associated with this effect, 4-methylimidazole, being formed by the interaction of sugars with ammonia in the rumen. (FLM)

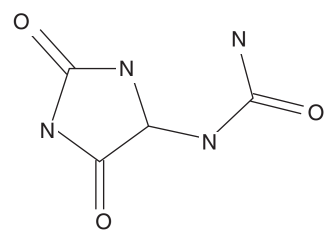
Alkaline phosphatase An enzyme found in intestinal contents that catalyses the release of phosphate from a wide variety of phosphorylated cellular metabolites and co-factors (e.g. sugar phosphates, nucleotides, ATP). It is also found in tissues such as liver, bone, and kidney which are sources of plasma alkaline phosphatase. In bone it is thought to contribute to crystal formation. (NJB)

Alkaloids A class of plant secondary compounds generally characterized as containing at least one basic heterocyclic nitrogen atom and usually possessing some type of physiological activity. They are found in approximately 15% of all vascular plants. Alkaloids are a heterogeneous group of compounds, subdivided and further classified by a similar basic chemical structure containing the nitrogen atom. Alkaloids comprise several thousand different structures and possess a wide variety of physiological activities and potency. Some of the key sources of plant material containing alkaloids affecting animal nutrition are listed in the table. (DRG)

Alkalosis A pathological condition in which the arterial plasma pH rises above 7.4. The range of alkalosis that is compatible with life is 7.4–7.7. An example is metabolic alkalosis resulting from excessive loss of gastric acid during prolonged vomiting. This also involves considerable loss of potassium in the urine. Treatment is by intravenous infusion of isotonic saline containing supplementary potassium chloride to correct both the chloride and potassium deficits. The bicarbonate excess corrects itself. (ADC)

All-*trans* retinoic acid A metabolic derivative of vitamin A (all-*trans* retinol) or β-carotene via the intermediate formation of all-*trans* retinol. Retinoic acid interacts with nuclear retinoic acid receptors (there are four) to affect appropriate genes, which result in cellular differentiation. (NJB)

Allantoin $C_4H_6N_4O_3$, a degradation product of purines. It is an intermediate in the production of uric acid that can be converted in part to urea except in birds and reptiles.



(NJB)

Alkaloids.

Alkaloid class	Plant or organism	Physiological effect
Diterpene	*Delphinium*	Neurotoxic
Indole	*Claviceps*, *Peganum*, *Phalaris*	Neurotoxic, vascular
Indolizidine	*Swainsona*, *Astragalus*, *Physalia*	Glycosidase inhibitor, teratogenic
Piperidine	*Conium*, *Lupinus*, *Nicotiana*	Neurotoxic, teratogenic
Pyridine	*Nicotiana*	Neurotoxic
Pyrrolizidine	*Senecio*, *Crotalaria*, *Heliotropium*	Hepatotoxic, pneumotoxic, photosensitization
Quinolizidine	*Lupinus*, *Thermposis*, *Cytisus*, *Baptisia*	Teratogenic, myotoxic, neurotoxic
Steroidal	*Solanum*, *Veratrum*, *Zigadenus*	Teratogenic, cholinesterase inhibitor
Tropane	*Datura*, *Atropa*, *Hyoscyamus*	Neurotoxic, blindness

Allowance Nutrient requirements represent the best estimates for the particular species, age and production system based on the available scientific evidence. The term 'allowance' takes account of the need to include a safety factor on top of 'requirements' to allow for variations in environmental conditions and individual variability in requirements. Allowances are usually set at 5–10% above requirements. (KJMcC)

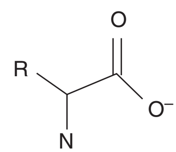
Aluminium The most abundant metal in the earth's crust. Its low solubility ensures that the concentration in most plant and animal tissues remains low. The only evidence of toxicity in farm animals comes from its interaction with essential nutrients, in particular phosphorus and magnesium in ruminants and iron in poultry, possibly leading to deficiencies in those elements in range livestock. Neurobehavioural disorders have been demonstrated at high aluminium intakes in laboratory animals, by those seeking to determine the role of aluminium in the development of Alzheimer's disease in humans. (CJCP)

Amadori products Intermediates in the reaction of phenylhydrazine with monosaccharides (e.g. glucose) to form glucose phenylosazones. Amadori products are undefined intermediates in Amadori rearrangement in the production of, for example, glucose phenylosazone from glucose phenylhydrazone. (NJB)

Amide A compound with the specific carbon–nitrogen linkage R·CON·R. The peptide bond between amino acids in proteins is an amide linkage. Familiar amides are the amino acids asparagine and glutamine in which an amine nitrogen ($\cdot NH_2$) is linked to a carboxyl-carbon, e.g. asparagine, $NH_2CO\cdot CH_2\cdot CH(NH_2)\cdot COOH$. (NJB)

Amine A compound with the specific carbon–nitrogen linkage $R\cdot CNH_2$. The simplest amine is methylamine ($CH_3\cdot NH_2$) in which one of the hydrogens of ammonia has been replaced by a methyl ($CH_3\cdot$) group. Free amino acids can be considered as amines. Some amines produced by decarboxylation of amino acids or modified amino acids are precursors of active hormones (e.g. histidine to histamine, 5 hydroxy-tryptophan to serotonin etc.). (NJB)

Amino acid Amino acids contain the elements C, H, N, O and S. Their basic structure in solution is ($R\cdot CHNH_3^+\cdot COO^-$) which is referred to as a 'zwitterion' because the alpha carbon ($\cdot CHNH_3^+$) has a positively charged nitrogen attached and the carboxyl group ($\cdot COO^-$) is negatively charged. The amino acid R group (side chain) can be aliphatic, contain hydroxyl (-OH) groups, have sulphur, have basic groups which contain nitrogen or have various aromatic rings. Amino acids are the basic units of which protein is constructed and amino acids can be modified to provide a wide variety of products that are required for an animal to function.



(NJB)

See also: individual amino acids

Amino acid metabolism Although there are hundreds of naturally occurring amino acids, only 20 are normally found as components of protein. Other amino acids not found in protein are products (e.g. taurine) or intermediates (e.g. ornithine or citrulline) in essential metabolic processes. Amino acids have the general formula, $R\cdot CHNH_2\cdot COOH$. In solution they are 'zwitterions', meaning that the $\cdot COO^-$ is negatively charged and the $\cdot NH3^+$ is positively charged. The metabolism of amino acids involves their incorporation into a wide variety of proteins, their release from protein during protein turnover and their use in the production of essential peptides (e.g. glutathione) and as precursors of other amino acids and essential metabolites. In the body approximately 1% of all amino acids are found as free amino acids while 99% are bound in protein, with a small fraction found as polymers such as peptides and hormones.

For animals, the main source of amino acids is the diet, though in some animals (especially ruminants) amino acids are produced by gut microflora during fermentative digestion and then become available for the animal's use. Amino acids are absorbed from the small intestine as free amino acids or as di- and tripeptides and released into the blood mostly as free amino acids but some peptides. Cellular uptake of each amino acid is dependent on transporter(s) for neutral amino acids (both sodium dependent and sodium independent) and for cationic and anionic amino acids.

For non-ruminant animals, amino acids are classified as dispensable (i.e. can be synthesized at rates equal to the need), conditionally indispensable (i.e. can be made from the basic carbon skeleton with nitrogen provided by transamination) or indispensable (which must be supplied fully formed in the diet). The dispensable amino acids are alanine, glycine, serine, cysteine, aspartic acid, glutamic acid, proline, hydroxyproline and tyrosine. The conditionally indispensable amino acids are arginine (for birds, fish and young mammals), histidine, phenylalanine, tryptophan, leucine, isoleucine, valine and methionine. The indispensable amino acids are threonine and lysine, which do not participate in transamination reactions. Since animals cannot synthesize the carbon skeleton of the conditionally indispensable amino acids, these are normally required in the diet in addition to lysine and threonine. For ruminant animals, the same classification applies but a large proportion of the amino acids required can be derived from microbial synthesis in the rumen. Rabbits and laboratory rodents derive a portion of their amino acid needs by caecotrophy (*see* **Coprophagy**).

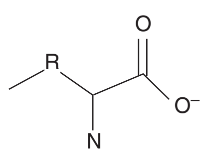
Part or all of the carbon skeleton of some amino acids (arginine, alanine, aspartic acid, cysteine, glutamic acid, histidine, hydroxyproline, isoleucine, methionine, phenylalanine, proline, serine, threonine, tyrosine and valine) provides carbon for the production of glucose (*see* **Gluconeogenesis**). These amino acids are called glucogenic amino acids. Both the liver and kidneys are involved in the production of glucose from amino acids and from three-carbon intermediates (pyruvate and lactate) from glucose catabolism. Other amino acids provide intermediates (acetyl-CoA) that are precursors of ketone bodies or give rise to them directly (acetoacetate) and are called ketogenic amino acids (leucine, lysine and tryptophan). Some amino acids give rise to both types of intermediates and are both glucogenic and ketogenic (isoleucine, phenylalanine and tyrosine). The main site of catabolism of amino acids is the liver but the catabolism of the branched-chain amino acids may involve both muscle and liver. The capacity for carrying out transamination with subsequent production of the branched-chain ketoacids is higher in muscle while the capacity to catabolize the branched-chain ketoacids via a branched-chain ketoacid dehydrogenase is greater in the liver.

Another example of inter-organ cooperation is seen in the transport of nitrogen from amino acid catabolism in muscle to the liver via the 'alanine cycle'. Nitrogen from the branched-chain amino acids and other sources is combined with pyruvate to produce alanine, which is transported to the liver: the nitrogen can then be incorporated into aspartic acid and then into urea. In urea production one of the two nitrogens in urea comes from ammonium and the other from aspartate. The nitrogen from amino acid catabolism in mammals is excreted in urine as urea (CN_2H_4O) and ammonium ion (NH_4^+). The production of urea is restricted to the liver and involves five enzymes, two of which are in the mitochondrial matrix. This subcellular division in the site of urea production requires transporters (ornithine/citrulline, malate, aspartate, glutamate) located in the inner membrane of the mitochondrion and gives rise to the potential for transporter control of urea synthesis. Other nitrogen-containing compounds found in urine (e.g. creatinine) are not part of a dedicated nitrogen excretion pathway.

In birds, the end-product of nitrogen excretion is uric acid ($C_5H_4N_4O_3$). Production of uric acid requires two one-carbon units from the folate system and thus competes with other systems requiring one-carbon units as part of their metabolism. Fish excrete nitrogen as ammonium or urea depending on whether their environment is fresh or salt water. The excretion of urea by saltwater fish is thought to be related to the higher osmotic pressure of salt water relative to that of the body.

A number of amino acids are precursors of such essential products as haem, purine, pyrimidine, hormone and neurotransmitters. Arginine, in concert with methionine and glycine, gives rise to creatine. Lysine in proteins is methylated by *S*-adenosylmethionine to trimethyllysine which, after the protein is broken down, becomes part of carnitine. Histidine gives rise to histamine. Histidine bound in certain proteins (e.g. actin and myosin) is methylated by *S*-adenosylmethionine to form 3-methylhistidine which, upon protein degradation, is released but cannot be re-used for protein synthesis. Because it is quantitatively excreted in the rat and human, it has been used to estimate muscle protein catabolism. Histidine, with β-alanine, forms the dipeptide carnosine: β-alanine also combines with 1-methylhistidine to form the dipeptide anserine and with 3-methylhistidine to form balenine. Phenylalanine is a precursor of tyrosine. Tyrosine provides the basic structure for DOPA, dopamine and norepinephrine. Tryptophan, after conversion to 5-hydroxytryptophan, is converted into serotonin. Methionine, via its conversion to *S*-adenosylmethionine, is a source of methyl carbons for numerous methylations. Additionally, after conversion to *S*-adenosylmethionine, methionine provides sulphur for the biosynthesis of cysteine (the carbon comes from serine), carbon for the biosynthesis of spermidine and spermine and carbon for purine synthesis via folate-dependent one-carbon metabolism. (NJB)

Amino nitrogen The amine nitrogen (-NH_2) attached to the α-carbon and, in some cases, the terminal carbon of an amino acid. The reaction of ninhydrin with α-amino nitrogen of free amino acids was an early basis for quantifying amino acids.



(NJB)

Amino sugars Monosaccharides (simple sugars) in which a single hydroxyl group (-OH) is replaced by an amino group (-NH_2). Glucosamine, galactosamine and mannosamine are examples. Glucosamine is a component of heparin, while the N-acetyl derivative is found in hyaluronic acid. Galactosamine, as the N-acetyl derivative, is a component of chondroitin. Mannosamine, as the N-acetyl derivative, is a component of sialic acid. (NJB)

Amino-oligopeptidase: *see* Aminopeptidase

Aminobutyric acid Aminobutyric acid can be found in two forms. α-Aminobutyric acid ($HOOC·CH_2·CHNH_2·COOH$) is produced by transamination of α-ketobutyric acid produced in the catabolism of threonine and methionine. γ-Aminobutyrate ($H_2NCH_2·CH_2·CH_2·COO^-$) is a neurotransmitter formed by the decarboxylation of glutamate. (NJB)

Aminopeptidase A **peptidase** that cleaves peptide bonds from the N-terminal of peptides, e.g. leucine amino peptidase (EC 3.4.11.1), which is attached to epithelial cells of the small intestine. (SB)
See also: Protein digestion

Aminotransferases Enzymes that are involved in transfer of an α-amino nitrogen from one amino acid to the ketoacid precursor of another amino acid. Aminotransferases can be found in many tissues and in the cytosolic as well as mitochondrial fractions of cells. The accepted vitamin co-factors for transamination reactions are **pyridoxine** 5′-phosphate (removal of -NH_2) and pyridoxamine 5′-phosphate (addition of -NH_2). (NJB)

Ammonia Ammonia (NH_3) is a gas at normal ambient temperatures. It is produced industrially and used as a fertilizer for crops by injection into the soil. It is toxic, even fatally, and is an irritant to membranes exposed to it. It reacts with water to become ammonium hydroxide (NH_4OH). In amino acid metabolism it can be released as ammonium (NH_4^+) from the amino acid glutamine by the enzyme glutaminase or from the amino acid glutamate by the enzyme glutamate dehydrogenase. Because ammonium can be incorporated into glutamate by the enzyme glutamate dehydrogenase or into glutamine by glutamine synthetase, ammonium nitrogen (NH_4^+) in the form of ammonium citrate ($C_6H_{14}N_2O_7$) can be used as a source of nitrogen for the biosynthesis of dispensable amino acids in non-ruminants. In the rumen, bacteria convert urea-N into ammonium-N which is then incorporated into microbial amino acids and protein, which are later digested and become available to the host in the form of absorbed amino acids. (NJB)

Ammonia treatment The feeding value of cereal straw for ruminants is improved by treatment with ammonium hydroxide. Ammonia is applied to straw (barley, oat, wheat) enclosed in a plastic sheet for 4–6 weeks (in temperate summer conditions). In tropical conditions, treatment of straw (rice, maize or sorghum) is achieved in 2–3 weeks. Ammonia is injected into straw stacks or large bales as gas (straw must contain at least 10% moisture) or solution (100 l of 300 g NH_3 l^{-1}). Treatment with gas can also be undertaken in ‘ovens’. ‘Oven’ treatment takes only 24 h and allows straw to be treated in cold winter conditions. Treatment increases organic matter digestibility (by *c*. 10% units, from *c*. 45%) and intake (by *c*. 30%) and increases nitrogen content (from 0.8 to 1.4% of dry matter), thereby increasing the activity and protein yield of rumen microbes. An added advantage of ammonia treatment is inhibition of spoilage organisms, thereby increasing the keeping quality of damp straw. Under tropical conditions, urea (or possibly urine) is used as a source of ammonia. Urea is converted to ammonia by the action of the enzyme urease present in straw. Jackbeans can also be used as a source of urease. (EO)
See also: Alkali treatment

Key reference

Sundstol, F. and Owen, E. (1984) *Straw and Other Fibrous By-products as Feed*. Elsevier, Amsterdam, 604 pp.

Ammoniated feeds: *see* Ammonia treatment

Ammonium: *see* Ammonia

Amylase An enzyme (α-amylase; 1,4-α-D-glucan-glucanohydrolase; EC 3.2.1.1) secreted in the saliva of omnivorous animals and from the pancreas. The enzyme hydrolyses starch and glycogen and produces the disaccharides maltose and isomaltose, and also maltotriose and α-limit dextrins. Preparations of α-amylase (EC 3.2.1.2) have been isolated from various sources, e.g. bacteria, barley malt and sweet potato, and are used for structural investigations of polysaccharides. (SB)

Amyloglucosidase An enzyme (EC 3.2.1.3) that acts on terminal units of α(1→4)-linked glucans from the non-reducing end, releasing glucose. (SB)

Amylopectin A branched polymer of **glucose** which has a role as a storage form of carbohydrate. Starch (from plants) and glycogen (from animals) consist of amylose, with linear chains of α(1→4) glycosidic bonds, together with amylopectin, in which linear chains of glucose are interspersed with branches due to α(1→6) glycosidic bonds. (NJB)

Amylose A linear polymer of glucose which has a role as a storage form of carbohydrate (energy reserve) found in both plants and animals. Found in **starch** (from plants) and **glycogen** (from animals), amylose consists of linear chains of glucose units with α(1→4) glycosidic bonds. (NJB)

Anabolic steroids Steroid hormones (often synthetic) that stimulate anabolic processes, in particular protein synthesis from amino acids, whilst inhibiting catabolism and in this respect act antagonistically to glucocorticoids. These agents promote retention of nitrogen, potassium and phosphate. The effect is to promote weight gain, providing nutritional status is adequate. May act by influencing the transfer of amino acids from tRNA to ribosomes. Often derived from testosterone esters or 17α-methyl dihydro-testosterone although oestradiol and its derivatives may also be effective. Typical examples used to promote growth in farm animals, particularly in beef cattle, are stilboestrol, trenbolone acetate, boldenone, nor-ethandrolone and ethylestrenol. The use of these agents in food-producing animals is banned throughout the European Union, and enforcement and monitoring are achieved by routine testing for residues and metabolites in meat and in animal tissue, faeces and body fluid samples. However, they are still widely used in other parts of the world. (MMit)

See also: Anabolism; Glucocorticoids; Growth; Muscle

Anaemia A reduction in the number of circulating red blood cells (erythrocytes) or in the haemoglobin content of circulating red blood cells. Symptoms include pale mucous membranes, increased heart and respiratory rate, poor growth rates and exercise intolerance. It is potentially fatal. Causes include:

- Chronic or acute haemorrhage, either external or internal, due to trauma, vascular damage, endo- or ectoparasites, Warfarin poisoning, platelet deficiency (e.g. in thrombocytopaenic pupura in piglets) etc.
- Excess erythrocyte destruction (haemolytic anaemia), initiated for example by infections such as babesiosis (red-water), *Clostridium oedematiens* (bacillary haemoglobinurea), or copper poisoning.
- Insufficient synthesis of either haemoglobin or red blood cells, caused by dietary deficiencies, e.g. iron in piglets, copper, vitamin B_{12} or cobalt, or by conditions affecting bone marrow, e.g. chronic bracken poisoning, radiation, certain drugs, leucoses.
- Poisoning, or dietary excesses, e.g. molybdenum, excess feeding of kale and other brassicas, chronic lead poisoning.

Vaccination is available against some of the infectious diseases that cause anaemia. Treatment may be specifically for the primary cause or symptomatic therapy. For acute anaemia, blood transfusion may be appropriate. Correction or supplementation of the diet is essential. (EM)

See also: Blood; Haemoglobin; Iron deficiency anaemia

Anaerobic digestion: *see* Fermentation; Rumen digestion

Analogues, of amino acids Carbon skeletons that are immediate precursors of amino acids. To function nutritionally, analogues must be converted to the amino acid at rates consistent with need. Hydroxymethionine is a synthetic source of methionine used extensively in the poultry industry. It supports growth roughly equivalent to that obtained with methionine. Most D-amino acids may be considered analogues of the physiological L-amino acids since all but lysine and threonine can be converted to the L-amino acid. The keto acids of all amino acids except lysine and threonine may be considered analogues since when used singly they can support growth approaching that with the amino acid. (NJB)

Analytical methods: *see* Chromatography; Gas–liquid chromatography; Mass spectrometry; Near infrared spectroscopy; Neutron activation analysis; Nuclear magnetic resonance; Proximate analysis of foods; Weende analysis; *also* individual constituents

Anchovy A small, schooling, pelagic fish found mainly inshore in bays and estuaries, but not in the open ocean. More than 130 species of anchovies are distributed in many parts of the world. They are important human food and animal feedstuffs (fish meal and oil) and also used as fertilizers. Anchovies swim through the water with their large mouths open and strain out small organisms (plankton) with fine, sieve-like structures called gill rakers. (SPL)

Angora goats Angora goats are named after the Turkish province, now known as Ankara, in which they originated. Like other breeds of domesticated goat (*Capra hircus*) they are thought to be descended from the bezoar or wild goat (*Capra aegagrus*). The distribution of Angora goats was, for many centuries, restricted to Turkey. In the mid 19th century they spread, firstly, to South Africa and shortly afterwards to the USA. Today they are found principally in the Middle East, southern Africa and Texas, with smaller numbers in other US states and in Argentina. In recent decades Angora goat populations have been established in a number of European states and in Australasia.

Mature female Angora goats (does) weigh about 40–45 kg and males (bucks) around 60–65 kg. They are farmed for their fibre, mohair (not to be confused with angora fibre, which comes from rabbits). Unlike all other goat breeds, which have coats comprising a mixture of coarse and fine fibres, Angora goats are single-coated: the mohair fleece is composed of only one fibre type and contains, or ideally should contain, no coarse hairs. In practice most mohair fleeces contain a small proportion of coarse hairy fibres known as kemps. These have a different morphology from the true mohair fibres and are regarded as a fault, because they cause problems in the manufacture of mohair garments and fabrics. Most Angora goats are white but some breeders specialize in the production of black or brown mohair. The typical mohair fleece is white, long and lustrous with wavy locks or staples. Mohair grows rapidly, at a rate of 2–2.5 cm per month, and the animals are generally shorn every 6 months to provide a fibre that meets the requirements of the processors and to prevent excessive soiling caused by the fleece trailing on the ground.

The average annual mohair production of adult does is between 4 and 6 kg of greasy fibre. The yield (i.e. the weight of the clean fleece, after scouring, as a percentage of the greasy weight) is typically around 75%, though this varies between different strains within the breed. Mohair fibre diameter increases with age, from less than 25 microns (μm) at the first shearing at 6 months of age to 35 μm or more at about 4 years old. It is now known that both fleece weight and fibre quality (fineness) are influenced by nutrition. High levels of feeding, particularly of high-protein diets, lead to the production of heavier fleeces with coarser fibres, i.e. there is an inverse relationship between quantity and quality.

Like other domesticated breeds, Angora goats are seasonally polyoestrus. Does come into heat at 21-day intervals during the breeding season which, in the northern hemisphere, extends from about August to February. Gestation length averages about 150 days.

The principal mohair-producing countries have dry climates and in these conditions the goats can be kept outdoors throughout the year. In other countries Angora goats are housed during winter or in the wet season. Their main nutritional requirements are met outdoors from grazing and indoors from conserved forage. Some supplementary concentrates are generally supplied during late pregnancy and in early lactation. (AJFR)

Animal fat The lipid isolated from animal fat depots, mainly triacylglycerols. Fat rendered commercially from beef and sheep carcasses is commonly called tallow. Beef tallow is hard and typically contains, as a percentage of total fatty acids, 26% palmitic, 17% stearic, 43% oleic and 4% linoleic acids. Pig fat, called lard, is softer due to its greater content of unsaturated fatty acids. It typically contains 26% palmitic, 14% stearic, 43% oleic and 10% linoleic acids. Since the occurrence of BSE in Britain, tallow from ruminant species has not been used in animal feedstuffs but has been replaced by alternative vegetable fats with similar physical properties (e.g. palm oil). (JRS)

Animal production level (APL) The amount of metabolizable energy (ME) required to support the productive state of the animal, relative to its requirement for maintenance. For ruminants, APL = (total ME requirement)/(ME for maintenance). (JMW)
See also: Plane of nutrition

Animal protein Protein from animal sources. The term includes products derived from milk, eggs, meat and fish. As dietary protein these products are distinguished from plant protein by a generally better quality, in terms of both digestibility and biological value. In general, animal protein sources have higher concentrations of essential amino acids, especially lysine and the sulphur amino acids, than most plant protein sources. (MFF)

Anions Anions can be inorganic or organic. They carry a negative charge. The major anions in blood plasma are bicarbonate (HCO_3^-), chloride (Cl^-), phosphate (PO_4^{2-}), sulphate (SO_4^{2-}) and organic acids ($R{\cdot}COO^-$). To maintain anion/cation balance, the anions are balanced by an equivalent charge in the form of cations (positive ions) such as potassium (K^+) and sodium (Na^+). (NJB)
See also: Acid–base equilibrium

Anoestrus A period of infertility, ovarian inactivity or sexual quiescence which may be seasonal (in sheep, goats, horses etc.) or induced by nutritional imbalances, stresses (such as heat, cold, confinement, poor management etc.), disease, lactation or old age. Nutritional causes of anoestrus include inadequate intake of energy, micronutrient imbalances and toxicoses. Xenobiotics that contribute to infertility include oestrogen-like compounds, phyto-oestrogens from some clovers, zearalenone from *Fusarium* moulds, ergot alkaloids, locoweeds (swainsonine), *Leucaena* (mimosine), mustard family (glucosinolates) and selenium deficiencies or toxicoses. (KEP)

Anorexia Lack of appetite, markedly low voluntary food intake or complete abstinence from food. There are numerous causes, including infectious or non-infectious disease, unavailability of acceptable, nutritious feed and certain mental disorders. Seasonal inappetence seen in winter in many species should not be regarded as anorexia. True anorexia is rare in non-human animals as there is natural selection against it. (JMF)

Antagonism A negative interaction between a nutrient and other nutrients or between nutrients and non-nutrients. The interaction may be related to uptake or to use. An example is branched-chain amino acid antagonism in which three- to fourfold increases in dietary leucine in a low-protein diet result in decreases in food intake and weight gain and in the blood and tissue concentrations of the other branched-chain amino acids, valine and isoleucine, and their keto acids. Another amino acid example is the lysine–arginine antagonism in which two- to threefold increases in dietary lysine result in an increase in the need for arginine. Antagonisms can be found in mineral interactions in which one mineral affects the rate and extent of uptake of another mineral such that more of the other mineral is required in the diet. Examples are zinc–copper, zinc–iron, calcium–zinc, calcium–iron, calcium–phosphorus, iron–copper and many more. (NJB)

Key reference

Shinneck, F.L. and Harper, A.E. (1977) Effects of branched-chain amino acid antagonism in the rat on tissue amino acid and keto acid concentrations. *Journal of Nutrition* 107, 887–895.

Antagonist A compound that blocks the physiological action of another compound. For example, acetylcholine released by parasympathetic nerves binds intestinal muscarinic receptors to stimulate motility. Atropine also binds these receptors but does not increase motility. Thus atropine can act as an antagonist by outcompeting acetylcholine for these receptors, effectively blocking acetylcholine actions. (JPG)

Anthocyanins These plant pigments are glycosides containing a nucleus (aglycone) called an anthocyanidin. Anthocyanidins are flavonoids, or water-soluble phenolic derivatives. They are generally red, crimson, blue, purple or yellow. They tend to be metabolically inert in animals but some have antioxidant activity. They form dimers (procyanidin) which can polymerize to form condensed tannins (proanthocyanidins). (PC)

Antibiotic Antimicrobial pharmaceutical, usually of plant or fungal origin. Although the primary use of antibiotics is in the treatment of infections, certain antibiotics are used as feed additives in order to improve growth and feed conversion. The modes of action of antibiotics used as growth promoters probably include reduction in sub-clinical disease, thinning of the wall of the intestine and, in ruminants, a change in the microflora and fauna in the rumen. In the late 1990s, some antibiotics previously licensed in the European Union for use as growth promoters (zinc bacitracin, virginiamycin, avoparcin) were banned because of fears that their use might encourage the development of antibiotic resistance and prejudice the treatment of human disease. All antibiotics must be used with care and the current data sheet should be consulted for dosage, contraindications and other precautions: many may be used by Category A manufacturers only. Some may be incorporated into feed blocks or used as top-dressing of feeds such as silage.

Flavophospholipol is licensed for use in pigs, domestic fowls, turkeys, rabbits, calves, growing and fattening cattle and fur animals. It is a phosphoglycolipid, and is not absorbed from the digestive tract, so is not metabolized by the animal. It changes the pattern of rumen microorganisms by inhibiting some Gram-positive bacteria and by reducing the formation of peptidoglycan.

Monensin is licensed for use in non-lactating cattle. It has had fatal effects when fed to horses, and when fed to cattle within 7 days before or after being treated with tiamulin. Monensin is an ionophore, and is poorly absorbed from the digestive tract, about two-thirds being lost unaltered in faeces. Ionophores facilitate the movement of ions across membranes by forming hydrophobic complexes with ions such as potassium and sodium, and in so doing disrupt bacterial cell walls, and possibly the cell walls of protozoa. They thereby change the pattern of rumen microorganisms, reducing the production of acetate, butyrate and methane, and increasing the proportion of propionate. Since methane is a waste product, the efficiency of rumen activity is improved. Ionophores also reduce the total mass of bacteria and thereby decrease the amount of dietary protein degraded.

Avilomycin is licensed for use in pigs, broiler chickens and turkeys. Salinomycin is an ionophore available for use in pigs and also used to prevent coccidiosis in broiler chickens. (WRW)

See also: Additive, feed; Growth promoters

Antibodies Long-chain globulin proteins produced by plasma cells in response to the presence of an antigen (foreign protein) as part of the body's defence system. Antibodies are made of two light and two heavy peptide chains. Constant regions are common to all antibodies; variable regions are specific to the antigen that stimulated their production, and can form a site that binds with that specific antigen to form an antigen–antibody complex. This aids the elimination or destruction of that antigen.

Antibodies are produced in five different classes, depending on the structure of the constant regions, and this determines the site in the body at which they have their action (*see* **Immunoglobulin**). Antigens that stimulate the production of antibodies can be from the environment, food, infection or vaccination.

Plasma cells in the mammary gland produce antibodies (IgA) shortly before parturition, that are concentrated in the colostrum and are also present in declining amounts in early lactation. Circulating antibodies (IgG) are also transported and concentrated in the colostrum. They provide the potential source of passive immunity to most of the domestic species. The relative importance of IgG and IgA varies with species. The greater the number of antigens the dam has been exposed to, the more antibodies there are likely to be in the colostrum, assuming adequate health and nutrition. (EM)

See also: Antigen; Colostrum; Immunity

Antigen Any substance that stimulates an immune response. Many different substances can act as antigens, but most are proteins of more than 20 amino acids. Microorganisms act as antigens but their complex structure provides many antigenic sites or epitopes. Large protein molecules may also have many epitopes. (EM)

See also: Antibodies; Immunity

Anti-infective agents Anti-infective agents in feedstuffs include natural phytochemicals and feed additives (e.g. antibiotics). Phytochemicals with anti-infective activity, especially against protozoa, include phenolic compounds and saponins. They cause lysis of protozoal cell membranes. Anti-infective phytochemicals in herbal products may become more important if use of antibiotics as feed additives is restricted. (PC)

Antimicrobial activity The ability to kill or impair the growth of bacteria or protozoa. Many natural toxins have antimicrobial action and most antimicrobial pharmaceuticals used today are of plant or fungal origin. Although many antimicrobials are used to treat infections, others impair the digestion of feed, especially in ruminants. Plants such as broom snakeweed (*Gutierrezia* spp.), pine needles and sage brush (*Artemesia* spp.) contain toxins that inhibit rumen fermentation and reduce animal production. (BLS)

Antinutritional factors Antinutritional factors (ANFs) are feed components that have negative effects on the intake or utilization of feeds, or that may be inherently toxic when ingested. Many common feeds, such as legume seeds, contain ANFs; many rangeland plants contain phytochemicals or toxins. The most important ANFs are alkaloids, haemagglutinins (lectins), phenolics, phytates, phyto-oestrogens, saponins, tannins and trypsin inhibitors.

Alkaloids are cyclic organic compounds containing nitrogen. When ingested they may cause feed refusal, abortion, birth defects, wasting diseases, agalactia, and death. There are marked animal species differences in reactions to alkaloids, which may be due to differences in rumen microbial metabolism or in the absorption, metabolism or excretion of alkaloids or may be directly related to alkaloid affinity to target tissues such as binding at receptor sites. Alkaloids constitute the largest class of plant secondary compounds, occurring in 20–30% of perennial herbaceous species in North America. Major categories of toxic alkaloids include pyrrolizidine (e.g. *Senecio*), quinolizidine (e.g. *Lupinus*), indolizidine (e.g. *Astragalus*), diterpenoid (e.g. *Delphinium*), piperidine (e.g. *Conium*), pyridine (e.g. *Nicotiana*) and steroidal (*Veratrum*-type) alkaloids. Management schemes to prevent losses are usually based on recognizing the particular toxic plant, knowing the mechanism of toxicity, and understanding the temporal dynamics of plant alkaloid concentration and consumption by livestock. Once these are understood, losses may be reduced by maintaining optimal forage conditions, adjusting grazing pressure and the timing of grazing, strategic supplementation, changing livestock species and herbicidal control.

Phenolic compounds are produced by a wide range of plants. Low molecular-weight (MW) plant phenolics are often converted to tannins when plants mature. When ingested, phenolics reduce feed intake and weight gain. After ingestion, phenolics are absorbed, producing negative effects on physiological functions. Conversely, hydrolysable tannins may be converted to low MW phenolics in the gastrointestinal tract of ruminants and may be toxic (*see* **Tannins**).

Phytates are divalent mineral ions complexed with organic phosphorus in seeds. Phytate phosphorus is poorly available to non-ruminant livestock. Most (50–70%) of the phosphorus in cereal grains is in the form of phytic acid. Phytates may be soluble (e.g. sodium or potassium) or insoluble (e.g. calcium). Phytates readily complex with phytic acid and inositol in cereal grains, and these chelates then bind much of the phosphorus and zinc in grains, while complexing to a lesser extent with copper, cobalt, magnesium and calcium. Phosphorus deficiency is characterized by distorted appetite, reduced weight gains and impaired reproduction. Zinc deficiency is manifested by reduced weight gains and skin lesions. Through microbial fermentation in the rumen, ruminants are capable of cleaving phosphorus from phytates, making it available to the animal. Phytates are particularly high in maize and in wheat by-products, and are also present in most other cereal grains. Adding the industrial enzyme phytase to pig and poultry rations may be economically feasible, because phosphorus is relatively expensive to supplement; it also reduces phosphorus elimination in faeces.

Phyto-oestrogens are plant oestrogens that affect reproduction. Phyto-oestrogens inhibit release of reproductive hormones and compete with oestrogen at cellular receptors. Hence, livestock consuming forages containing phyto-oestrogens exhibit reductions in fertility, including abnormal oestrous cycles and ovulation, and defective development of reproductive organs and genitalia. Forages that typically contain phyto-oestrogens include lucerne and clover (*Trifolium* spp.). Cattle are much less sensitive to phyto-oestrogens than are sheep, which appear to activate phyto-oestrogens in the rumen to more potent compounds and may also have more sensitive oestrogen receptors. Poultry may also be affected by phyto-oestrogens; there is some evidence that quail are adversely affected by phyto-oestrogens in range plants.

Saponins are steroidal or triterpenoid glycosides that have considerable biological activity. Saponins have a bitter taste, reducing the palatability of feeds. They may also reduce the digestion and absorption of nutrients, including minerals. These effects occur primarily in non-ruminant livestock. Nevertheless, saponins in some range plants from the *Caryophyllaceae* (pink) family (e.g. *Drymaria*, *Agrostemma*, *Saponaria*) or in snakeweed (*Gutierrezia* spp.) can have toxic effects in ruminants, including loss of appetite, weight loss, diarrhoea, abortion and photosensitization. The primary livestock feed with significant amounts of saponins is lucerne (*Medicago sativa*), which causes frothy bloat. The concentration of saponins in lucerne changes seasonally, with the highest amounts in midsummer.

Tannins are high-MW phenolic compounds that bind strongly with proteins and other macromolecules such as starch, cellulose or minerals. Two major classes of tannins are hydrolysable and proanthocyanidins (condensed tannins). Tannins reduce feed intake because of astringency (i.e. reduced acceptability) and reduce digestibility by the formation of largely indigestible complexes in the digestive tract. Deleterious effects vary depending on the type of tannin and the tolerance of the animal, but concentrations above 10–20% may be toxic to ruminants. Clinically affected ruminants may show signs of kidney failure and elevated serum urea nitrogen. Non-ruminant animals may have reduced growth rates with low (i.e. $< 5\%$) concentrations; higher concentrations may be fatal. Tannins are common in plants, occurring in both gymnosperms and angiosperms. Woody species and broadleaf plants are more likely to contain tannins than are *Gramineae*. Compounds such as polyethylene glycol (PEG) may be added to feed and water to bind and inactivate tannins, allowing high-tannin feeds to be used for grazing or pen-fed livestock. For ruminants, tannins may have some positive effects through complexing with high quality protein (allowing it to bypass rumen degradation) or through increased nitrogen recycling to the rumen.

Trypsin inhibitors are plant proteins that inhibit the pancreatic enzyme trypsin, which is partly responsible for protein digestion. Trypsin (and other protease) inhibitors bind tightly to trypsin and chymotrypsin, inhibiting their proteolytic activity. Trypsin inhibitors occur primarily in legume seeds, particularly soybeans, but are also found in low concentrations in cereal grains such as wheat, oats, buckwheat, barley and maize. There are two classes of trypsin inhibitors: the low-MW Bowman-Birk inhibitor and the larger Kunitz inhibitor. The anti-tryptic activity is destroyed by moderate heat, which may be applied during the processing of plant materials. The Bowman-Birk inhibitors are more heat-stable than the Kunitz type. Excessive heating may reduce protein quality through non-enzymatic browning reactions. Ruminant livestock are less affected than non-ruminants, because most trypsin inhibitors are degraded slowly in the rumen though some may escape the rumen and enter the small intestine. In poultry, trypsin inhibitors cause pancreatic enlargement and reduce feed efficiency and growth rates; in pigs and calves, growth rates are depressed from reduced protein digestibility without accompanying pancreatic enlargement. Trypsin inhibitors from soybeans may be added to bovine colostrum, resulting in increased immunoglobulin absorption in calves. (JAP)

See also: Alkaloids; Haemagglutinins; Lectins

Antioxidant Antioxidants can be organic or inorganic and nutrient or non-nutrient in nature. They function to protect animal tissue against highly reactive oxygen-containing products produced chemically and by metabolism. These so-called reactive oxygen species (ROS) can be organic or inorganic compounds in which oxygen is a critical component. Their production is linked to the use of oxygen as the primary electron acceptor in aerobic metabolism. Compounds such as superoxide anion ($\cdot O_2^-$), hydrogen peroxide (H_2O_2), hydroxyl radical ($\cdot OH$), alkoxyl radical ($RO\cdot$) and peroxyl radical ($ROO\cdot$) attack cellular lipid, protein, DNA and carbohydrate. Chemical attacks on the unsaturated fatty acids of cellular membranes produce products such as the peroxyl radical ($ROO\cdot$), which initiates a chain reaction that can lead to compromised cell membranes and eventually cell death.

The antioxidants available to the cell are vitamin E, vitamin A, carotenoids, vitamin C and glutathione. Vitamin E is a fat-soluble vitamin involved in inhibiting chain reactions initiated when peroxyl radicals react with long-chain unsaturated fatty acids that contain three or more double bonds. An identifiable product of this attack is malondialdehyde, which can be measured by assays dependent on thiobarbituric acid (TBA). TBA products have been used as indicators of oxidative damage to membrane lipids. The chain reaction producing malondialdehyde is terminated when a peroxyl radical (ROO·) reacts with α-tocopherol to produce an α-tocopherol radical intermediate that reacts with another peroxyl radical to produce a non-radical product such as α-tocopherylquinone. To be effective, tissue α-tocopherol concentration must be above a critical threshold. Below the threshold peroxyl radicals propagate and deplete α-tocopherol while above the threshold peroxyl radicals are suppressed by the more than adequate α-tocopherol reserve. The average tocopherol concentration in membranes is one α-tocopherol per 500–1000 phospholipid molecules (Liebler, 1993).

Another nutrient antioxidant is vitamin C (ascorbic acid). It is not known whether the role of ascorbic acid is solely in the recycling of the α-tocopherol radical produced by the interaction of a lipoperoxyl radical (ROO·) or whether it has an additional role.

Another nutrient-based antioxidant is reduced glutathione (GSH), which is made up of three amino acids in a peptide linkage, γ-glutamyl-cysteinyl-glycine. The SH in the GSH refers to the cysteine portion of the molecule, which is involved in oxidation/reduction reactions. In its role as an antioxidant, GSH is converted to oxidized glutathione (GSSG). The enzyme glutathione reductase is involved in interconversion of GSSG to GSH, i.e. GSSG → 2GSH. The reducing equivalents required to convert oxidized glutathione to reduced glutathione come from glucose-6-phosphate via the production of NADPH + H which is converted to NADP when GSSG is reduced to 2GSH. GSH is involved in conversion of the α-tocopherol radical to α-tocopherol with the production of GSSG from 2GSH. This could not be shown in animals fed diets deficient in vitamin E. The direct use of glutathione in protection against oxygen-based damage is the selenium-containing enzyme glutathione peroxidase. This enzyme is involved in the destruction of hydrogen peroxide HOOH (H_2O_2) and lipoperoxides ROOH. Here 2GSH react with HOOH to produce $2H_2O$ and GSSG. When HOOH is not catabolized by glutathione peroxidase it can, in the presence of ferrous iron (Fe^{2+}), produce the hydroxyl radical ·OH, which is the most reactive oxygen metabolite and thought to be involved in tissue damage as indicated by production of malondialdehyde from unsaturated fatty acids and O-tyrosine from protein-bound phenylalanine. (NJB)

Key reference

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Antiparasitic agents Parasites may colonize either the internal or external medium of animals, or occasionally both, but are present in greatest numbers outside their host animal vector. Currently treatment of infected animals is usually based on anthelmintic agents but resistance is increasing, particularly in nematode worms. Attention is turning to prophylactic measures, such as the provision of uninfected pasture, and biological control, in particular by treatment of the parasite with fungi in its native pasture environment. (CJCP)

Antiprotozoal agents Protozoa are single-celled organisms that are often present in soil and may be transmitted to farm animals when feeding or by insect vectors. Many infect the digestive tract; others penetrate vital organs. A variety of drugs are available to treat protozoal diseases but they can be difficult to eradicate. Some antibacterial and antifungal agents have a limited effectiveness in treating protozoal infections. Chemoresistance is also emerging and new drugs must be targeted for effective chemotherapy. (CJCP)

Apo-enzyme An enzyme form that requires a co-factor in order to function. The intact enzyme protein without the enzyme co-factor bound to it is called the apo-enzyme. When the enzyme co-factor is bound to the enzyme protein this combination is called the holo-enzyme. An example is the red blood cell enzyme transketolase. The vitamin co-factor thiamine diphosphate binds to the enzyme and aids in the reaction but is not permanently changed by the reaction. This relationship is different from that of other vitamin dependent co-substrates such as NAD or NADP, which are changed to NADH and NADPH, respectively, as a result of the enzyme reaction. (NJB)

Apolipoproteins Proteins that are essential components of the lipid transport system in the body, which involves chylomicrons and the lipoproteins HDL, LDL, IDL and VLDL (high-density, low-density, intermediate-density and very low-density lipoproteins). Two general types of lipoproteins are identified: those that are integral (e.g. apo B-100), which cannot be removed and are critical to structure and function; and those that can be exchanged (e.g. apo A, apo C etc.). Apolipoproteins also act as enzyme co-factors and as ligands for lipoprotein receptors on cell surfaces. (NJB)

Apparent digestibility Digestibility determined simply from the difference between the amount of a nutrient consumed (I) and the amount excreted in the faeces (F), expressed as a proportion of the intake. Thus apparent digestibility = (I − F)/I. It is also determined at the terminal ileum by measuring the loss of the nutrient in ileal digesta (D); thus apparent digestibility at the terminal ileum = (I − D)/I. Unlike **true digestibility** or **real digestibility**, apparent digestibility ignores losses of endogenous origin. (SB)
See also: Digestibility

Appetite An instinctive desire for food or drink, or any other instinctive desire necessary to maintain life. Regarding feeding, appetite is an object or objective, such as obtaining a food or foodstuff. For example, during a meal, the appetitive phase is the goal-directed behaviour focusing on acquiring food, while the consumatory phase is the act of ingestion. During the consumatory phase, mechanisms are initiated that help to terminate the meal. The degree of disposition towards obtaining food may vary greatly, so that the appetite may be a subtle or overwhelming compulsion.

Hunger is often used synonymously with appetite, but differs in several aspects. Hunger may be viewed as the ‘stimulus to eat’ that arises from internal cues which provide information about energy or essential nutrient status. Hunger may be considered the motive to eat, in the same way that thirst is considered to be the motive to drink. Appetite may arise from the same internal cues that are responsible for hunger, as well as from the sight or smell of food, or from psychological desires or cravings. Appetite often implies a greater selectivity toward the food(s) consumed than hunger.

In contrast to food intake, which can be quantified in terms of the amount of food consumed per unit time, appetite is difficult to quantify and so the mechanisms controlling appetite are not differentiated from the mechanisms that control food intake. Food intake is controlled, both on a long-term, day-to-day and within-meal basis. On a long-term basis, adult animals will adjust their food intake to maintain a relatively stable body weight. On a day-to-day basis, animals will eat a relatively constant amount of energy each day and will correct for daily perturbations in energy intake. Circadian, diurnal or specific daily feeding patterns also contribute to how and when food is consumed within a day – these patterns can vary greatly between species. Within a meal, there are mechanisms that initiate the meal, sustain the meal and terminate the meal. Stimuli arising from within the body (internal) as well as from environmental (external) stimuli may be involved in initiating a meal. Very little is known about the internal stimuli that initiate a meal. None the less, these stimuli are probably energy metabolites in nature, and signal information regarding energy or essential nutrient (e.g. glucose) stores. The internal stimulus responsible for initiating the meal probably gives rise to the feeling of appetite or hunger. External stimuli that may be involved in initiating a meal can include social eating habits, the sight or smell of food, or other environmental factors. Signals from long-term energy stores such as adipose tissue also influence feeding, as low levels of insulin or leptin enhance feeding.

The appetite for food is controlled by the central nervous system (CNS), but is also responsive to metabolic, humoral and vagal signals originating from the periphery. Metabolic modulators include small transient drops in blood glucose that precede a meal, as well as hepatic glucose and fatty acid metabolism. Hormonal signals include factors such as amylin, apolipoprotein AIV, enterostatin, oestrogen, leptin, glucagon, glucocorticoids, insulin and somatostatin. The vagus nerve transmits information to the brain regarding gastric or rumen distention and the release of gastrointestinal peptides during a meal.

While it is generally thought that animals eat to meet their energy demands, there are numerous circumstances when this is not true. Highly palatable diets often cause animals to overeat and become obese, while extremely unpalatable diets will cause animals to undereat. A diet extremely deficient in an essential nutrient will cause anorexia if it is the only diet available. At the same time, animals fed mildly protein-deficient diets may overconsume the diet in an attempt to obtain more protein. Appetite is also suppressed during infection and cancer. Cytokines such as tumour necrosis factor-α, interleukin-1 and interleukin-6 appear to be the primary cytokines responsible for infection- and cancer-induced anorexia.

Neurotransmitters such as norepinephrine, serotonin, dopamine, histamine and GABA have all been shown to be involved in the control of feeding. Neuropeptides or peripheral peptides that act at CNS sites to affect food intake include agouti-related protein, amylin, α-melanocyte-stimulating hormone, bombesin, cocaine and amphetamine-related transcript (CART), corticotropin-releasing factor, enterostatin, galanin, glucagon, glucagon-like peptide, insulin, melanin concentrating hormone, opioids, orexin (hypocretin), neuropeptide Y, somatostatin, thyrotropin-releasing hormone and urocortin. Differences in the role and importance of these neurotransmitters and neuropeptides vary with species.

Numerous brain areas are involved in the control of appetite. The hypothalamus plays a critical role, particularly the arcuate nucleus, paraventricular nucleus, lateral hypothalamus, ventromedial hypothalamic nucleus and the dorsomedial nucleus. The caudal brainstem also plays an important role in feeding, as it contains the motor neurones that function as the central pattern generator for the rhythmic and stereotyped movements of ingestion (e.g. mastication, licking, lapping). The caudal brainstem also receives afferent fibres from the mouth, stomach and small intestine. Higher cortical brain areas are involved in multiple aspects of food intake, including making food associations, such as learned preferences and learned aversions, controlling motor movements necessary for finding or catching food, or making appropriate food choices.

Specific appetites arise from the animal's attempts to maintain an adequate intake or prevent a deficiency of dietary essential nutrients such as protein, vitamins and minerals. For example, animals maintain a level of protein intake above their requirement when allowed to select between different foods – this is often considered a specific appetite for protein. Animals deficient in a specific essential nutrient will select foodstuffs or diets containing the deficient nutrient over foodstuffs lacking the needed nutrient – this is also considered a specific appetite and serves to restore homeostasis in deficient animals. All specific appetites except sodium appetite appear to require post-absorptive feedback and learning before an animal will display a specific appetite for a given food. That is, the animal must first consume and absorb a specific food that contains adequate quantities of the needed nutrient. The brain then senses some event associated with the repletion of the limiting nutrient or the restoration of homeostasis. This 'positive post-absorptive event' is then associated with some aspect of the consumed food (usually taste) and will direct the animal toward obtaining and consuming this specific food during subsequent meals. In contrast, sodium appetite is innate and does not require post-absorptive feedback or learning. Animals deficient in sodium will immediately recognize foods containing this nutrient.

Perverted appetites or pica involve the intake of inedible or non-nutritive material such as earth, hair, bone, etc. The purpose of pica is unknown, but under some circumstances pica may occur during expression of a learned taste aversion or during states of nutrient deficiency. (NJB)

Appetite disorders Appetite disorders may be secondary effects of diseases, most of which cause a reduction in food intake, or they may be diseases themselves, such as anorexia. Many diseases cause a fever, with elevated body temperature. A reduction in food intake occurs, which is presumed to derive from a direct effect of the elevated temperature on the brain. Diseases involving abdominal discomfort, e.g. ovarian cancer, also depress intake: the reduction in intake should alleviate the discomfort, particularly if the food was the source of the problem. Other diseases are metabolic, i.e. in the body as distinct from the digestive tract, and again a reduction in intake is an innate response to metabolic imbalance or discomfort. In a normal animal, this is most likely to be due to the food but, even if it is not, intake will still be reduced. On the other hand, there are certain metabolic abnormalities that lead to an increased intake; for example, insufficient insulin secretion, as in diabetes, does not allow normal cellular uptake of glucose, with the result that certain cells (liver, hind-brain) signal their shortage of energy to the intake-controlling circuits of the brain. Appetite disorders are not likely to be transmitted genetically as they cause infertility and premature death. (JMF)

See also: Anorexia

Appetite stimulant A single compound or group of compounds that flavours a feed to increase the appetite. These include yeasts, mixtures of herbal extracts, distillery or brewing by-products and simple sugars. Appetite refers to the desire of an animal or bird for food or water, but is generally used to refer to a long-term effect. A number of compounds have been reported to be effective in the diets of young pigs but the literature is somewhat conflicting. Poultry have < 1% of the taste buds found in humans or other farm animals and these stimulants are ineffective. (SPR)

See also: Flavour compounds

Apple The juice of apples (*Malus* spp.) is extracted for apple juice or cider, leaving a residue of apple pomace that contains the remaining tissue, skins, pips and stalks. Pomace may be fed directly to livestock, dried, or sold moist. Some pomace has absorbents (e.g. wood shavings) added to aid juice extraction, which increase the fibre content and reduce the nutrient concentrations. Apple pomace is palatable and suitable for feeding to adult ruminants but it is low in protein (*c.* 5%) and in minerals. It is also low in dry matter (DM) and has only the moderate energy level of ~10 MJ ME kg^{-1} DM for cattle. Moist apple pomace can be stored for up to 6 months covered in clamps and its bulk density when moist is < 150 kg m^{-3} and when dried < 350 kg m^{-3}. The pectin and pentosan contents make it unsuitable for young ruminants, piglets and poultry. Maximum DM inclusion rates as a percentage of diet are 20% for dairy and beef cattle, 10% for lambs and 5% for ewes, sows and finishers. (JKM)

Aquaculture The cultivation of aquatic organisms (fish, molluscs, crustaceans, unicellular algae, macroalgae and higher plants), using extensive or intensive methods in order to increase the production or yield per unit area or unit volume to a level above that obtained naturally in a particular aquatic environment (Mariculture Committee of the International Council for the Exploration of the Sea, 1986). The term does not apply to the impoundment of aquatic organisms in order to gain access to favourable markets; nor does it include culture of essentially terrestrial organisms (e.g. terrestrial plants grown hydroponically).

Aquaculture includes pond, raceway, cage, pen and raft culture. Marine (as opposed to freshwater) aquaculture has been termed ‘mariculture’. Aquaculture encompasses the culture of aquatic organisms for stock enhancement, ocean ranching and ornamental purposes. The objectives of aquaculture are to increase production above levels occurring in natural ecosystems and to provide a more stable temporal supply of food organisms of consistently higher food quality under greater human control than can be supplied through the natural fisheries. These objectives are realized through selection of species or strains with higher feed conversion efficiencies, higher growth rates, later maturity and greater resistance to disease.

Commercial aquaculture is an ancient practice, though large-scale farming is relatively recent. The earliest known treatise on aquaculture is the *Classic of Fish Culture* in 500 BC by Fan Lei, a Chinese politician turned fish culturist who attributed his accumulation of wealth to pond production of carp. Oyster culture is known to have been practised in Japan and Greece *c.* 2000 years ago. Seaweed culture is much more recent, the earliest known text being published in 1952 in Japan. Fish farming was first carried out in Europe by the Etruscans.

Aquaculture has become the world's fastest growing food production sector for over a decade, with cultivation of 206 different animal and plant species. Total aquaculture production in 1998 was 39.4 million metric tonnes (Mt), valued at US$52.5 billion and growing at an average percentage rate of 11% per year since 1984. Finfish have contributed over half of the total aquaculture production by weight (20 Mt), followed by molluscs (9.1 Mt), aquatic plants (8.5 Mt), crustaceans (1.5 Mt) and others (0.3 Mt). Inland aquaculture, mostly carp culture, currently accounts for about two-thirds of the total production (excluding seaweed production), but mariculture is growing rapidly.

In 1998 Asia produced 35.81 Mt, over 90% of total global production. The world's top ten aquaculture producing countries in 1998 were China (27.1 Mt), India (2.03 Mt), Japan (1.29 Mt), the Philippines (0.95 Mt), Indonesia (0.81 Mt), Korea Republic (0.80 Mt), Bangladesh (0.58 Mt), Thailand (0.57 Mt), Vietnam (0.54 Mt) and Korea DPRP (0.48 Mt). Other countries include USA (0.44 Mt), Norway (0.41 Mt), Chile (0.36 Mt), Spain (0.31 Mt), France (0.27 Mt) and Italy (0.25 Mt). Major aquatic organisms currently under culture include several species of carp, scallop, clam, oyster, mussel, prawn, marine shrimp, salmon, trout, sea bream, sea bass and tilapia. Based on anticipated human population growth, it has been predicted that aquaculture production of food fish must exceed 50 Mt by 2025, assuming a global per capita fish consumption of 13.5 kg per year. (RHP)

Further reading

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Aquatic environment Aquatic environments encompass both freshwater (lakes, rivers, wetlands) and saline (oceans, estuaries, salt lakes and sloughs) conditions. They display a wide range of thermal regimes, pH, salinity and other chemical characters, clarity, and degree of movement, all of which determine the type of organisms that occupy them. A stagnant pond, for example, is a very different aquatic environment from a fast-flowing river or exposed ocean coast. Although aquatic habitat is usually judged to be physically more stable than the aerial or terrestrial environment, it is none the less subject to periodic changes. In temperate latitudes, seasonal thermal changes may be considerable, from freezing to 30°C or more. Water levels rise and fall seasonally, or more frequently in the case of tides, periodically exposing some inhabitants to air. Estuarine habitats may experience large fluctuations in salinity within hours. The organisms that live in these environments influence the physical properties to some extent, as in trapping or producing sediment, obscuring clarity of the water, or changing the content of oxygen and other chemical constituents. (CB)

Aquatic organisms Organisms living in fresh, brackish and sea water are generally divided into plankton, nekton, benthos and neuston (invertebrates, fish, mammals, etc.). Most fish and aquatic invertebrates are poikilotherms (body temperature conforms to external environment) with their metabolic rate increasing as the water temperature increases. Marine invertebrates are osmoconformers; marine fish, however, maintain their plasma hypotonic to that of the seawater medium by drinking, reducing urinary water loss and excreting salt through the gills. Freshwater fish osmoregulate by pumping out water while retaining the salts. External respiratory surfaces (gills) must be kept moist for gas exchange.

In the marine environment, many small free-floating eggs are often released and externally fertilized. The larvae are widely dispersed and feed on plankton, thus reducing the need for a large yolk sac within the egg. High mortality rates are associated with these planktonic larvae. In a freshwater environment, generally eggs are either retained by the parent or associated with the bottom and contain a large yolk sac, which produces more highly developed larvae or juveniles at hatch.

Aquatic animals usually excrete nitrogenous wastes in the form of ammonia, a soluble toxic substance requiring large amounts of water for its removal. (DN)

Aquatic plants Vegetation that is normally associated in nature with standing water, either permanently or at least for prolonged periods during the year. The plants may be wholly submerged, or with photosynthetically active parts entirely or partly submerged. In the broad sense of the term 'plants', they are represented by flowering plants, ferns, bryophytes, algae and fungi. As marine plants are generally categorized separately, the term 'aquatic' is often applied to only the freshwater species. The distinction between true aquatic plants and those that inhabit wet soils is unclear and ultimately relies on whether the plant requires some degree of submersion or merely tolerates it. Some intrinsically terrestrial plants can be relegated to aquatic habitats by poor competitive ability on drier soils, e.g. *Taxodium* (bald cypress). Herbaceous vascular plants dominate the aquatics, spanning a large number of families and ranging in size and habit from minute floating species, e.g. *Lemna* and *Wolffia* (duckweeds), to tall emergent forms, e.g. *Oryza* (rice) and *Typha* (cattails). Freshwater algae comprise at least 15,000 species but are mostly microscopic and inconspicuous. Fungi are small filamentous species.

Aquatic plants are important in stabilizing shorelines and purifying water. Ironically, where water movement is minimal, they often contribute to the destruction of their aquatic habitat by accruing sediment, towards hydrarch succession to terrestrial conditions. Aggressively growing macrophytes can be nuisances, clogging waterways and producing anoxic conditions after death. The large biomasses of such plants, e.g. *Eichhornia* (water hyacinth), have sometimes been used as a supplement to silage and other livestock feed. (CB)

Further reading

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Arabinogalactans Branched heteropolysaccharides with molecular weight 16,000–100,000, having varying proportions of D- or L-arabinose, and D-galactose; arabinose may be present in the furanose or pyranose ring form, galactose in the pyranose form. The backbone frequently consists of galactose residues. Arabinogalactans are usually water soluble and they may be covalently linked with protein. They may contain small amounts of rhamnose and uronic acids. They are the major hemicelluloses in plants. (JAM)

See also: Arabinose; Dietary fibre; Galactose; Hemicelluloses

Arabinose A five-carbon sugar, $C_5H_{10}O_5$, molecular weight 150, in L- or D-form and as a pyranose or furanose ring. Does not occur free in nature. A major component of plant polysaccharides. Absorbed in the small intestine by passive diffusion. (JAM)

Arabinoxylans Branched heteropolysaccharides with molecular weight 6000–30,000, having varying proportions of arabinose (usually in L form and as the furanose ring) and xylose (in D form and as the pyranose ring). Arabinoxylans frequently contain linear chains of xylose residues and may include small amounts of uronic acids. They are water soluble and are the major constituents of plant cell walls, particularly in cereals and grasses. (JAM)

See also: Arabinose; Carbohydrates; Dietary fibre; Hemicelluloses; Structural polysaccharides; Xylose

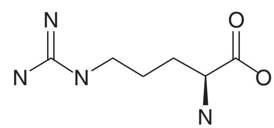
Arachidic acid Eicosanoic acid, a saturated long-chain fatty acid, $CH_3{\cdot}(CH_2)_{18}{\cdot}COOH$, shorthand designation 20:0. It is found in groundnut oil, rape oil, butter and lard. (NJB)

Arachidonic acid 5,8,11,14-Eicosatetraenoic acid, molecular structure $CH_3{\cdot}(CH_2)_4(CH{=}CH{\cdot}CH_2)_4{\cdot}(CH_2)_2{\cdot}COOH$, a long-chain unsaturated fatty acid, shorthand designation 20:4, found in fish and groundnut oils. It is an essential fatty acid for the cat family, but can be produced from linoleic acid in many animals. This makes linoleic acid an essential fatty acid and without it a deficiency of arachidonic acid is expected. Arachidonic acid is found in high concentration in membranes as part of the phospholipid fraction. Metabolically it is a precursor of the prostaglandins, thromboxanes and leukotrienes. (NJB)

Arctic char (*Salvelinus alpinus* (L.)) The most northerly adapted of the salmonid fish, with a circumpolar natural range. There are both anadromous and strictly freshwater forms. Eggs should be incubated at less than 8°C, and the optimum temperature range for growth is 10–13°C. Iceland is the major producer of cultured Arctic char. A major problem for culture to date has been highly variable growth rates. (RHP)

Arginase A cytoplasmic enzyme that catalyses the catabolism of the amino acid L-arginine to urea and L-ornithine. The enzyme is found in the liver of ureotelic animals (human, dog, cat, rat, pig, etc.) but not in uricotelic animals such as birds, in which nitrogen is excreted mainly as uric acid. In ureotelic animals the highest activity of arginase is found in the liver but it can also be found in other tissues such as the kidney, brain, mammary gland and red blood cells. (NJB)

Arginine An amino acid ($NH_2{\cdot}NH{\cdot}C{\cdot}NH{\cdot}(CH_2)_3{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 174.2) found in protein. It can be synthesized from arginosuccinate (via citrulline). The arginine synthesized in the liver is used primarily for urea synthesis, with lesser quantities used for the synthesis of creatine, polyamines and nitric oxide. Arginine synthesized in the kidney can be used for body protein synthesis, but avian and most reptilian species cannot synthesize arginine in either kidney or liver tissue and this makes arginine a dietary essential amino acid for these species. Young mammals can synthesize sufficient arginine to achieve growth rates that are about 50% of maximal, whereas adult mammals do not require arginine in the diet because biosynthesis is sufficient to satisfy their needs. Feline species, however, do not synthesize arginine efficiently and therefore require arginine in their diet.



(DHB)

See also: Citrulline; Urea cycle

Arsanilic acid Formerly used as a feed additive, as a coccidiostat in broilers and as a growth promoter in pigs and broilers, which makes use of its antibacterial properties. Feed efficiency is increased but residues of arsenic occur in meat and offal. (JMF)

Arsenic A mineral element (As) with an atomic mass of 74.92. It is found naturally in small amounts in sea water and rocks. Soils contain from 1 to 40 mg kg^{-1} but can accumulate more where arsenical pesticides and herbicides are used. Vegetables and grains contain < 0.5 mg kg^{-1}; freshwater fish contain an average of 0.75 mg kg^{-1} and seawater shellfish may contain much higher concentrations. Arsenic compounds can leach into ground water and contaminate well water. This has prompted some regulatory agencies to suggest a limit of 10 μg As l^{-1} drinking water for human consumption.

Arsenic as arsenate or arsenite is readily absorbed from the intestine and some of the As is converted to the methylated form in the liver before being excreted in the urine. There is no known metabolic function for As and it is generally considered to be a toxic substance. However, some investigators have found evidence, though weak, that As might have limited nutritional benefit in certain animal species, especially ruminants. The phenylarsenic compounds are the least toxic and are used as feed additives in the diets of pigs and poultry as a growth stimulant, whereas the water-soluble inorganic compounds are the most toxic, resulting in their use as pesticides. Although the element is also considered a carcinogen its trioxide form has been used to induce remission of acute promyelocytic leukaemia in humans. Low concentrations of selenium and As have been shown to induce hypomethylation of DNA in isolated intestinal cell models. This mechanism is thought to give selenium its anti-carcinogenic properties. Whether As has similar properties is not known. Natural antagonists to intestinal absorption and organ accumulation of As are other dietary minerals such as selenium.

Although the inorganic forms of As are more toxic than the organic forms, it has been reported that cattle and sheep can tolerate various inorganic As compounds in dietary concentrations up to 280 mg kg^{-1} for 60 days or more without ill effects. Pigs also tolerate rather high amounts of dietary arsenic, but have reduced food intake at concentrations > 500 mg kg^{-1}. (PGR, CJCP)

See also: Selenium

Further reading

Anke, M., Glei, M., Arnhold, W., Drobner, C. and Seifert, M. (1997) Arsenic. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements*. Marcel Dekker, Inc., New York, pp. 185–230.

Nielsen, F.H. (1990) Other trace elements. In: Brown, M.L. (ed.) *Present Knowledge in Nutrition*. International Life Science Institute, Washington, DC, pp. 294–307.

Arsenicals Arsenic-based compounds used as pesticides in crops and livestock, especially for tick control. Arsenical pesticides present significant hazards to animal health, causing gastroenteritis and a rapid drop in blood pressure. (CJCP)

Artificial drying Artificial drying of crops ('parching' over fire) dates back to biblical times. Green crop drying is normally associated with artificially drying with hot air. This method allows green crops to be preserved independent of weather conditions, at high nutritive quality with low conservation losses (as low as 3% of the dry matter). While dried grass accounted for 200,000 t in 1972 in the UK, this process declined in popularity during the 1980s due to the high cost of fossil fuels. Almost 300 l of oil is required to dry 1 t of dried grass from a crop of 80% moisture content. Composition of leafy dried grass can be dry matter (DM) 90%, crude protein 18.7% DM, metabolizable energy 10.6 MJ kg^{-1} DM. Barn drying provides a method of blowing cold air through a stack of cured hay bales to ensure that the moisture content of the dried hay is < 12%. Hay preservatives and drying agents allow for increased flexibility in haymaking systems. Under certain conditions, they can greatly increase the efficiency of nutrient preservation. The most common preservatives are organic acid-based formulations. Drying agents available are usually carbonate-based products, which may also contain fatty acid esters. (RJ)

Artificial rearing of mammals The process of substituting intensive technology for the normal care and nutrition provided by the dam in neonatal life. The most extreme need applies when offspring have been removed directly from the womb by hysterectomy to establish minimal-disease flocks or herds. It also has a function for neonates deprived of maternal care by an accident, a breakdown in maternal health or because of failure of the dam to lactate. The boundary between artificial rearing and very early weaning is not exact. Very early weaning following a very short lactation may facilitate the breaking of the disease chain from parent to offspring, particularly if this is accompanied by intensive medication of the offspring. Some success is claimed for reducing the incidence of some pig diseases such as porcine respiratory and reproductive syndrome and enzootic pneumonias.

For successful artificial rearing, the complex physiological needs must be met. The environment must be controlled so that the nutritional, social and physical environment provided by the dam can be simulated in the essential aspects. The immune system of the neonate at birth is naive. Rearing is greatly facilitated if the neonate can receive passive immunity via colostrum or by an equivalent dose of relevant **immunoglobulins** extracted from blood. At birth the gut is permeable to proteins and the globulins can be absorbed directly into the bloodstream. The benefits may be sustained well towards adult life. Offspring that are totally deprived of colostrum need 'hospital quality' care. This should include protection from air- and food-borne pathogens, a stable temperature and isolation from other livestock. The process of normalization of the environment needs to be very gradual and in step with the development of active immunity.

Nutrition during artificial rearing is critical to its success. The closer the artificial diet is to the composition of the natural milk of the species, the better the outlook. Growth rates tend to be more normal if the artificial diet is offered in a liquid rather than a solid form. Liquid feeding requires particularly diligent hygiene. In ruminants, liquid diets carry an additional benefit because they stimulate the reflex closure of the oesophageal groove and allow the food to bypass a non-functioning rumen. The reflex is assisted by a husbandry routine that raises the expectation of being fed. The protein source in the artificial diet is critical. The casein in milk has clotting properties in the presence of the stomach enzyme rennin, and this attribute aids **digestion**. Proteins other than those of milk are often less suitable partly because they do not clot and are usually less soluble. Those of vegetable origin tend to be difficult to digest, because the molecules are larger than those of the milk proteins and they may provoke an immune reaction. Milk fats are easily digested, particularly if emulsified, but in dry diets lipids rich in medium-chain fatty acids tend to be the most readily digested. Lactose not only supplies energy but is also readily fermented in the gut, encouraging the development of a friendly, lactobacillus-based flora. (VRF)

Artificial rumen A vessel in which rumen contents can be incubated under conditions resembling those of the rumen *in vivo*. It may be a closed or open system operating batchwise or a continuous-flow stirred tank reactor (CFSTR) or chemostat that will achieve a steady state. Such systems allow study of the products of rumen fermentation, the population dynamics of rumen microflora or studies of the degradation kinetics of components of forage and feeds, methanogenesis etc. The most complex of these continuous fermenters involve dialysis of the products to mimic absorption and gaseous exchange. Temperature, pH and redox potential may be monitored or controlled. The system may be used to study isolated pure cultures or mixed microbial and protozoan ecosystems. Artificial rumen systems allow study of the time course of change of substrates, gases and organisms. They are usually kept anaerobic using hydrogen and reducing agents. Simple batch systems are more easily managed. The 'Rusitec' is an artificial rumen system devised by Czerkawski (1986). (IM)

Reference

Czerkawski, J.W. (1986) *An Introduction to Rumen Studies*. Pergamon Press, Oxford, UK, 236 pp.

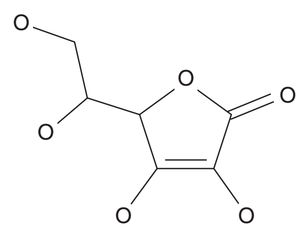
Artificial sweeteners: *see* Attractants; Flavour compounds

Ascites (or hydroperitoneum) A non-inflammatory peritoneal effusion, seen as an accumulation of serous fluid in the abdominal cavity. Though ascites can be part of generalized vascular oedema (vascular hypertension or hypoproteinaemia), more typically it results from chronic passive congestion of the portal venous system of the liver, often as a sequel to hepatic diseases such as cirrhosis or veno-occlusive disease. Other traumatic, neoplastic or vascular diseases that obstruct venous or lymphatic draining can also cause ascites but are relatively rare. Ascites must be differentiated from other accumulation of fluid in the peritoneal space, including exudates from inflammatory diseases or urine from a damaged urinary system.

There are nutritional, infectious, immunological and toxic diseases that result in liver disease and ultimately cirrhosis. As cirrhosis is a non-specific change, definitively identifying the inciting cause is often a diagnostic challenge. Toxins that are commonly associated with liver disease in livestock include copper (sheep are most susceptible), gossypol, pitch (clay pigeons), cocklebur, lantana, sacahuista, lechugilla, some vetches, blue-green algae, aflatoxins and pyrrolizidine-containing plants (*Senecio*, *Crotolaria*, *Amsinkia*, *Cynoglossum*, *Echium*, *Symphytum* and *Heliotropium* spp.). One of the common lesions of pyrrolizidine alkaloid intoxication is fibrosis and obliteration of the heptic central vein (veno-occlusive disease).

Avian ascites or broiler pulmonary hypertension syndrome is a disease of rapidly growing broilers. Birds 3–4 weeks old are the most commonly affected and flock mortality can be nearly 20%. Ascites syndrome worldwide costs about US$1 billion, with an average incidence of 4.7% in broiler flocks. Affected birds are stunted and lethargic, with abdominal enlargement and lack of appetite. Postmortem changes include marked right ventricular dilation and hypertrophy, arterial hypertrophy, ascites (serous fluid distension of the abdomen), pulmonary congestion and oedema. Although the aetiology of ascites syndrome is not completely known, it is closely associated with right congestive heart failure. Other proposed contributing factors include chronic oxygen deficits (housing at elevations of 3000 m), poor ventilation, high-energy diets and salt, monensin or furazolidone supplements. Of all these aetiologies, those that contribute to rapid growth appear to be most closely linked to broiler ascites. A likely pathogenesis is that rapid growth and increased oxygen requirements lead to cellular oxygen deficits, pulmonary arterial hypertension, right heart failure, passive congestion of the abdominal organs and ascites. A comparable syndrome with similar nutritional and genetic contributing factors is seen in turkeys (round heart disease). Other toxins have also been shown to cause ascites in birds. Severe ascites and oedema were reported in the 1960s when thousands of birds were poisoned with polychlorinated dibenzo-*p*-dioxin 'chick oedema factor'. Poisoned birds developed extensive hepatic necrosis and cholangiolar hyperplasia and portal hypertension. Heart failure is common in ascites produced in birds poisoned with high-salt diets or furazolidone. Ducklings and turkeys appear to be most susceptible to furazolidone toxicosis. (BLS)

Ascorbic acid L-Ascorbic acid is vitamin C, $C_6H_8O_6$. It is required in the diet of primates, guinea pigs and some bats and birds. In humans a dietary deficiency results in the classical symptoms of scurvy in which wound healing is impaired and subcutaneous haemorrhages are seen as well as muscle weakness, swollen gums and loose teeth. L-Ascorbic acid is a major water-soluble antioxidant involved in oxidation/reduction reactions in the body (ascorbic acid ⇌ dehydroascorbic acid + 2H). It participates in many processes, including collagen synthesis, in epinephrine synthesis from tyrosine and absorption of iron.

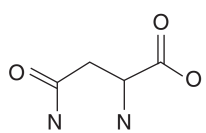


(NJB)

Ash The mineral elements in a feed, or in biological tissue, measured by burning off ('ashing') the organic matter and weighing the residue (the ash). During ashing the organic matter in the material under test is oxidized and minerals present in organic combination are changed to inorganic form. The measurement does not provide any information on the specific elements present and ash may include carbon from organic matter as carbonate when base-forming minerals are present in excess. As with the measurement of any feed component, it is important that a representative sample of the feed be used. The sample should be ground so that it will all pass through a sieve with 1 mm diameter openings; the sample should then be thoroughly mixed. A portion (2–3 g) is then dried to constant weight at 103°C and the moisture content determined. A portion (approximately 2 g) of the dried feed is weighed into a crucible (nickel or porcelain) and placed in a muffle furnace. The temperature is raised, stepwise, to 600°C. Ashing is allowed to proceed overnight (18 h), after which the crucible is transferred directly to a dessicator, cooled and weighed and the ash content of the sample determined as the weight remaining. (CBC)

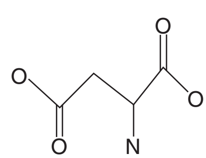
Asian sea bass (*Lates calcarifer*) A commercially important fish species farmed in several Asian countries and northern Australia. They belong to the family Centropomidae and are commonly known as baramandi, bhetki or giant sea perch. Asian sea bass are widely distributed in tropical and subtropical areas of the Indo-Pacific region inhabiting a wide variety of freshwater, brackish and marine habitats, including streams, lakes, estuaries and coastal waters, but spawning only in inshore marine waters. These predatory fish feed initially on small crustaceans and later switch to fish. Juvenile sea bass may be cannibalistic. (RMG)

Asparagine An amino acid ($NH_2 \cdot CO \cdot CH_2 \cdot CH \cdot NH_2 \cdot COOH$, molecular weight 132.1) found in protein. It contains both an amino and an amide group. It can be synthesized in the body from aspartic acid.



(DHB)

Aspartic acid A dicarboxylic amino acid ($COOH \cdot CH_2 \cdot CH \cdot NH_2 \cdot COOH$, molecular weight 133.1) found in protein. It can be synthesized in the body from oxaloacetate and an amino donor.



(DHB)

Aspergillosis A fungal infection (mycosis) caused by a number of *Aspergillus* spp. It is primarily a respiratory infection, especially in birds, but can affect the digestive and reproductive tracts. Clinical findings include dyspnoea, gasping and polypnoea, with microscopic evidence of fungal growth in affected tissues. Mastitis and abortion may occur in ruminants. (PC)

Associative effects of foods The effect of one food on the utilization of another given with it; for example, the change in digestibility of feed A attributable to the presence of food B. Thus, a diet of equal parts of dry matter (DM) from coarse forage (DM digestibility 0.45) and a concentrate mix (DM digestibility 0.75) will not necessarily have a DM digestibility of 0.6. This means that the metabolizable energy value attributed to an individual feed is not necessarily its value when used as a dietary component.

Although associative effects occur in all species, they are most important in ruminants given concentrates and roughages together. Ruminants have a unique capacity to digest cellulose, which allows them to consume poor quality forages, such as crop residues. However, to meet production targets for milk and meat, the poorer the quality of the forage the more necessary will be supplementary carbohydrate feeds. Starch is rapidly fermented in the rumen, causing a fall in the pH of the rumen liquor which, in turn, inhibits the cellulose-fermenting enzymes. This depresses the breakdown of the cellulose contained in the forage component of the diet. The effects will be greater when large amounts of concentrate are added and the forage component includes mature grasses or crop residues. Adding concentrates to an all-roughage diet can either reduce or increase roughage intake, thus giving a ‘substitution’ or ‘replacement rate’, defined as the change in roughage DM intake per unit change in supplement DM intake.

True associative effects of foods are not easy to estimate, especially when mature forage or crop residues are a major dietary component. Such feeds are also generally deficient in protein, thereby restricting the growth of cellulolytic bacteria and limiting the rate and extent of fibre digestion. Many of the starchy feeds will probably also contain protein degradable in the rumen, which will tend to correct this deficiency. To maximize rumen efficiency from widely divergent foods, a combination of rapid and slowly degradable proteins is needed. The overall effect of combining forages and concentrates depends on the amount of each in the diet and on the quality of the forage (Galyean and Goetsch, 1993).

Many feeds are subjected to some form of physical processing. For grains, this is usually either rolling or grinding, which allows the rumen microbes easier contact with the grain contents, potentially resulting in an increase in the extent and rate of digestion. With fodder, particularly roughage, whilst grinding increases the surface area open to microbial attack in the rumen, it removes the ability of the animal to select the more nutritious plant components. It can also make the feeds more dusty and, therefore, less palatable.

Positive associative effects of foods can also be described as synergy, when the effect of the combination in the diet is greater than when either food is fed alone. Benefits can be measured either as increased intake or as digestibility, or a combination of both. (TS)

Reference

Galyean, M.L. and Goetsch, A.L. (1993) Utilization of forage fibre by ruminants. In: Jung, H.G., Buxton, D.R., Hatfield, R.D. and Ralph, J. (eds) *Forage Cell Wall Structure and Digestibility*. USDA Agricultural Research Service and the US Dairy Research Center, Madison, Wisconsin.

Ataxia A gait disorder in which the movement of the animal is uncoordinated, typified by a swaying gait. It occurs in young lambs and goat kids suffering from swayback, which is caused by copper deficiency. (WRW)

See also: Copper; Gait disorders

Atherosclerosis A condition in which atheromas, consisting of fatty material, occur in the wall of arteries. It is not normally a problem in farm animals. (WRW)

Atlantic salmon (*Salmo salar* (L.)) A typically anadromous salmonid fish of the North Atlantic, ranging from the Arctic circle to Portugal in the eastern Atlantic and from Iceland and Greenland to Connecticut in the western Atlantic. Eggs are spawned in late autumn in freshwater streams. The fry hatch the next spring and migrate to sea as smolts after 1–8 years, depending upon latitude. Landlocked forms, living the full life cycle in fresh water, also occur. Over 98% of Atlantic salmon production worldwide is cultured. (RHP)

See also: Salmon culture

Attractants Animals have innate preferences and aversions that can be used to make feeds attractive or repellent. Sweet flavours are commonly added to foods for young animals, especially weaned piglets and calves, as most animals have an innate preference for sweetness. This flavour normally indicates the presence of sugars which are readily available sources of energy. Even in the absence of such sugars, sweet flavours can induce animals to prefer foods containing them, as long as they do not also have antinutritional factors such as high fibre, toxins, or nutritional imbalances. There is a belief (or hope) that the inclusion of palatability agents in a food will increase feed intake but this has rarely been demonstrated to last for more than a few days. However, improving the attractiveness of one food when it is offered as a choice with one or more other foods may increase the short- and long-term preference for the flavoured food, depending on the relative nutritional value of all the foods on offer. (JMF)

Atwater factors These factors describe the **metabolizable energy** per gram of protein, fat and carbohydrate (4, 9 and 4 kcal, respectively). They are used in relation to human diets but are not commonly used in animal nutrition. (JAMcL)

Automatic feeding Mechanical methods of providing feed to animals without human intervention. For poultry, the most common form is the chain feeder, in which compound feed, as mash or crumbled pellets, is conveyed round the house in an open-topped metal duct. The feeder is controlled by a time clock so that animals can be fed at

Intensively reared poultry normally have both feed and water provided automatically.

fixed times, even when the stockman is not available. This system allows equal access to feed by all the birds and is normally used for breeding birds in lay and for layers during rearing. Spin feeders distribute pellets over the floor of the house. These are only suitable for birds on restricted intake, such as broiler breeders during rearing, to ensure maximum distribution in the minimum time. With pan feeders a central auger conveys feed into a number of suspended feeding dishes known as pans. These can be adjusted to hold a given quantity of feed to ensure that all the pans receive the same amount of feed. As the last pan empties, it triggers the drive mechanism to refill the pans. Pans are the preferred system for *ad libitum* feeding, as in broiler houses.

For pigs, the most usual system for *ad libitum* feeding is similar to pan feeders, having an overhead conveyor that replenishes self-feeders, which are hoppers in which the feed flows by gravity into a trough to which the pigs have continuous access. For restricted feeding, predetermined amounts of meal or pellets are released into troughs, or on to the floor of the pen. Liquid feeding systems are also easily automated for both *ad libitum* and restricted feeding. Electronic systems can be used to control the intake of loose-housed animals such as dry sows: each animal has an electronic tag which identifies it and triggers the release of a predetermined amount of food when the animal enters the feeding station, but also denies it access if it has already eaten all its allotted food.

A similar system is commonly used for dairy cows, which are fed a predetermined ration when they enter the milking stall. Fully automatic systems are less common for other farm animals, though self-feeding and controlled grazing are widely used for cattle and sheep, and many systems of feeding are mechanized. (KF)

Availability 'Availability' and 'bioavailability' are terms used to describe the percentage of a nutrient in a feed ingredient that is digested, absorbed and metabolically utilized so that it is available for growth, maintenance, reproduction or production (milk, eggs, work). 'Relative bioavailability' refers to how well a nutrient in a feed ingredient is used relative to a known standard. For example, a growth assay might be used to compare the utilization of threonine in soybean meal to that of threonine fed as pure L-threonine, which is completely available. This is commonly a slope ratio assay, which involves feeding at least three doses of L-threonine in the linear area of the growth response curve (usually between 40 and 70% of the requirement). A criterion of response such as weight gain or protein accretion is then related to supplemental threonine intake to generate a standard slope. Graded doses of soybean supplying similar amounts of threonine are also fed and again the response is related to threonine intake. The slope for soybean meal threonine is divided by the slope for standard L-threonine to provide an estimate of relative bioavailability. A similar procedure can be used with a single level of soybean meal. In this assay, the resulting weight gain is inserted into the regression for free threonine to give the bioavailable threonine intake. This value is then divided by the actual measured threonine intake to arrive at an estimate of relative bioavailability.

With amino acids, relative availability determined by growth assay should be similar to true digestibility measured directly. However, growth assays do not work well for many nutrients, such as phosphorus, iron, manganese and vitamin A. For such nutrients, response criteria are needed that respond linearly to graded doses of the nutrient in question, such as bone ash, haemoglobin, bone manganese concentration and liver accumulation of vitamin A, respectively.

The term 'available' is used in a more restricted sense in connection with lysine, to describe the percentage of lysine in a feed ingredient that is not chemically conjugated in ways that make it unusable in metabolism. 'Available lysine' used in this sense does not include any measure of its digestibility.

(DHB)

See also: Nutrient bioavailability

Available: *see* Availability; Bioavailability

Avidin A natural glycoprotein found in egg white. It tightly binds biotin and has been shown to induce biotin deficiency in chicks and rats when fed raw. There are also anecdotal reports of avidin-induced biotin deficiency in other livestock. As avidin is easily denatured by heat, cooking or biotin supplementation is recommended when animals are fed raw egg whites. (BLS)

Ayu (*Plecoglossus altivelis*) Also known as 'sweet fish' or 'pond smelt', a member of the salmon family, native to East Asia. This anadromous fish spawns in fresh water and after a year returns to the sea, where it feeds on benthic organisms such as diatoms and blue-green algae. Ayu are cultured in either freshwater or seawater ponds and their optimum water temperature range is 15–25°C. Larvae hatched in captivity require acclimation to sea water before being fed live food organisms such as rotifers and artemia. The average market size is 50–150 g.

(SPL)

B

B-complex vitamins The B-vitamin complex is a group of eight water-soluble vitamins which, like all vitamins, must be provided in sufficient amounts in the diet. They are thiamine, riboflavin, niacin, pyridoxine, folate, biotin, pantothenic acid and vitamin B_{12}. Each of these is intimately involved as a coenzyme or co-substrate in one or more reactions in cellular metabolism. For example, thiamine is converted to thiamindiphosphate and pantothenic acid to coenzyme A. Co-factors such as these are not changed as a result of the chemical reaction in which they participate. These enzyme co-factors play critical roles in metabolism. Because of their participation in cellular metabolism they are widely distributed in nature. (NJB)

Backfat The layer of subcutaneous fat lateral to the spine. The thickness of this layer is a good predictor of the total body fat content of the carcass and this measure is often used in grading the carcasses of pigs, for which a common point of measurement is the P_2 position, 6.5 cm lateral to the spine at the level of the last rib. (SAE)

Bacteria: *see* Gastrointestinal microflora

Bagasse The fibrous residue remaining after sugarcane has been milled and the juice extracted. It is normally used as a fuel in sugar mills, in the manufacture of fibreboard or paper, as animal bedding and as a ruminant feed. Untreated bagasse has a very low digestibility but this can be improved by treatment with high-pressure steam or alkali (sodium hydroxide). (EO)
See also: Sugarcane

Bakery products Wastes from bread, cake, biscuit and pasta making. Typically these are high in starch and oil but composition varies and each product should be analysed before it is used in animal diets. These products can be fed to ruminants and non-ruminants but their high levels of oil can reduce rumen fibre degradation rates. They are an excellent source of energy but the quality of the protein and starch can be reduced by heat processing. Fresh products are very palatable but should be used before they become mouldy or rancid. Palatability may be reduced when the products are dried and ground. The main factors limiting the use of bakery products are the high oil content and risk of contamination from packaging. Their high oil concentrations can reduce the vitamin E level of the diet. (JKM)

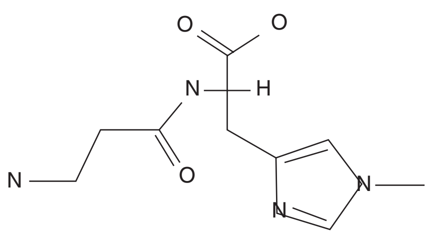
Composition of bakery products.

		Nutrient composition ($g\ kg^{-1}$ DM)				Energy ($MJ\ kg^{-1}$ DM)	
	Dry matter ($g\ kg^{-1}$)	Crude protein	Oil	Starch	Sugar	MER	MEP
Bread	650–680	120–125	30	260–280	75–80	14	16
Bakery waste	500–890	10–150	10–250	200–600	50–250	9–19	18.5
Confectionery	800–900	5–200	10–250	0–100	150–250	12–18	–

MEP, metabolizable energy for poultry; MER, metabolizable energy for ruminants.

Bale A large bundle of material bound with twine or wire. There are four basic types of bale: (i) the traditional small rectangular hay bale 0.35 m × 0.45 m × 0.9 m weighing 20–30 kg; a small round bale 0.45 m × 0.60 m; (iii) a large square bale 1.5 m × 1.5 m × 2.4 m weighing 400–700 kg; and (iv) a large round bale 1.2 m × 1.2 m weighing 400–700 kg. For ensilage, bales are either wrapped in polythene film or placed into polythene bags and sealed, to ensure anaerobic conditions. (DD)

Balenine β-Alanyl 3-methylhistidine, the dipeptide formed of 3-methylhistidine with β-alanine. It has also been called ophidine. Protein-bound histidine in muscle is methylated in the 3 position and is released as free 3-methylhistidine when actin and myosin are broken down in normal protein turnover. Other compounds of similar structure are carnosine (β-alanylhistidine) and anserine (β-alanyl 1-methylhistidine). Balenine is found in the blood and tissues of pigs.



(NJB)

Bamboo Plant of the family *Gramineae* (grasses), chiefly of warm or tropical regions. Bamboos are the largest grasses, sometimes reaching 30 m in height. The stalks are round with evergreen or deciduous leaves. Uses include wood for construction, paper production and fuel. The sprouts are eaten as food. Bamboo may be fed to ruminants either fresh or as silage of boiled bamboo shoot shell. Bamboo has a high potential nutritional value and rumen degradability. The addition of wheat bran increases the rumen degradability of dry matter and protein. In bamboo seed, the carbohydrate and vitamin C contents are highest in *Bambusa arundinacea* and the protein content is highest in *Dencrocalamus strictus*. In bamboo leaves, the dry matter (DM) is 550–600 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 180–190, ether extract 5–40, crude fibre 220–290 and ash 118–170, with MER of 11.3 MJ kg^{-1} DM. (JKM)

Key reference

Bhargava, A., Kumbhare, V., Scrivastava, A. and Sahai, A. (1996) Bamboo parts and seeds for additional source of nutrition. *Journal of Food Science and Technology* 33, 145–146.

Banana (*Musa* × *paradisiaca* L.) Bananas and plantains (cooking banana) are grown in the tropics as staples for human consumption and for export. By-products fed to livestock are surplus and reject fruit, peels, leaves and pseudostems.

Banana (and plantain) fruit are mainly starch (*c.* 70% in dry matter), some of which is converted to sugars with ripening. As protein (< 4% in dry matter), minerals (especially Na) and fibre contents are low, supplementation is necessary when feeding. Normal usage is for pigs; supplementation with a protein source of appropriate amino acid spectrum is important. Ripe bananas promote higher growth than green ones, probably because of 'active' tannins in unripe bananas. Cooking slightly improves green bananas for pigs. Chopped green bananas are highly palatable for cattle, but less so for sheep and goats. For ruminants, urea is a suitable (and less expensive) source of much of the supplemental protein. Banana-based diets require fibre supplementation to ensure normal rumen function. Bananas can be ensiled. Peels can be fed when ripe, but not green. Leaves are fed to ruminants during scarcities, but low protein and high tannin make for low digestibility and low intake. The pseudostem of banana comprises fleshy leaf sheaths that surround the stem, and also stem after the fruit is harvested. It is high in moisture (> 90%) and is fed, freshly chopped, to ruminants and pigs. The dry matter is low in protein (< 4%) and mostly nitrogen-free extractives (*c.* 60%). Ensiling is also possible.

(EO)

Key references

Babatunde, G.M. (1992) Availability of banana and plantain products for animal feeding. In: *Roots and Tubers, Plantains and Bananas in Animal Feeding*. FAO Animal Production and Health Paper No. 95. Food and Agriculture Organization, Rome, pp. 251–276.

Gohl, B. (1981) *Tropical Feeds*. Food and Agriculture Organization, Rome, 515 pp.

Barley Barley (*Hordeum sativum*) is a member of the *Gramineae* (grass) family. It is cultivated primarily for its grain, which is used for human and animal food. The grain (kernel) comprises the seed and pericarp (seed coat) and is surrounded by a hull (or husk) representing 0.1–0.15% of the grain weight. The hull is composed of two structures, the palea and lemma, collectively referred to as glumes, and these fuse with the outer coat of the developing grain to produce a covered kernel. The chemical composition and nutritive value of barley grain (see table) is influenced by the presence of the hull.

Livestock feeding represents the single most important market for the world's barley production (~ 50% of the total), the remainder being used for human food consumption and for malting purposes. Barley contains little of the gluten protein whose elastic properties are important in bread making. Barley flour is therefore used to make unleavened or flat bread, and porridge in North Africa and parts of Asia, where it is a staple food grain.

By-products of barley arise mainly from the brewing, distilling and pearl barley industries. Brewing gives rise to two main by-products: malt culms (or malt sprouts) and brewers' grains. Malt culms comprise the dried rootlets and sprouts of germinated barley grains produced in the malting process. Brewers' grains are the spent grains from the mashing and filtration and are widely used to replace both forage and concentrates in the diets of ruminants. The production of malt whisky from the distillation of barley malt alone or a mixture of cereals (grain distillation) produces a number of wet and dry by-products for use in the animal feed industry. These include distillers' wet spent malt (malt draff) or grains (grain draff) and light grains (dried draff), pot ale syrup, malt distillers' dried solubles, superdraff and distillers' (malt or grain) dark grains. Also produced are malt culms (dried rootlets and shoots) and malt residual pellets, consisting of pelleted malt culms, thin and broken grains (after dressing) with barley hulls and dust. Barley feed is the by-product arising from the preparation of pearl barley for human consumption. This comprises three grades of dust produced during processing and contains approximately 140 and 100 g kg^{-1} dry matter (DM) of protein and fibre, respectively. Dried brewers' grains and distillers' dark grains can be fed at a level of 20% diet DM in growing cattle and dairy cows and 10% diet DM for calves and sheep. Their high unsaturated fatty acid contents may cause a reduction in fibre degradation in the rumen and a depression in feed intake. Copper toxicity may arise from feeding distillers' grains to sheep. For pigs, the use of distillers' grains is generally restricted to feeding to sows, due to the high fibre content.

Barley is grown primarily for animal feeding and brewing: by-products of brewing are also used for animal feeding.

Chemical composition and nutritive value of barley grain and barley by-products (as g kg^{-1} dry matter unless specified). (After MAFF, 1990.)

Feed type	DM (g kg^{-1})	CP	Starch	NDF	GE (MJ kg^{-1} DM)	Energy value (MJ kg^{-1} DM)		
						Ruminants[a]	Pigs[b]	Poultry[c]
Barley grains								
All seasons	864	129	562	201	18.5	13.3	15.4	–
Winter	857	130	585	178	18.5	13.5	15.4	14.3
Spring	869	128	572	207	18.5	13.2	15.5	–
Barley by-products								
Fresh brewers' grains	250	218	38	619	21.3	11.5	–	–
Draff	248	211	18	673	21.5	10.2	–	–
Distillers' dark grains	907	275	26	420	21.3	12.2	–	–
Malt culms	906	290	57	556	18.9	11.1	–	–
Pot ale syrup	483	374	–	6	20.0	15.4	–	–
Forages								
Straw (all seasons)	867	41.5	10.9	811	18.4	6.4	–	–
Straw (spring)	862	42.6	17.8	811	18.5	6.6	–	–
Straw (winter)	874	37.6	2.2	809	18.3	6.2	–	–
Whole-crop silage	394	90.3	234	575	19.1	9.1	–	–

[a] As metabolizable energy; [b] as digestible energy; [c] apparent metabolizable energy (corrected to zero).
CP, crude protein; DM, dry matter; GE, gross energy; NDF, neutral-detergent fibre.

In addition to the use of barley and barley by-products in livestock diets, barley may also be grown as a forage crop or ensiled as a whole-crop forage. Barley straw is also produced following harvesting of the grain and can be utilized for feed purposes. (ED)

Further reading

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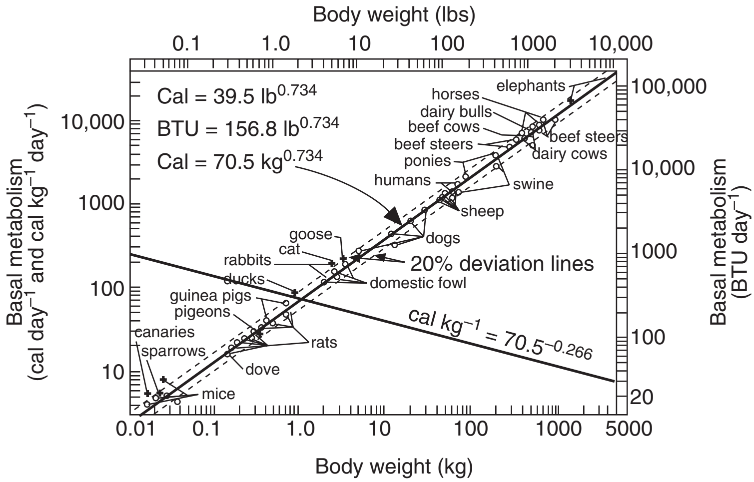
Basal metabolism The irreducible energy cost of maintaining the body during complete rest. It was originally intended to provide a standard condition of measurement for human subjects, which would make possible comparisons between individuals, ages, sexes, races, social groups etc. The conditions for measuring basal metabolic rate (BMR) are that the subject must be in a thermoneutral environment, have not eaten for 12 h and be lying down but not asleep; usually it is measured soon after the subject has awoken from a night's sleep. Compliance with these conditions demands a cooperative subject and is virtually impossible with animals. Nevertheless, the concept of basal metabolism still provides a useful starting point, not only for interbreed and interspecies comparisons, but also for consideration of the additional energy needed for food ingestion, digestion, lactation, pregnancy, exercise and environmental discomfort, all of which increase metabolic rate above the basal level. Nor is BMR the minimum level; the rate drops, for example, during sleep and in starvation. Metabolic rate is higher in growing animals and productive adults than in those fed maintenance rations, and although it is obviously greater in large than in small animals, the latter have a much greater BMR per unit weight. Brody's (1945) classic graph, reproduced here, shows that when body weights and 'basal' metabolic rates are plotted on a double logarithmic grid, the results from mature animals of different species ranging from mice to elephants fall close to a straight line. Brody's regression equation, converted into SI units, may be written as:



Brody's (1945) graph relating basal metabolism of mature species to body weight.

BMR = 3.41 × (weight in kg)$^{0.734}$ Watts
or
BMR = 295 × (weight in kg)$^{0.734}$ kJ/24h.

It is emphasized that the 'basal' metabolic rates considered by Brody do not fulfil the conditions as originally defined for humans. They probably most nearly represent either fasting metabolism of animals that are free to stand or lie at will but not recently fed, or resting metabolism of normally fed animals lying down. The interspecies comparison may not be so exact as it at first appears from Brody's graph; the dashed lines on either side represent 25% divergences of BMR from the predicted values. More recent measurements suggest that for some species BMR tends to be consistently different from the values predicted by the Brody relationship (approximately 20% higher in cattle and 20% lower in sheep). Brody's regression does, however, demonstrate that tissue of small animals is metabolically more active than that of large ones; BMR per unit of body weight of mice is 25 times as great as that for elephants. The exponent 0.734 found by Brody is frequently rounded to 0.75, and body weight to the power 0.75, known as metabolic body size, is often used for interspecies comparisons. (JAMcL)

Further reading

Blaxter, K.L. (1989) *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge, UK.

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Beak In birds, synonymous with rostrum or bill. The beak includes the upper and lower projecting mandibles, which are covered by horny layers of keratinous tissues and grow continuously. When food is gathered by the beak, it is mixed with saliva containing digestive enzymes secreted from glands around the mouth. (MMax)

Bean Beans include field bean (*Vicia faba*, L. spp.), horse bean (*V. faba* var. *equina* Pers) and broad bean (*V. faba* var. *minuta* (Alef) Mansf.). Beans are legumes mainly grown for human consumption but some varieties are grown for animal feed. There are winter and spring varieties of bean which have contrasting agronomic characteristics suitable for different sites, but yield and harvest date differences are small. Beans are a good source of protein and energy, with high levels of lysine, but they are low in methionine and cysteine. Spring varieties are higher in protein than winter varieties. Beans are rich in thiamine and phosphorus and are often used to replace peas in animal diets. They contain tannins and trypsin inhibitors, which may reduce protein digestibility, though new low-tannin varieties are grown. Urease, phytates, haemagglutinins and glucosides are regularly present in raw beans. These anti-nutritional factors limit dietary inclusion rates, particularly in diets for non-ruminants, but they can be inactivated by heat processing. Field beans can be included in dairy, beef and ewe diets at 20% of total diet, in finisher pig and sow diets at 10%, in grower pig diets at 7.5%, and in lamb, calf and breeder and layer chicken diets at 5%. A blend of extruded beans and full-fat rapeseed (50:50) known as 'Extrupro' is used as a high-energy and high-protein supplement for all ruminants. The dry matter (DM) content of spring beans is 840–880 g kg^{-1} and the typical nutrient composition (g kg^{-1} DM) is crude protein 210–290, crude fibre 70–90, ether extract 10–25, ash 25–41, neutral detergent fibre 100–211, starch 300–400 and sugars 15–55, with MER 10.5–14.0 and MEP 13.5 MJ kg^{-1}.

(JKM)

Beckmann process This technique, named after the German chemist Ernst Beckmann, uses alkali to hydrolyse the ester bonds between lignin and cell wall polysaccharides to improve the degradability of cereal straws. Cereal straw is soaked for up to 2 days in a dilute (1.5%) solution of sodium hydroxide and then washed to remove excess alkali, prior to feeding. (FLM)

See also: Alkali treatment

Beef Meat from cattle, mostly from specialized beef breeds.

Beef cattle Cattle used to produce meat. Beef cattle are produced either for sale or for on-farm consumption throughout most of the inhabited world, except in areas of Africa infested with tsetse fly where trypanosomiasis prevents all but a few resistant breeds from being kept, and areas where the Hindu religion is practised (India) as cattle are considered to be sacred and are not eaten.

Ideally beef cattle are large, well-muscled animals, with good conformation (i.e. muscling around the shoulders and especially the hind quarters), fast rates of growth, and good feed conversion ratios. These attributes are found to varying degrees in most specialist beef cattle breeds, which include Aberdeen Angus, Hereford, Belgian Blue, Charollais and Limousin. These all originated in Europe but, as they have been exported worldwide, further selection for local conditions (especially hot climates) has created a number of sub-breeds. Whilst under ideal temperate conditions these are far better suited to the production of beef than many general-purpose native cattle, under tropical conditions and stresses they are not as productive, and may be subject to devastation in situations such as drought. To avoid this, cross-breeding of imported improved breeds with local cattle can be used, or where conditions are particularly unfavourable the improvement of the local cattle is normally the best option. A good example of this is the Chinese Yellow Breed which has an excellent feed conversion ratio and can survive on poor quality feeds such as rice straw which is plentiful in China. Many improved breeds cannot be productive on such a poor diet so improvements in productivity depend on selection within the breed, supported by limited cross-breeding programmes.

Large scale cross-breeding programmes have created tropical beef breeds such as the Brahman, Droughtmaster, Brangus and Santa Gertrudis. Brahman were created by selecting and crossing productive tropical cattle, whilst the other three were developed by cross-breeding the Brahman with European breeds such as Shorthorn and Aberdeen Angus.

Animals used for beef production normally come from one of two sources: specific beef breed dams mated to beef breed sires; or dairy cow dams mated to beef breed sires. Animals that are 100% dairy or of multipurpose breeds can also be used for beef, depending on the circumstances and the availability of bloodstock, though with poorer productivity.

The systems in which beef cattle are kept vary from extensive ranches to intensive feedlots. In between these extremes are other systems such as suckler cow production, family farm fattening of store cattle, and smallholder (backyard) rearing. Ranches are found where land is cheap and feeds are of low nutritive value, whereas feedlots are found where feedstuffs are cheap (often near to agri-industrial wastes) but land is expensive (often due to its location near to major cities). Backyard production occurs where families fatten a small number of cows on whatever vegetation, wastes and residues are available.

Typical feeding regimes for beef cattle combine fodder, either fresh or preserved, with some concentrates. Fresh, grazed grass is used where the climate permits, with such cereals and by-products as are available and cost-effective. Straw can also be used as a bulk feed if the rest of the ration is designed to cover its deficiencies. It is important not to feed too much concentrate which causes fat to be laid down rather than lean tissue. The shorter the production cycle the greater the risk of this. However, in some cultures fatty meat is preferred. MMal

Beet, fodder: *see* Fodder beet

Beet, sugar: *see* Sugarbeet

Behaviour, feeding: *see* Feeding behaviour

Behenic acid Docosanoic acid, a saturated long-chain fatty acid, $CH_3{\cdot}(CH_2)_{20}{\cdot}COOH$, shorthand designation 22:0. It is found in oils such as groundnut and rapeseed oils, some milk fats and marine animal oils. (NJB)

Benzoic acid $C_7H_6O_2$, an unsaturated six-carbon ring with a carboxyl carbon attached. It is found in berries and gum benzoin and is used as a food preservative. Benzoic acid is not apparently catabolized by animals but is conjugated with glycine in the liver to form hippuric acid, which is excreted in urine. Hippuric acid makes up a greater fraction of urinary nitrogen in grazing ruminants than in simple-stomached animals. (NJB)

Beta agonists Beta agonists (β-adrenergic agonists) are substances that activate β-adrenergic receptors. They include both the naturally occurring catecholamines (i.e. dopamine, norepinephrine and epinephrine) and synthetic compounds that are structurally similar to them. Epinephrine appears to be the natural agonist for these receptors. Norepinephrine also activates them but only at high (pharmacological) concentrations. Norepinephrine is instead thought to act via α-adrenergic receptors (the other major class of catecholamine receptors). The β-adrenergic receptors are further broken down into three classes: β1, β2 and β3. There are both broad-based and selective pharmacological agonists for each type. The classic β-agonist is isoproterenol. Synthetic β-adrenergic agonists such as clenbuterol, cimaterol and ractopamine have major effects on the growth and metabolism of skeletal muscle and adipose tissue of food animals. (NJB)

β-Alanylhistidine: *see* Carnosine

Beta-oxidation The metabolic processes involved in catabolism of free fatty acids. Even-chain fatty acids are cleaved into a common two-carbon intermediate, acetyl-CoA. Odd-chain fatty acids produce mainly two carbon units (acetyl-CoA) but the terminal three-carbon unit is released as propionyl-CoA. Since this process occurs in the mitochondrion, all cells (with the exception of the mature mammalian erythrocyte) are thought to catabolize fatty acids in this way. (NJB)

Betaine A water-soluble compound, $(CH_3)_3{\cdot}\overset{+}{N}{\cdot}CH_2{\cdot}COO^-$, widely distributed in plant and animal tissues. In metabolism, betaine is derived from the oxidation of choline in a two-step process. One of the methyl groups of betaine can be used by the liver enzyme betaine homocysteine methyltransferase to methylate L-homocysteine to form L-methionine. The remaining two methyl groups of betaine are converted into one-carbon units of the folate system. (NJB)

Bicarbonate Bicarbonate is formed in animals from CO_2 produced in the catabolism of carbohydrates, fats and amino acids. The carbon dioxide produced is dissolved in water and, with the aid of the erythrocyte enzyme carbonic anhydrase, carbonic acid (H_2CO_3) is produced. Carbonic acid can dissociate into bicarbonate HCO_3^- and hydrogen H^+ ions. The carbonic acid–bicarbonate system ($H_2CO_3 \rightarrow H^+ + HCO_3^-$) is one of the three major blood buffering systems. This system differs from the haemoglobin and protein buffer systems because the blood concentration of CO_2 is maintained and is continually replenished. It is controlled by respiratory rate and the plasma concentration of HCO_3^- is controlled by the kidney. Bicarbonate plays a major role in maintaining the pH of blood near 7.4. (NJB)

Bifidobacteria: *see* Gastrointestinal microflora

Bile Bile is made in the liver, stored in the gallbladder and secreted into the small intestine at the level of the duodenum. It contains sodium and potassium salts of the bile acids cholic acid and chenodeoxycholic acid. The salts of deoxycholic acid and lithocholic acid are also found in bile but these bile acids are the result of microbial metabolism of cholic acid and chenodeoxycholic acid, respectively, in the intestinal contents. The bile pigments, bilirubin and biliverdin, are products of haemoglobin degradation. Limited amounts of inorganic salts, fat, lecithin, fatty acids and cholesterol are also found in bile. The bile acids are conjugated with one of two amino acids: glycine or taurine. These conjugates are referred to as glycocholic and taurocholic acids. Bile acids can be reabsorbed from the intestinal tract at the level of the ileum and returned to the liver by the portal circulation, from which they can be secreted again in bile; this is called the enterohepatic circulation. Bile enhances lipid digestion due to the formation of fatty acid-containing micelles that can diffuse through the unstirred water layer on the mucosal surface where the fatty acids are subsequently taken up by the enterocytes. (NJB)

Binding agents Materials added to compound feed at relatively low rates of inclusion (0.05–2.5%) to increase the durability and hardness of the pellets. Improved durability allows further mechanical handling during transport, transfer into storage systems and feeding. Hardness is important to avoid pellet destruction due to pressure when stored in bulk bins. It is not always correlated with durability.

Binding agents are also thought to increase press capacity and pelleting efficiency as some allow more fat and steam to be added to the meal during conditioning. The table below gives common binding agents. (MG)

Binding proteins Proteins that specifically interact with some other molecule (e.g. another protein) or atom (e.g. a mineral). Binding proteins are varied in their function. They can be involved in a variety of physiological functions. Interaction of a binding protein with its ligand can result in a conformational change in the binding protein that alters its function. Enzymes can be considered specific binding proteins for substrates and, when they bind them, cofactors.

Regulation of gene expression (DNA or RNA binding proteins)

Transcription factors can regulate the production of messenger RNA (mRNA) by turning on or off the expression of specific genes. RNA binding proteins can influence the production of mature mRNA by affecting RNA splicing, polyadenylation (addition of multiple adenosine residues to an mRNA precursor) or RNA transport. In addition, RNA binding pro-

Binding agent	E number
Citric acid	E330
Sodium, potassium and calcium stearates	E470
Silicic acid (precipitated and dried)	E551a
Colloidal silica	E551b
Kieselguhr (diatomaceous earth, purified)	E551c
Calcium silicate (synthetic)	E552
Sodium aluminosilicate (synthetic)	
Kaolin and kaolinitic clays (free from asbestos and containing at least 65% complex hydrated aluminium silicates whose main constituent is kaolinite)	E559
Natural mixtures of steatite and chlorite free of asbestos	E560
Vermiculite	
Lignosulphonates	E565

teins are critical in mRNA translation into protein. RNA binding proteins are critical for the function of the ribosome, for putting the proper amino acid on to a specific tRNA (aminoacyl tRNA synthetases) for binding to specific regions of mRNA.

Cell signalling

Protein–protein interactions are critical for transmission and decoding of hormone signals by cells. Examples include binding of hormones to their receptor (insulin binding to the insulin receptor) and for the interaction of the hormone receptors with other proteins that transmit the signal into specific cellular actions.

Transport of compounds

Binding proteins exist for certain vitamins (vitamin D binding protein) or minerals (transferrin) and are important in moving such compounds between organs and cells or, in some cases, within cells.

Cell structure

A variety of filament systems organize the cytoplasm of cells and can alter cell shape. An example is microtubules (MTs) made of the protein tubulin. MTs form hollow fibres that are used to transport proteins to different locations in the cell. MTs are also important in chromosome separation during cell division. A variety of MT binding proteins exist that can alter MT function. (RSE)

Bioavailability That proportion of a dietary nutrient that is absorbed and may then be utilized by an animal for physiological function(s). The method of assessing bioavailability depends on the species and its physiological state. The animals that are of most interest to nutritionists are usually those that are growing or producing (meat, milk, eggs, etc.). Consequently, growth, efficiency of feed utilization, output of milk or eggs or changes in tissue concentration of some nutrient (e.g. calcium in bone) are frequently chosen as parameters of measurement.

In most bioavailability assays the chosen parameter is used to compare a test feedstuff or nutrient to a standard, which is usually the nutrient in its pure and fully available form. The test may use a single measurement (mean ratio method) or a set of several intakes of the standard (slope ratio assay). In the simplest slope ratio assay, a purified or semi-purified standard such as reagent grade compound, crystalline amino acid, etc., is fed in a series of diets to give three or more levels of a nutrient that produce a linear increase in the chosen criterion (e.g. growth) in response to increasing amounts of the nutrient. The test material is also incorporated into one or more diets at levels that would be expected to yield a linear response but are less than the known or estimated optimum dietary level for maximal response. Provided that there is a linear relationship between the nutrient intake (x) and the animal's response (y) with both the test and the standard nutrient sources, the relationships can be expressed as $y_{test} = a_{test}x + b_{test}$ and $y_{std} = a_{std}x + b_{std}$, respectively, where a_{test} is the slope and b_{test} is the intercept of the regression equation with the test source and where a_{std} and b_{std} are the slope and intercept with the standard nutrient source. It is also assumed that the two lines generated by these equations intersect at 0,0. To ensure the validity of the assay, this assumption is tested in the analysis of the results. Therefore the ratio of the slopes, $100\ a_{test}/a_{std}$, is an estimate of the bioavailability of the test nutrient, when the bioavailability of the standard is assumed to be 100% (Littell *et al.*, 1995).

Variations of the slope ratio method include the standard curve and mean ratio assays. In the former case, several data points are generated with the standard nutrient source to obtain a standard linear response. A single level of the test feed is given such that the intake of the nutrient falls within the range of the standard. The response value (y_{test}) is then compared with the value expected from the same amount of pure nutrient, using the regression equation for the standard source. Thus, bioavailability = $100\ y_{test}/(a_{std} \times x_{test})$. In some cases, a direct comparison of a test source of a nutrient is made to a standard source of that nutrient, each having only one data point. In this case, the validity of the assay is heavily dependent on the amount of the nutrient in the test source compared with the standard. If the amount is small, the assay is usually less accurate. It is important to recognize that, in addition to the nutrient of interest, the test feed may contain other constituents that contribute, positively or negatively, to the animal's response. This difficulty can be minimized by arranging that the diets used to establish the standard curve are deficient only in the nutrient being tested and that antinutritional factors in the test feed are inactivated.

Sometimes, the bioavailability of certain nutrients for fish is more easily estimated by conducting controlled digestibility trials. Although this does not technically fulfil the definition of bioavailability it is useful because, for many nutrients, digestibility is the main component of availability.

More accurate estimation of the true digestibility of a given nutrient may be determined by the use of isotopes. The method has been particularly useful in determining true absorption of various essential minerals, especially of trace minerals. Ideally the source of the nutrient in question is one in which the nutrient has been biosynthesized in the presence of either a stable or radioactive isotope and is therefore intrinsically labelled with the nutrient. The concentration of the intrinsic label in both diet and faeces can be used to calculate the true digestibility of the nutrient tested. In the presence of another isotope of the same nutrient that has been previously injected into the bloodstream of the subject animal and allowed to reach equilibrium, one can calculate the endogenous loss of the nutrient via the intestine. (JSJr)

See also: Availability; Nutrient bioavailability

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Biogenic amines Decarboxylation products of amino acids with hormone-like actions. Histamine is formed by decarboxylation of L-histidine. Histamine affects cells by binding to histamine receptors (H_1, H_2 or H_3) found in peripheral tissues and the brain. Tyrosine is converted to L-dopa (dihydroxyphenylalanine), which is decarboxylated to dopamine which, in turn, can be hydroxylated to become norepinephrine. These processes are carried out in catecholamine-secreting neurons and in the adrenal medulla. The products act on α- and β-receptors. Tryptophan is hydroxylated to 5-hydroxytryptophan which is decarboxylated to form serotonin (5-hydroxytryptamine), which is found in the brain and in serotonergic neurons. It has its effect through cellular serotonin receptors. In the pineal gland, serotonin is converted to melatonin. The neurotransmitter γ-aminobutyrate is derived from the decarboxylation of glutamic acid. (NJB)

Biological value (BV) A measure of protein quality. The term has a strict definition, but is also used more loosely as a synonym for protein quality. BV is calculated by measuring the faecal and urinary nitrogen losses of two groups of growing rats: one given a protein-free diet, the other a diet containing the test protein at a concentration of 10%:

$$BV = 100\,(Ni - (Nu - Nu_e) - (Nf - Nf_e))\ /\ (Ni - (Nf - Nf_e))$$

where, for the rats given the test diet, Ni is the nitrogen intake, Nu is urinary nitrogen excretion, Nf is faecal nitrogen excretion; and, for the rats given the protein-free diet, Nu_e is urinary nitrogen excretion (endogenous urinary nitrogen), Nf_e is faecal nitrogen excretion (metabolic faecal nitrogen).

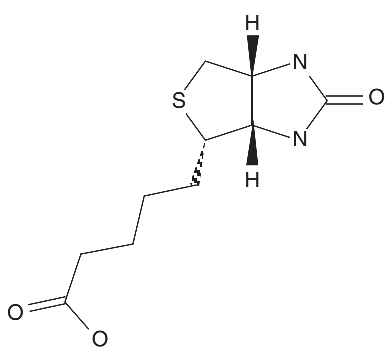
Thus, endogenous urinary nitrogen and metabolic faecal nitrogen are added to the nitrogen retained to give the total amount of nitrogen utilized. This is divided by the nitrogen truly absorbed (i.e. faecal nitrogen is corrected for endogenous loss) to give the biological value, which is therefore independent of digestibility. BV is related to the simpler measure, **net protein utilization** (NPU):

$$BV = NPU \times \text{true digestibility.}$$

Although originally designed and strictly defined as a test with rats, it has also been adapted for use with other animals. (MFF)
See also: Protein quality

Biotechnology A technology that uses biological systems and processes to produce substances of medical, biological, nutritional and other commercial significance. It includes use of cell and tissue culture, cell fusion, molecular biology, and recombinant deoxyribonucleic acid (DNA) technology to generate unique organisms with new traits or organisms that have potential to produce specific products. The most common applications include fermentation to produce antibiotics, brewery products and cheese. Genetic engineering allows the isolation of a desired gene and its insertion into the DNA of another organism which is then grown for the commercial production of insulin, hormones, vaccines etc. The same technology is used to produce microorganisms that degrade hazardous wastes, as well as genetically modified plants and animals. (SPL)

Biotin $C_{10}H_{16}N_2O_3S$, one of the water soluble B-vitamins. It is the vitamin co-factor for pyruvate carboxylase, which forms oxaloacetate, and for acetyl-CoA carboxylase, which is the first step in fatty acid biosynthesis. It is also the co-factor for propionyl-CoA carboxylase which is involved in the conversion of propionate to succinate, which can be a source of glucose carbon. In addition it is a co-factor in the carboxylase step of leucine catabolism. It is normally synthesized in adequate quantities by the intestinal bacteria. It occurs normally in a variety of foods.



(NJB)

Birth weight The weight of an animal at the moment it is born. Within species, this weight will depend on the breed of the animal's parents and the genetic material that it inherits from them. The uterine environment also has a significant effect on birth weight. If an embryo is transferred from one female to a smaller one, the birth weight of the resulting newborn is likely to be lower than if it had been carried to term by its own dam. Manipulation of ova and embryos prior to transplanting has been known to increase birth weights by up to 50%, resulting in severe problems at parturition. Fetal requirements for energy, protein and minerals increase rapidly, especially during the last third of gestation. Because of this, restricting energy intake to the mother can reduce birth weight; while increasing the energy intake of the ewe in the last 6 weeks of pregnancy, for example, can increase the birth weight of lambs. Specific nutritional deficiencies can cause debility, deformation and death of the newborn, rather than reduced birth weight per se. As litter size increases, the birth weight of each individual in the litter tends to decrease. Early parturition results in lower birth weights. Newborn animals of lower than average birth weight are more likely to die. (PJHB)

Biuret Biuret is the common name for imidodicarbonic diamide or carbamylurea, $NH_2{\cdot}CO{\cdot}NH{\cdot}CO{\cdot}NH_2$. It reacts with an aqueous solution of copper sulphate and sodium hydroxide to give a purple-coloured complex. Proteins and some amines react in a similar manner to biuret, thus forming the basis of the colorimetric method for the quantitative determination of proteins. The method is simple, robust and reliable but lacks selectivity since all proteins react in a similar manner. (JEM)

Black gram An annual dicotyledonous plant (*Vigna mungo*), native to central Asia, grown for forage, silage and hay. It is an important feed for livestock in India, with dietary inclusion rates of up to 17% (Saran *et al*., 2000). It is also grown in chicken pastures. Fodder is derived mainly from the stem and leaves but the seeds, pods and pod husks are also used. Black gram is usually fed to cattle as a fodder but it may also be consumed by other species, including chickens. The silage of black gram in the dough stage has a dry matter (DM) content of 273 g kg^{-1}, with crude protein (CP) at 139 and crude fibre (CF) at 191 g kg^{-1} DM. The pods of the black gram plant have much lower levels of CP at 90 and CF at 299 g kg^{-1} DM. Black gram seeds have a CP level of 261–268 and a very low CF level of 53–56 g kg^{-1} DM. The pod husks have a CP level of 166 and CF 246 g kg^{-1} DM. (JKM)

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Blindness Nutritional problems that cause blindness in animals generally do so by interfering with the function of the nervous tissue comprising the visual centre of the cerebral cortex, the optic nerve or the retina. Thiamine deficiency can result from inadequate dietary thiamine in non-ruminants or, in ruminants, from the presence of thiaminases (e.g. from eating high-concentrate diets, bracken fern or raw fish), which destroy thiamine before it can be absorbed. Polioencephalomalacia, or degeneration of the cerebral cortex, ensues, destroying vision. Sulphur toxicity can also induce polioencephalomalacia. Lead poisoning, from ingestion of used crankcase oil and grease or discarded lead batteries, results in loss of visual cortex function. Arsenical compounds, once used as pig growth promoters and to control swine dysentery, can, in large amounts, cause degeneration of the optic nerve. Vitamin A deficiency causes retinal degeneration, leading to night blindness. Eventually the optic nerve may become involved and vision lost completely. Water deprivation followed by rapid replenishment of water (also known as sodium toxicosis) can cause oedema of the brain tissues, blocking vision. In the nervous form of ketosis, blood glucose levels may fall to the point at which the function of the visual cortex is depressed, resulting in partial blindness. (JPG)

See also: Lead; Night blindness; Thiamine

Bloat Bloat is most commonly observed in ruminants, as a disorder of rumen function that causes swelling or tympanites of the rumen. It sometimes occurs in pigs, when the small intestine becomes colonized by gas-producing bacteria. In cattle it can be observed as an acute swelling between the last rib and the hip on the left side. The animals are restless, find lying uncomfortable and may eventually die of heart failure or of suffocation due to inhaling rumen contents.

Bloat in ruminants is caused by consumption of either large quantities of rapidly digested carbohydrate (gassy, feedlot or cereal bloat) or pasture legumes (pasture or frothy bloat), which create a stable foam in the rumen. Gassy bloat is usually due to sudden consumption of cereals, particularly if they have been excessively processed, which accelerates bacterial digestion. This may occur if an animal loses its appetite for a period, and then compensates by overeating. This type of bloat can be treated by releasing the gas with a stomach tube or in an emergency by a rumen trocar and cannula. Sometimes bloat can be caused by an obstruction in the oesophagus, such as a piece of food that is stuck. This can often be removed by passing a stomach tube to release the gas.

Pasture bloat is of more economic importance as it can affect a large group of animals at the same time. Lucerne is the most likely of all legumes to cause bloat, with cows sometimes dying within a few hours of entering a field for grazing, but it can also be caused by young leafy grass that has recently received nitrogen fertilizer. Some legumes contain tannins, which reduce the speed of protein digestion and probably discourage animals from grazing those plants. Tannins are present in sufficient quantities in bird's-foot trefoil to prevent the production of a stable foam, and their content in white clover increases sufficiently at flowering to make it safe to graze. If a mixed grass-and-clover sward has enough clover to cause bloat (probably more than 50% of the herbage by mass), it should not be grazed for long periods but should either be conserved, if there is sufficient mass, or rested for a few weeks until the clover inflorescences appear, after which it can be grazed or conserved.

Cows are most likely to become bloated in the late evening after a day's grazing and also after a wet period when they avidly graze to make up for lost time. Wet grass reduces saliva production, and the saliva contains a mucin that disperses foam in the rumen. Herbage that has been frozen is particularly likely to cause bloat, as the rupture of plant cell walls releases a lot of potassium. Potassium-rich feeds, such as molasses, are notorious for causing bloat, whereas grasses rich in sodium appear to be less likely to cause it. The precise mechanism has not yet been determined but may relate to the stimulation of saliva production by sodium-rich feeds, and the foam-dispersing properties of the salivary mucin.

Forage supplements will usually slow down the rate of digestion and reduce bloat but, if there is adequate herbage, grazing supplements may not be eaten by some cows in sufficient quantities, particularly if they are based on straw or other low quality forages. Mineral oils also help to disperse the foam and can be added to a concentrate feed or sprayed on to the pasture or the cows' flanks, to be licked off as needed. Linseed oil is often used. A proprietary product, poloxalene, also breaks up the foam and can be used as a drench for clinical cases or included in feed blocks as a preventive measure. Often simply walking the cow from the field to the farmstead to receive medication will alleviate the swelling. It is important to keep a bloated cow on her feet if possible, as death can follow soon after recumbency.

There are reported breed differences in the susceptibility of cattle to bloat: Jersey cows are particularly prone to the disorder. Cows can get used to feeds that are liable to make them bloat; this may be by altering their behaviour to spread their meals out more evenly over the day. Lactating cows are particularly susceptible, due to their high intakes. Pasture bloat remains a serious problem in countries like New Zealand, where the cattle rely on pasture with little or no fertilizer applied and a high legume content. (CJCP)

Blood The fluid transport system of the body, circulating within the cardiovascular system. It transports nutrients from the gut, oxygen from lungs, hormones from endocrine glands to body tissues and waste products from the tissues to excretory organs. Blood also aids in the maintenance of pH, fluid and electrolyte balance in the body, aids temperature control and is important in defending the body against pathogens.

Blood can be divided into a cellular component and a fluid component. These can be separated by centrifugation. The cellular component normally makes up 30–55% of blood volume, depending on species. The fluid component, plasma, will coagulate on exposure to air, to form serum and a fibrinogen clot. With platelets (thrombocytes), and by the action of the coagulation cascade, fibrinogen forms a clot when blood vessels are damaged. This can act as a self-defence mechanism to prevent further blood loss.

Cells that are found in the blood fall into three groups: red blood cells (erythrocytes), white blood cells (leukocytes) and platelets (thrombocytes). There are around 500–1000 times as many red blood cells as white. Erythrocytes are biconcave disc-shaped cells making up around 32% of blood volume. Mammalian erythrocytes have no nuclear material but those of birds, fish and reptiles do. They are formed from cells that originate principally in the bone marrow and survive in circulation for 3–4 months. Structurally they are envelopes containing haemoglobin, the iron-containing pigment that colours the blood and absorbs oxygen. Oxygen is transported from oxygen-rich areas, the lungs, to oxygen-deprived areas where O_2 is exchanged for CO_2, which is then returned to the lungs.

Leukocytes, which are larger than erythrocytes, are nucleated and are involved in body defence. They are divided into two major groups: granulocytes, which originate from bone marrow precursors, and lymphocytes, which come from lymphatic tissues around the body.

Granulocytes include neutrophils (polymorphonuclear leukocytes), which are phagocytic cells that are present in circulating blood but also able to migrate from blood vessels into tissues. Classically, numbers rise in response to bacterial infection. Eosinophils, with red-staining granules, are also phagocytes but are associated with parasitic infections and some allergic conditions. Basophils contain histamine that is secreted during allergic reactions. Monocytes are phagocytic and migrate from blood vessels to tissues, where they are called macrophages; they tend to be involved in chronic infections.

Lymphocytes are present in circulating blood but are also found in lymphoid tissues, e.g. Peyers' patches in the intestinal wall, spleen, tonsils and lymph nodes. They are involved in specific immunity, either as B cells in the humeral response, e.g. antibody-secreting cells (plasma cells), or as part of the cell-mediated immune system.

Blood groups are recognized in animals and are used in thoroughbred identification. Blood transfusions can be used, particularly to treat blood loss or shock, but usually only once, due to the formation of antibodies to the 'foreign' blood group.

Some of the measurements made on blood include: (i) haematocrit or packed cell volume (PCV), which measures the proportion of blood that is in cells; (ii) red, white and total (TBC) blood cell counts; (iii) differential white blood cell counts, which determine the different types of white blood cell present and can give an indication of the morphology; (iv) haemoglobin levels – in total for the blood and, in combination with red cell counts, for individual red blood cells (MCH); and (v) blood chemistry, enzyme and hormone levels.

Disorders of the blood include anaemia (lack of red blood cells), leukaemia (a malignant disease of lymphoid tissue that is especially common in the cat, where, unlike in humans, there is rarely an increase in numbers of leukocytes in the blood) and thrombocytopaenia (lack of platelets – causes include poisoning). Haemolytic disease of the newborn can result from an incompatibility between the blood of the sire and dam and is thought to be the cause of some late abortions in cattle. In foals, puppies and piglets, antibodies in colostrum cause haemolysis of red cells; exchange transfusions have been performed to save severely affected foals. Haemophilia is rare, but is seen in dogs and cats. Haemolysis is the destruction of red cells with the release of haemoglobin; some infections and poisons can cause this. Blood circulation can carry pathogens or pathogenic substances round the body, leading to pyaemia, septicaemia, viraemia or toxaemia.

(EM)

See also: Anaemia; Haemoglobin; Immunity

Blood flow The degree to which an organ or tissue, via its network of capillaries, is perfused by blood. Blood flow can be measured by the flow (as ml min^{-1}) in the artery supplying it, or in the vein draining it, using various tracer dilution techniques, or by an ultrasonic or electromagnetic flow probe implanted around the blood vessel. (DS)

Blood meal A deep red/brown granular powder obtained from blood collected at slaughterhouses. It is processed by gentle heating until fully coagulated; the excess water is drained off by pressing and finally the residue is dried and ground. It is occasionally further ground to form a very fine powder known as blood flour, which is more soluble although harder to handle. Blood meal is a good food material that is readily eaten by all animals, although it can be unpalatable at first. Modern drying methods apply heat gently, which allows blood meal to be produced with a minimum of heat damage. The dry matter is almost pure protein, with high concentrations of essential amino acids except isoleucine. Excessive heat substantially reduces its digestibility but mild heat improves its value to ruminants by reducing solubility in the rumen.

Under *The Bovine Spongiform Encephalopathy (No. 2) Order 1996 (SI 1996 No. 31663)* it was still permitted to feed blood meal to both ruminant and non-ruminant animals in the UK and Europe, although this practice was not common. However, following the *Processed Animal Protein Regulations 2001* of 1 August 2001, this practice is no longer permitted in the EU for animals kept, fattened or bred for the production of food.

Typical analysis for blood meal.

Component (units)	Weight
Dry matter (g kg^{-1})	900
Metabolizable energy (MJ kg^{-1} dry matter)	13.2
Crude protein (g kg^{-1} dry matter)	940
Ash (g kg^{-1} dry matter)	10
Oil (ether extract) (g kg^{-1} dry matter)	10

(MG)

Blood plasma The fluid portion of unclotted blood consisting of 93% water and 5–7% protein with electrolytes, nutrients such as glucose, amino acids, lipids and some vitamins, hormones, metabolic waste products and small amounts of gases. Albumin, fibrinogen and globulins are the three major proteins. Globulins (particularly IgG) are produced by the humeral immune system in response to the stimulus of specific antigens and can be a source of passive immunity. (EM)
See also: Immunity

Boar An entire male pig (*see also* **Pigs**). In the growing phase, boars require higher quality diets than castrates or gilts because of their higher protein deposition rate. They also have a lower appetite and thus can usually be fed *ad libitum* to slaughter without incurring carcass grading penalties. Their higher protein:fat ratio in liveweight gain makes them the most efficient type of pig in terms of feed utilization, and the preferred option in countries where age at slaughter is low enough to minimize the risk of boar taint in the meat. When used as breeding animals, their feed requirements will depend on liveweight, housing temperature and mating frequency. Under practical farm conditions, boars are usually fed a restricted amount of 3–4 kg day^{-1} of the same diet as the gestating sows, given in one or two daily meals. Both extreme overfeeding and underfeeding can adversely affect libido, while prolonged underfeeding can also reduce sperm production. Adequate levels of calcium, phosphorus and biotin are essential for soundness of legs. Semen quality can be beneficially affected by dietary supplements of *n*-3 fatty acids and by antioxidants such as vitamin E and selenium. (SAE)

Body composition Body composition can be defined either in chemical or tissue-related terms. In an agricultural context, it is not always easy to define what should be considered as 'the body' because there are a number of major components of liveweight, such as the gastrointestinal tract, that are of little value. The degree to which these are included or excluded in an analysis can cause confusion when different results are compared. For some purposes, the empty body, that is liveweight minus gut contents, is an appropriate base line. After slaughter, the empty body minus the major internal organs may be regarded as the eviscerated body. If the skin and hair are removed and an allowance is made for the evaporative loss of cooling, then a 'carcass weight' is obtained. **Carcass** weights may be reported with the head on or off.

The simplest chemical description of body composition is in terms of proximate analysis – dry matter (or water content), fat (lipid), protein (usually as N × 6.25) and ash. With small species, it is practicable to homogenize the entire body and take aliquots for analysis. More detailed analyses can reveal the status of the reserves of macro- and micronutrients.

Studies of tissue-related composition are often undertaken to give a link between the chemical composition and the economic value of the carcass. The major differences in body composition amongst animals of the same species usually relates to the ratio of fat (lipid) to fat-free (lipid-free) body, or that of 'adipose tissue depots' to 'lean tissues'. Elsley *et al*. (1964) showed a remarkable stability between the ratio of bone to muscle and in the ratios of lean parts of the carcass to one another in sheep and pigs that had been grown on profoundly different nutritional regimes. The composition of the fat-free component of the body appears relatively constant both within and across species. This applies whether the fat is defined as chemically determined fat (lipid) or as dissectible fat. Blaxter (1989) gave percentage values for the concentration of water and protein in the fat-free (lipid-free) body for a number of species. These were, respectively, for hens, 71.9 and 22.1, for rabbits 72.8 and 23.2, for sheep 71.1 and 21.9, for pigs 75.6 and 19.6, for oxen 71.4 and 22.1 and for the horse 73.0 and 20.5. The close similarity suggests a powerful functional relationship across all species.

Factors affecting the proportion of fat in the body

Fatty tissue is late maturing and is characteristically increased in mature animals. Young animals prioritize lean growth and tend to be vulnerable if food becomes scarce, because they have small energy reserves. A feature of early selection for domestic animals was to prize those that had a propensity to fatten easily, because these had a greater survival capability and in adverse times were a ready food source for starving humans. Modern selection techniques have favoured leaner animals to such an extent that some functionality has been lost. For example, in domestic pigs, sows have become so lean that they cannot sustain a normal or extended lactation. Hill sheep too are disadvantaged if they are excessively lean, since they lose some of the insulating value of subcutaneous fat when over-wintering and the ewes have difficulty maintaining body condition if required to suckle in the early spring.

Entire males are usually leaner than females, which in turn are usually leaner than male castrates. The quest for carcass leanness has led to a reversal of castration policy in some countries and male pigs are left entire in several countries. Bulls too are left uncastrated in some production systems for the same reason, though this can bring management difficulties because of their unpredictable aggressiveness.

Nutrition can greatly affect the ratio of fatty tissues to lean body mass. Fat proportions are greatly increased in growing pigs and poultry when the diet is deficient in protein or in critical amino acids. Generous feeding on high-energy diets can have the same effect, whilst restricted feeding usually produces a leaner carcass but slower growth rates.

Although changes in nutrition have little effect on the composition of lean tissues, the fatty acid composition of the adipose tissue of non-ruminant animals can be profoundly altered by the nature of the dietary fats. Diets rich in polyunsaturated fatty acids such as *n*-6 linoleic or linolenic acids can transfer high concentrations of these fatty acids to the depot triglycerides. The very long-chain *n*-3 fatty acids of fish oils (eicosapentaenoic and docosahexaenoic) can also be incorporated in the triglycerides of the adipose depots of pigs and poultry. Some nutritionists believe that this could confer a nutritional advantage to the animal fat as a component of human diets. (VRF)

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Body condition A simple, often largely subjective assessment of the fat and muscle of an animal, to judge its readiness for slaughter or breeding. It may be expressed as a body condition score. (MFF)

Body density: *see* Specific gravity

Body fat A term used to describe both the amount of lipid in the body and the amount of **adipose tissue**, which consists of a matrix of connective tissue, blood vessels and specialized cells (adipocytes) in which lipid is stored, mainly as triglycerides. The adipose tissue is subdivided into the subcutaneous, abdominal, intermuscular and intramuscular depots. Subcutaneous fat is not uniformly distributed and in some species may be concentrated in specialized depots such as the hump or tail. The main abdominal fat stores are the omental and perirenal depots. Fat pads also surround other organs. Inter- and intramuscular fat are important to the cooking and eating qualities of meat. (MFF)

Body fluids A general term embracing both intracellular and extracellular water and including blood, urine, saliva, sweat and other secretions, water in the digesta and water associated with tissues. The term is particularly used with reference to the maintenance of normal hydration and osmotic balance. (KJMcC)

Body temperature: *see* Temperature, body

Body water Body water includes all water contained in the body fluids and body tissues of the animal, though the term is sometimes taken to exclude water in the alimentary tract. Total body water can be estimated in living animals by dilution techniques (usually using labelled water, ^2H_2O or ^3H_2O). Body water content can be measured after slaughter by desiccating samples of the homogenized carcass. The water content of animals varies inversely with their fat content, generally decreasing with age. The water content of the fat-free body is more constant but also decreases somewhat with age.

(MMacL)

Bomb calorimeter An instrument for measuring the heat of combustion (i.e. the gross energy) of a small sample of combustible material (e.g. food, body tissue, faeces). The bomb itself is an airtight stainless steel container inside which the pre-weighed sample (usually compressed into a small pellet) is placed so that it is in contact with a firing device. Oxygen is admitted at high pressure through a valve and the bomb is then placed in the calorimeter vessel, which is a copper can containing water. This entire system is then placed on an insulated stand inside an outer vessel whose walls form a temperature-controlled water jacket. The temperature of the calorimeter and bomb is allowed to equilibrate with that of the water jacket and the bomb is then 'fired' by means of a brief electric pulse. The sample is completely oxidized in its oxygen-rich environment and the heat from its combustion causes a proportional rise in the temperature of the system comprising the bomb, calorimeter vessel and water. An automatic control system is used to cause an equal rise in the temperature of the water jacket, which ensures that there is no heat loss from the calorimeter system; its temperature rise is thus a measure of the heat of combustion of the sample. It is necessary to calibrate the device by means of test firing with samples of a substance of known heat of combustion. The whole procedure takes about 30 min for completion and can yield estimates of heat of combustion accurate to 0.5%. (JAMcL)

Further reading

McLean, J.A. and Tobin, G. (1987) Indirect calorimeters. In: *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, pp. 24–30.

Bone density The amount of mineral per unit of bone volume. The classical method for measurement of bone density is based on Archimedes' principle, requiring weights of the bone in air and in water. Anatomical features of bone such as the medullary cavity, trabecular spaces and the Haversian system create inaccuracies in measurements. Clinical techniques such as dual-energy X-ray absorptiometry (DXA) are used to estimate bone mineral density, but these measurements are based on area (cm^2) not volume (cm^3). Estimates of bone density by DXA are highly correlated with ash density, but bone mineral density estimates are only weakly associated with fracture incidence in humans. (TDC)

Bone diseases Nutritionally related bone diseases fall into one of three categories: those affecting the growth plate; failure to remodel mature bone properly; and diseases characterized by retention of cartilage plugs within bone.

Rickets is the failure to mineralize endochondral cartilage of growth plates; it is usually caused by vitamin D or phosphorus deficiency in young animals. Calcium deficiency may also induce rickets. Manganese and copper deficiency reduce elongation of growth-plate cartilage by reducing proteoglycan and collagen synthesis.

Bone is continuously undergoing resorption and replacement by new bone in a process called remodelling. Osteoporosis, primarily the result of calcium deficiency, occurs when bone is resorbed but is not replaced by new bone. Since bone is a major depot of calcium this serves as a means of maintaining calcium homeostasis. Osteodystrophy and osteomalacia occur when bone is resorbed and is replaced by bone matrix but not by bone mineral and are typically associated with vitamin D or phosphorus deficiency. In osteochondrosis (mammals) and tibial dyschondroplasia (birds), areas of physeal or epiphyseal cartilage fail to mineralize and remain as weak points within the bones. This is associated with diets (and genetics) that encourage very high rates of growth. (JPG)

See also: Rickets

Bone formation Bone formation involves a coordinated series of steps including synthesis, secretion, posttranslational modifications, and repair (maintenance) of a complex extracellular matrix which can become mineralized with hydroxyapatite-like crystals. Preosteoblast cells proliferate and differentiate as they become embedded in an extracellular matrix. The embedded, fully differentiated osteoblasts are called osteocytes. Signals directing the extent and location of new bone formation are mediated by osteoblasts, but formation is coupled with removal of pre-existing calcified hyaline cartilage in growth plates (endochondral ossification), or stimulation of systemic hormones and growth factors that modulate osteoblast proliferation (bone modelling, by endochondral and intramembranous ossification), or removal of existing mineralized bone by osteoclasts (bone remodelling). Additional signals may originate with embedded osteocytes that direct localized responses to mechanical loads or fracture healing responses.

The bone extracellular matrix is composed of 40% collagen (primarily type 1 collagen) and 10–15% non-collagen proteins, which include proteoglycans (85% chondroitin sulphate, 7–12% core protein and 5–7% keratan sulphate), glycosylated proteins and gamma-carboxylated proteins. The helical structure of collagen (*see* **Collagen**) provides tensile strength and, upon mineralization by growth of hydroxyapatite-like crystals within the helix, compressive strength. Proteoglycans (also called ground substance) are complex branched polymers with negatively charged side-chains that maintain the hydration state of the matrix.

Mineralization follows secretion of the extracellular matrix with initiation and growth of hydroxyapatite-like crystals ($3Ca_3(PO_4)_2 \cdot Ca(OH)_2$). The mineralized matrix functions in both structural and storage roles. Deposition and resorption of mineral responds to changes in mechanical loads and to systemic signals involved in calcium and phosphate homeostasis.

Two systemic hormones, parathyroid hormone and 1,25 dihydroxyvitamin D_3, are involved in bone formation through their direct action on osteoblast metabolism. Osteoblasts also mediate systemic signals that are transmitted through local signalling pathways to osteoclasts. For example, agents that increase bone resorption, such as PTH, bind to receptors on osteoblast cells, which release a localized factor to stimulate osteoclastic activity and hence increased bone resorption. These signalling arrangements function to couple bone formation and resorption for modelling and remodelling of bone. (TDC)

Bone meal Bone meal and products made from bone are most commonly used as sources of phosphorus. Phosphates of rock origin (rock phosphate or lime phosphate) may, unless thoroughly treated, contain dangerously high levels of fluorine, whereas those from bone are completely safe. Bone meal for use as a phosphorus supplement is produced by heating, drying and finely grinding fresh, defatted bones from warm-blooded land animals. This extracts most of the protein and fat to leave monohydrogen phosphate ($CaHPO_4 \cdot xH_2O$), also known as monocalcium phosphate. This process is now tightly controlled within the EU under *The Processed Animal Protein Regulations 2001* of 1 August 2001 and now includes treatment with dilute hydrochloric acid (4%) over a period of at least 2 days, after which the resultant liquor is treated with lime to form a precipitate of dicalcium phosphate. Because of these new regulations the most common sources of phosphorus now used in animal feed within the EU are from de-fluorinated natural phosphates and composed of equal parts of monocalcium and dicalcium phosphate ($CaHPO_4$-$Ca(H_2PO_4)_2 \cdot H_2O$). (MG)

Bone resorption: *see* Bone formation

Boron A non-metallic element (B) with an atomic mass of 10.811. It does not occur free in nature but combines readily with oxygen to form boric acid, $B(OH)_3$, and borate salts, $B(OH)_4^-$. Boron also forms esters with oxygen-containing compounds, or will link with four oxygen atoms in adjacent hydroxyl groups to form identifiable biological compounds. Some of these B-containing compounds can be isolated from nature, including boromycin, an antibiotic produced by certain bacteria. Certain plant species have an absolute requirement for B, and recent experimental results suggest that B serves a physiological function in animals as well.

Chicks raised on diets marginally deficient in vitamin D and without B showed more anomalies in bone maturation than chicks fed marginal vitamin D and adequate B (3 mg kg^{-1}). However, B would not substitute wholly for vitamin D. Additional dietary B (5 mg kg^{-1}), compared with no B, enhanced body weight gain in broilers.

Recent studies also have shown that B deprivation is detrimental to normal development of the embryos of the South African clawed frog (*Xenopus laevis*), the zebrafish (*Danio rerio)* and rainbow trout (*Oncorhynchus mykiss*). Dietary requirements for farm animals have not been established.

(PGR)

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Botanical composition Plants are made up of a number of components, of which the most important are meristematic tissue, parenchyma and lignified tissue. The first two are important as food material and are most plentiful in leaves, young stems, storage organs and seeds. Lignified tissue has little or no feeding value.

Plants with upright stems and aerial buds can only be grazed or cut once, whereas those that tiller can usually be defoliated several times during the growing season. Whereas annuals only produce tillers above ground (stolons), perennials can also produce underground tillers, or rhizomes. In temperate climates the growing season lasts as long as ambient temperatures are sufficient to maintain growth. However, first flowering is controlled by a combination of the amount of vegetative growth and increasing day length. The grazing season, as distinct from the growing season, is dependent on rainfall being insufficient to cause damage through treading. In spring, tillers develop rapidly and, if there is no defoliation, this is followed by the growth of tall inflorescence-bearing stems. Vegetative development is arrested at this stage but, if conditions are right, a second flowering occurs in late summer. This is followed by a reduction in tillers during the winter. In the semi-arid tropics lack of grazing material, often caused by drought, is the major limitation to grazing. For herbivores, leaves and young stems are the major source of nutrients, with conservation of forage and supplementary feed gaining in importance as their nutritive value, or availability, falls.

The nutritive value of a grass sward will depend not only on rainfall and fertilizer applications but also on the frequency of defoliation, either by cutting or grazing. The more often defoliation takes place, the greater is the proportion of young leaves and shoots in the aerial part of the plant. Lignification of stems will be minimized. Fewer defoliations, whilst resulting in increased lignification, will lead to an increased yield of dry matter.

Storage organs in food crops are generally modified stems or roots, with non-lignified secondary thickening. They are normally harvested and stored for use in the winter period. For livestock, this group includes such crops as fodder beet and mangels. Modern conservation techniques and a consequent reduction in the use of rotations has reduced the importance of these crops as livestock feed but many are valued as vegetable crops.

Seeds contain only small quantities of cellulose, making them edible by both humans and animals. They usually contain very little water and, if kept dry, they remain dormant, allowing long-term storage. The most important crops in this group are the cereals and oilseeds. Seeds are valuable sources of starch, protein and fats (oils). Many of the crops grown for their seeds for human consumption also contribute valuable by-products for livestock feeding (e.g. oilseed cakes; bran and other miller's offals; straws and stovers).

(TS)

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Hopkins, A. (2000) *Grass: Its Production and Utilization*. Blackwell Science, Oxford.

Botulism Intoxication caused by toxins elaborated by *Clostridium botulinum*, a Gram-positive, spore-forming anaerobic bacterium which inhabits soils, litter, feed and the digestive tract. There are seven types of *C. botulinum*, producing specific toxins: A, B, C, D, E, F and G. Types A, B and E are most important in humans, type C in most animal species and D in cattle. The incidence of botulism is highest in birds. Botulism causes progressive motor paralysis, characterized by progressive weakness and paralysis, and death by respiratory or cardiac paralysis. (PC)

Bovine spongiform encephalopathy (BSE) A fatal degenerative disease of cattle, related to other transmissible spongiform encephalopathies such as ovine scrapie, and Creutzfeldt-Jakob disease of humans. Neurones in the brain are progressively destroyed, leading to apprehension, hypersensitivity, ataxia and coma of affected animals, usually after several years of incubation. BSE can be transmitted to a wide variety of mammals by feeding diseased tissues. As the infective agent is not destroyed by cooking, there is concern to avoid human infection. The disease in cattle reached epidemic proportions in the UK in the early 1990s due to the inclusion in compound feeds of meat and bone meal made from carcass offal that included infected material, and it has occurred sporadically in other countries. It was controlled in the UK by banning the use of meat and bone meal in animal feed. Similar bans on the inclusion of meat products in animal feeds, and regulations excluding older cattle, bovine offals and nervous tissue from the human food chain, are now in force in many countries. Animal feeding practices have had to adjust to the loss of these valuable but potentially dangerous feedstuffs. (RFEA, AJFR)

See also: Blood meal; Bone meal; Meat products

Further reading

Hunter, N. (2000) Transmissible spongiform encephalopathies. In: Axford, R.F.E., Bishop, S.C., Nicholas, F.W. and Owen, J.B. (eds) *Breeding for Disease Resistance in Farm Animals*. CAB International, Wallingford, UK, pp. 325–339.

Bracken fern (*Pteridium aquilinum*) A perennial rhizome-forming herb found in many parts of the world. Its fronds are palatable to livestock but contain several toxins that cause disease syndromes. The toxins include a thiaminase, ptaquiloside, an unidentified bone marrow suppressant, and possibly a cyanogenic glycoside. Ptaquiloside is a carcinogen that causes urinary tract neoplasms in cattle that have grazed bracken for several weeks. This has been called enzootic haematuria, as affected cattle often bleed into the urinary tract. Poisoned animals also develop leucopaenia, thrombocytopaenia and anaemia. Bracken fern poisoning in horses is primarily neurological, probably caused by thiamine deficiency. Sheep are relatively resistant to bracken poisoning but some develop bright blindness due to degeneration of the retinal neuroepithelium. (LFJ)

Brackish water Water that is less salty than sea water (34–35 g l^{-1}). Brackish waters are usually found in those portions of estuaries where fresh and salt water mix. This mixing zone is typically called the middle estuary; it is bracketed by the lower estuary, which is characterized by oceanic influences and is essentially sea water, and the upper estuary, where there is a tidal influence but no intrusion of sea water. (RHP)

Further reading

Fairbridge, R.W. (1980) The estuary: its definition and geodynamic cycle. In: Olausson, E. and Cato, I. (eds) *Chemistry and Biogeochemistry of Estuaries*. Wiley Interscience, New York, pp. 1–35.

Bran The collective name for the layers of tissue (pericarp, testa and aleurone) removed during the processing of cereal grains (e.g. wheat bran during flour processing). An important by-product for animal feeding that is generally low in starch content and energy value. (ED)

See also: Cereals

Branched-chain amino acids The three indispensable amino acids L-leucine $(CH_3)_2{\cdot}CH{\cdot}CH_2{\cdot}CHN^+H_3{\cdot}COO^-$, L-isoleucine $CH_3{\cdot}CH_2{\cdot}CH{\cdot}(CH_3){\cdot}CHN^+H_3{\cdot}COO^-$ and L-valine $(CH_3)_2{\cdot}CH{\cdot}CHN^+H_3{\cdot}COO^-$. They are closely related in structure and metabolism, sharing the same enzyme (the branched-chain keto acid dehydrogenase) in their catabolic pathway. This enzyme complex is found in both the liver and extrahepatic tissues. The three interact in metabolism, such that an excess of leucine alters the utilization of the others: this is called an amino acid antagonism. In cases where only one keto acid of the amino acid is used, it will adequately serve as a source of the amino acid. (NJB)

Branched-chain fatty acids Branched-chain fatty acids are not widely distributed but are found in rumen contents, where they are produced during the catabolism of **branched-chain amino acids** by rumen microorganisms. Isobutyric acid, $(CH_3)_2{\cdot}CH{\cdot}COOH$, is derived from the catabolism of L-valine; and isovaleric acid, $(CH_3)_2{\cdot}CH{\cdot}CH_2{\cdot}COOH$, is derived from the catabolism of L-leucine. (NJB)

Branched-chain keto acids The transamination products of the branched-chain amino acids leucine, isoleucine or valine. The transamination partner may be one of the other branched-chain keto acids or α-ketoglutarate. The transamination product of leucine is α-ketoisocaproate, $(CH_3)_2{\cdot}CH{\cdot}CH_2{\cdot}CO{\cdot}COO^-$; that of isoleucine is α-keto-β-methylvalerate $CH_3{\cdot}CH_2{\cdot}CH{\cdot}(CH_3){\cdot}CO{\cdot}COO^-$; while that of valine is α-ketoisovalerate, $(CH_3)_2{\cdot}CH{\cdot}CO{\cdot}COO^-$. (NJB)

Brassicas The brassica family includes **cabbages**, Brussels sprouts, **cauliflowers**, **kales**, **turnips**, forage **rape**, radishes and **mustard**. Oilseeds include rapeseed, also known as canola (*Brassica napus*, *Brassica campestris*) and **mustard** seed (*Sinapis* spp.). All of the brassica family contain glucosinolates which degrade readily to thiocyanates, isothiocyanates, nitriles and their alkyl, alkenyl and aryl residues. These can cause adverse effects such as goitre in animals and humans. Some of the forage materials, such as kale, also contain *S*-methylcysteine sulphoxide (40–60 g kg^{-1} dry matter) which degrades in the rumen to yield dimethyl sulphoxide and then dimethyldisulphide, which causes haemolytic anaemia. The glucosinolates and their aglycones smell and taste pungent, flavouring the meat, milk and eggs of animals that consume them. The oils of rapeseed and mustard seeds can contain substantial proportions of erucic acid but new cultivars have low concentrations of erucic acid (< 50 g kg^{-1} of the oil) and glucosinolates (< 10 μmol g^{-1} seed). (TA)

Bread: *see* Bakery products

Breadfruit A round green seedless fruit approximately 20 cm in diameter, produced by the breadfruit tree, which grows up to 20 m high and has large tough lobed leaves. The fruit is cooked and used by people in a similar manner to potatoes, and is a staple food in the Pacific islands. It is related to jackfruit (*Atrocarpus integrifolia*). Breadfruit can be fed to all classes of livestock but is often used for pigs. Dried fruit is ground to make meal for storage. The meal has a pleasant odour and is a good source of energy. Breadfruit meal has low protein, fat and fibre contents but is very high in carbohydrates (see table).

Typical composition of breadfruit products (g kg^{-1} dry matter).

	DM(%)	CP	CF	Ash	EE	NFE	Ca	P
Breadfruit, ripe	29.8	5.7	4.9	6.8	1.0	81.6	0.12	0.15
Breadfruit meal	84.9	3.2	5.5	3.1	0.9	87.3	0.08	0.16
Breadnut, fibre and skins	13.4	6.5	18.1	11.2	4.5	59.7		
Breadnut, seeds and shells	31.4	11.1	14.3	4.0	6.0	64.6		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Breadfruit is seedless but another variety, called the breadnut, contains seeds. Fruits of the breadnut have a rough surface covered in conical spines, unlike the smaller bumps on the surface of a breadfruit. Both the seeds and pulp of the breadnut are edible. The breadnut fruit has higher protein, fat and fibre contents than the breadfruit, particularly so in the case of the seeds. (LR)

Reference

Gohl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series, No. 12. FAO, Rome.

Brewery by-products Malt culms and brewers' grains are the main by-products of brewing malted or unmalted cereal grains, particularly barley, and other starch-rich products. Other by-products include spent hops, waste beer and brewers' yeast, the latter usually being incorporated with other by-products such as brewers' grains. The by-products of brewing malted barley are shown in the figure.

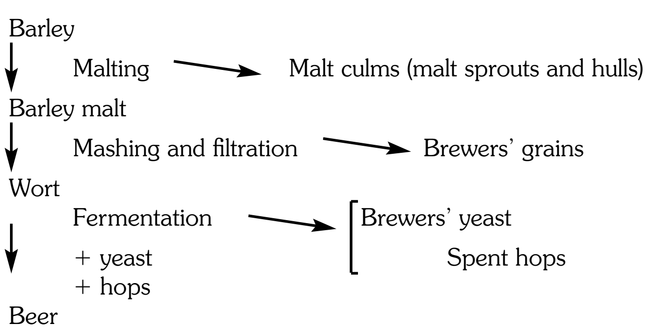
Malt culms, also called malt sprouts, comprise the dried radicle (rootlets) and plumule (sprouts) of the germinated barley grains and generally represent approximately 5% of the weight of malted barley. They are a good source of protein (290 ± 56.9 g kg^{-1} dry matter, DM), with a high fibre (556 ± 50.7 g neutral-detergent fibre kg^{-1} DM) content and an estimated energy (ME) value of 11.1 ± 0.95 MJ kg^{-1} DM. Because of their high fibre content, they are generally fed only to ruminants and then, because of their bitter taste, only at low levels. Wet brewers' grains, also called draff, are the spent grains and the insoluble fraction, including protein, following the removal of the wort, and may also contain residues of maize and rice. Fresh brewers' grains have a low DM content (250 ± 31.3 g kg^{-1} fresh weight) and high protein and fibre contents (218 ± 34.2 and 618 ± 63.9 g kg^{-1} DM, respectively). They are widely used in ruminant feeding as a forage or concentrate feed replacer or for buffer feeding and have an estimated energy (ME) value of 11.5 ± 0.65 MJ kg^{-1} DM. They can be fed in their fresh state or following ensilage or drying. (ED)

Further reading

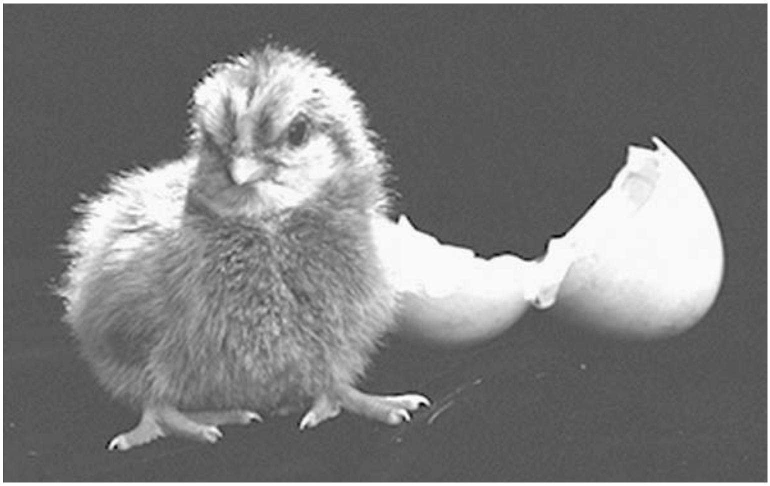
MAFF (1990) *UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs*. Rowett Research Services, Aberdeen, UK, 420 pp.

Moss, A.R. and Givens, D.I. (1994) The chemical composition, digestibility, metabolisable energy content and nitrogen degradability of some protein concentrates. *Animal Feed Science and Technology* 47, 335–351.

Broiler chickens Domestic fowl (*Gallus gallus*) that are produced specifically for meat production. The term 'broiler' originally referred to a size of bird that was suitable for rapid oven cooking (as opposed to roasting and frying) but now refers to all strains and sizes of chicken that are reared only for their meat. Broiler chicken strains were first produced around 1950 by crossing White Cornish (also known as Indian Game) with Plymouth White Rock breeds. However, specialist poultry breeding companies now hold and select their own pedigree lines of birds that are primarily used in their selection programmes to produce commercially available broiler chickens. The efficiency of poultry meat production is improved if the broiler chickens are fast growing and deposit mostly lean tissue, rather



By-products of brewing malted barley.



Day-old chicks require a temperature of 32°C, decreasing to 22°C at 20 days of age.

than fat, in their body growth. Continued selection and development of broiler strains has given birds that grow very fast, compared with other strains and breeds of chicken, and tend to be slaughtered at weights that are less than half of their mature body weight.

Poultry breeding companies produce two lines of birds that provide either the females or the males. The two lines are housed together to produce fertile hatching eggs, which are then transported to machine incubators for a 21-day incubation period. The hatched chicks, each weighing about 45 g, are taken to a rearing farm, where they are grown to their slaughter weight. Slaughter weights can vary from 1 to 3 kg, depending upon market requirements, but most broiler chickens are slaughtered at about 2 kg.

Most broiler production systems use solid floors covered with a thin layer of absorbent litter material, such as wood shavings or straw. Rearing in cages is possible for birds that are to be slaughtered around 1 kg, but not suitable for heavier weights of broilers. Floor-rearing sites may rear large numbers (tens of thousands) of birds in one flock and individual birds are allowed to move around freely within the rearing house. Day-old chicks have only a thin layer of down covering their body and have not enough feather growth to enable them to control their body temperature adequately until they are about 20 days of age. Additional heat needs to be given to the birds during this time: either the whole rearing area is heated to the required temperature or a number of small localized areas of heat are provided, using heaters with a high radiant heat output. Day-old chicks require a temperature of 32°C and this requirement decreases by about 0.5°C per day until they reach 20 days of age. Thereafter the broiler chickens are able to withstand a range of temperatures, although the most efficient conversion of food inputs into bird growth occurs at a house temperature of 18–24°C. For this reason, many broiler chickens are produced in controlled environment houses in which a combination of good insulation, to retain the body heat emitted from the birds, and powered ventilation, to bring in cooler outside air, is used to maintain a desired optimum temperature. Other systems of partial environmental control and outdoor production may also be used but these often incur higher production costs. Controlled environment housing must have precise control of ventilation rates to remove toxic gases (carbon monoxide, ammonia, etc.) and water vapour from the house. This type of building allows for control of light: long day lengths with relatively dim light are frequently used in commercial broiler production systems. Systems of cooling incoming air can also be used in controlled environment houses that are operated in climates with high ambient temperatures.

Broiler chickens are allowed *ad libitum* access to feed and water during their rearing period. Containers need to be distributed frequently and evenly around the flock because many birds are not prepared to walk long distances to the feeders and drinkers. Feed is moved mechanically within the house within pipes that supply and fill small pans or in open tracks that slowly move feed around the house and give feeding access to the birds throughout their length. Pipes are used to convey water to hanging drinkers that allow up to 20 birds to drink at once or to small cup or nipple drinkers designed for single bird use.

Broiler chickens remain in the rearing unit until they reach their slaughter weight. They are then caught and transported to a slaughter and carcass processing facility. One slaughter and processing site may receive birds from many rearing sites. The transport of live chickens is relatively expensive and so the broiler rearing farms are often clustered in fairly close proximity to the slaughterhouse.

Compound feed mills supply a number of the broiler rearing units. A single feed is usually supplied at any one time, though the nutrient composition of the feed is changed as the chickens grow. Broiler feeds are almost invariably based on cereals or other high-starch feeds, but a variety of other feedstuffs may be included to meet the birds' requirements for amino acids, fatty acids, minerals and vitamins. The feeds are mostly pelleted. In general, intakes of pelleted feed are higher than for mash feed and feed efficiency is improved. This also provides an opportunity to heat-treat the feed, thus reducing contamination by potentially harmful bacteria such as *Salmonella*. Typically a broiler chicken starter feed contains around 12.8 MJ metabolizable energy (ME) kg^{-1} and 230 g protein kg^{-1}, whereas a broiler finisher feed contains around 13.2 MJ ME kg^{-1} and 190 g protein kg^{-1}.

Poultry breeding companies are continually improving the growth potential of their commercial broiler stocks, so it is difficult to define the characteristics of broiler growth. Commercial flocks also vary in their growth performance due to a variety of management, health and dietary variables that occur between flocks. However, a male broiler chicken should reach 2 kg in approximately 34 days having eaten 3.1 kg of feed, and a female bird should reach 2 kg in approximately 38 days having eaten 3.4 kg of feed.

(SPR)

See also: Chick; Chicken

Key references

Hunton, P (1990) Industrial breeding and selection. In: Crawford, R.D. (ed.) *Poultry Breeding and Genetics*. Elsevier, Amsterdam.

Sainsbury, D. (1992) *Poultry Health and Management*, 3rd edn. Blackwell Scientific Publications, London.

Brouwer formula A formula for calculating **heat production**, proposed by Professor E. Brouwer, and recommended for general use in 1965 by an international committee of scientists. As first published the equation relates heat production (M, kcal) to oxygen consumption (O_2, litres), carbon dioxide production (CO_2, litres), methane production (CH_4, litres) and urinary nitrogen (N, grams):

$$M = 3.666 \times O_2 + 1.200 \times CO_2 - 0.518 \times CH_4 - 1.431 \times N$$

In SI units the equation is:

$$M\ (kJ) = 16.18 \times O_2 + 5.02 \times CO_2 - 2.17 \times CH_4 - 5.99 \times N$$

The equation has become widely accepted for those farm animals that excrete urinary nitrogen in the form of urea (i.e. most of them). Slight variations on the formula are more appropriate for use with poultry (based on uric acid) and fish (based on ammonia).

(JAMcL)

See also: Indirect calorimetry

Further reading

Brouwer, E. (1965) Report of the Sub-committee on Constants and Factors. In: Blaxter, K.L. (ed.) *Energy Metabolism. Proceedings of the 3rd Symposium.* Academic Press, London, pp. 441–443.

Brown adipose tissue (BAT) A specialized adipose tissue found most prominently in some newborn vertebrates. Brown fat has mitochondria that can become uncoupled so that the protons produced from substrate catabolism, which are normally used for ATP production, are released and the energy that is normally utilized for the conversion of

ADP to ATP is lost as heat. This specialized fat participates in non-shivering **thermogenesis** and because it is highly vascularized the heat produced is distributed to the body via the blood. (NJB)

Browning Browning, known as non-enzymatic browning, carbonyl-amine browning or the Maillard reaction, occurs when a reducing sugar is heated in an aqueous medium with amino acids or proteins. The reaction involves a condensation between the aldehyde group of a reducing sugar and a free amino group of an amino acid. In free amino acids or proteins, the ϵ-amino group of lysine is involved. The result is a decrease in the digestion and absorption of dietary lysine. (NJB)

See also: Maillard reaction

Key reference

Lawrie, R.A. (1970) *Proteins as Human Food*. Butterworths, London.

Browsing Eating of leaves and twigs from trees and bushes. Most livestock species prefer either to browse or to graze, though many (including cattle and goats) are adaptable. In semi-arid rangelands, leaves and fine stems are usually available into the dry season, with the new season growth starting just before the onset of the rains. Browse plants often contain phenolic compounds. (TS)

Brunner's glands Small glands in the **duodenum** that produce an alkaline secretion of sodium bicarbonate ($NaHCO_3$) that enters the duodenum through ducts located between the villi. The secreted bicarbonate, together with that from pancreatic secretions, neutralizes the hydrochloric acid in the digesta that enter the duodenum from the stomach. The glands are lacking in birds. (SB)

Brush border The brush-like surface structure, formed by numerous microvilli, on the membrane of the villi (the finger-like projections of the gut epithelium). The structure of the brush border substantially increases the absorptive surface area of the small intestine. Together with valve-like folds of the intestines, and the finger-like villi, the brush border increases the absorptive surface about 600-fold. A number of specific hydrolytic enzymes, including peptidases (aminopeptidases, dipeptidase and tripeptidase) located in the brush border and carbohydrases (maltase, isomaltase, sucrase, lactase, trehalase) attached to the brush border, complete the degradation of proteins and carbohydrates into amino acids and monosaccharides, respectively. Enterokinase, which initiates the activation of pancreatic enzymes in the duodenum, is also secreted from the brush border. (SB)

Buckwheat Buckwheat (*Fagopyrum esculentum*) is not a cereal but the seeds have similar nutritional characteristics to cereal grains. Buckwheat, also called saracen corn, has triangular seeds with a fibrous hull (~ 20% of seed weight) surrounding a kernel, which is generally used for flour manufacture. By-products of buckwheat include buckwheat hulls and buckwheat middlings but only the latter are generally suitable for feeding. Straw is also produced following seed harvest.

Buckwheat may be grown as a green forage crop. It is high in carbohydrates with, typically, 549 and 129 g starch and crude fibre kg^{-1} dry matter (DM), respectively. The protein content is low (131 g kg^{-1} DM) and both the seed and by-products tend to be deficient in calcium. The grains are used for animal feeding and are processed by grinding before feeding to most classes of livestock except poultry, to which they are fed whole. Their low palatability means they are generally mixed with other cereals before feeding. Buckwheat middlings have a high feed value and are rich in protein (~ 300 g kg^{-1} DM) and are generally used as part of the diet of dairy cows. The hulls are generally used only as fuel, bedding or packaging. (ED)

Further reading

Centraal Veevoederbureau (1991) *Veevoedertabel*. CVB, Runderweg 6, Lelystad, The Netherlands.

Buffalo: *see* Water buffalo

Buffer A molecule that controls pH, modulating the concentration of protons (H^+) in solution by either releasing or taking up protons. Buffers can be inorganic (e.g. carbonic acid, H_2CO_3) or organic (e.g. acetic acid, $CH_3 \cdot COOH$) molecules that participate in acid/base reactions, giving off or taking up protons. Buffers vary in the pH they are able to maintain and their capacity to control pH. To work as a buffer the parent molecule must partially dissociate and come into equilibrium with its components, i.e. $CH_3 \cdot COOH \rightleftharpoons CH_3 \cdot COO^- + H^+$. It is the capacity of acetic acid in solution to dissociate into an acetate anion and a proton that makes it a buffer.

(NJB)

Bulk Approximately 25% of a typical poultry feed consists of components that cannot be digested by chickens. Certain ingredients may be added to increase the indigestible components and increase the bulk density of the feed and these are described as bulking agents or feed diluents. Examples of these materials are sand or clay, ground straw or sawdust, or cereal grain hulls such as wheat or oat bran.

Birds respond to an increase in the bulk density of their diet by increasing their voluntary feed intakes and so there is no change in their nutrient intakes. However, the figure shows that this compensation may not be exact. (SPR)

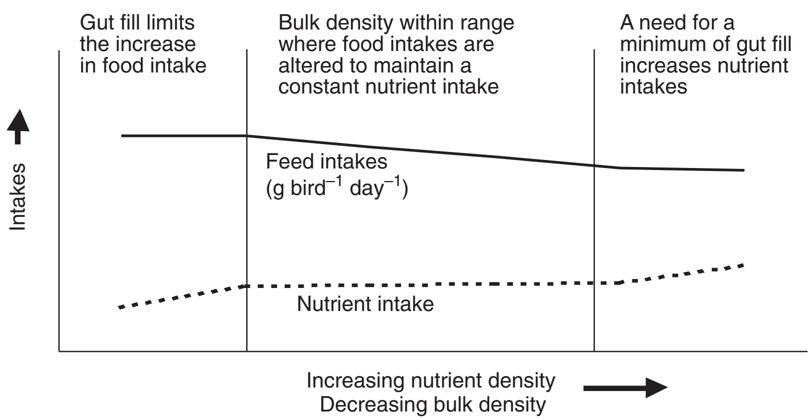
Key reference

Leeson, S. and Summers, J.D. (1997) *Commercial Poultry Nutrition*, 2nd edn. University Books, Guelph, Ontario.

Bulk density The bulk density of an individual sample of a feed such as a cereal is widely used in the feed trade as a measure of its probable metabolizable energy concentration, because the starch-containing endosperm in a grain has a higher density than the fibrous seed hull. However, there are many confounding factors and bulk density seems to be poorly related to energy concentration or nutritive value. Terms used to describe bulk density are bushel weight or specific weight (kg per hectolitre). The latter is used in international trading of cereals. For example, the accepted minimum for feed wheat is 72 kg hl^{-1} and for bread-making wheat is 76 kg hl^{-1}. (SPR)

Bull The mature male of any species of *Bovini* (cattle) and of certain other species. The term is usually applied after the animal has reached sexual maturity. The primary function of the bull is to produce spermatozoa and introduce them into the female reproductive tract at oestrus in order to fertilize any ova (sing. **ovum**, q.v.) that are shed some hours after the end of oestrus. The bull's reproductive tract consists of primary, secondary and accessory sex organs

The primary sex organs consist of a pair of testes, which are suspended in the scrotum between the hindlegs. The testes contain seminiferous tubules, which produce the spermatozoa, and cells that produce testosterone, which gives the bull its libido. The secondary sex organs are made up of the epididymis, where spermatozoa are stored and matured, and the duct system, including the penis, which transport the semen to the cow's vagina at mating. The accessory sex organs



comprise the seminal vesicles, prostate and Cowper's (bulbo-urethral) glands, which add buffers, nutrients, hormones and osmo-regulators to the semen.

After puberty, semen production is essentially a continuous process, although it can be impaired by severe malnutrition, which probably explains why there may be seasonal fluctuations in semen production of bulls living in harsh environments.

The bull's hormonal status means that it grows faster than the cow, reaches a higher mature weight and is more active, leading to higher maintenance requirements. (PJHB)

Key reference

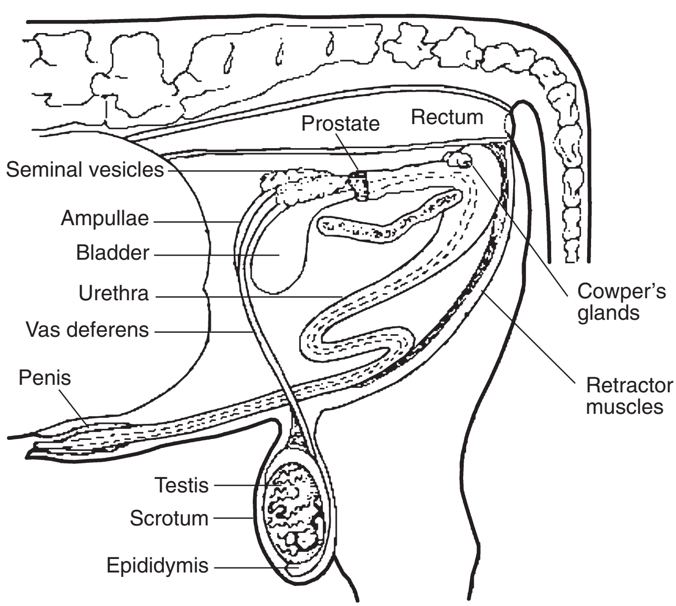
Peters, A.R. and Ball, P.J.H. (1995) *Reproduction in Cattle*, 2nd edn. Blackwell Science, London.

Butterfat The lipid fraction of milk, from which butter is made. Butterfat is secreted in the mammary gland as globules that are lighter than the whey fraction and therefore form a cream layer in whole milk. Butterfat consists of triglycerides that are synthesized in the mammary gland from glycerol and a mixture of fatty acids ranging in chain length from 4 to 22. Shorter-chain fatty acids (up to 16 carbon atoms) are synthesized in the mammary gland from acetic acid and β-hydroxy butyrate; longer-chain fatty acids are absorbed from the bloodstream for direct incorporation into milk triglycerides. The butterfat content of milk varies between species, being typically 3.9% in cows, 4.5% in goats and 7.4% in sheep. Milk from dairy cows is economically most important and butterfat content of milk from these animals is affected by genotype, stage of lactation and nutrition.

Cattle of the Channel Islands breeds produce milk with a higher butterfat content (5%) than the more numerous Holstein or Friesian breeds (3.9%); there is generally an inverse relationship between genetic merit for milk yield and butterfat content of milk.

Immediately after calving, cows produce colostrum, which has a very high fat content (6.7%). The butterfat content of normal milk declines over the first month of lactation and then increases steadily throughout the rest of lactation.

By far the greatest influence on butterfat content of milk comes from nutrition. Since acetic acid and β-hydroxy butyrate are major precursors for *de novo* synthesis of milk fat, dietary factors that influence the production of these acids in the rumen, such as digestible fibre intake, have direct effects on the butterfat content of milk. Intake of long-chain fatty acids is positively related to their content in



The reproductive tract of the bull (lateral view).

milk, but if dietary fat content exceeds 60 g kg^{-1} dry matter (DM), rumen digestion of fibre can be disrupted through the physical and detergent effects of long-chain fatty acids on fibre particles and rumen microorganisms, respectively. This problem can be overcome by feeding the fatty acids in a protected form as calcium salts, as small particles with a high melting point, or encapsulated in formaldehyde-treated casein.

Since the early 1980s, worldwide consumption of butterfat has declined due to the perceived adverse effects of saturated fats on cardiovascular disease; butterfat typically contains 60–70% saturated fatty acids. Increasing the proportion of unsaturated fatty acids in milk is difficult because unsaturated fatty acids are hydrogenated in the rumen, unless they are fed in a protected form.

Studies have shown that conjugated linoleic acid (CLA), found mainly in milk fat and ruminant meat, has powerful anticarcinogenic properties. CLA also reduces the incidence of atherosclerosis and diabetes, and repartitions energy away from body fat towards muscle tissue (Bauman *et al.*, 2001). This fatty acid, therefore, has tremendous potential for improving human health. CLA is produced in the rumen from incomplete biohydrogenation of linoleic acid and in the mammary gland by the action of delta-9 desaturase on vaccenic acid. The main factors that raise the CLA content of milk are grazing fresh pasture and increased intake of linoleic and linolenic acids. (PCG)

Reference

Bauman, D.E., Corl, B.A., Baumgard, L.H. and Griinari, J.M. (2001) Conjugated linoleic acid (CLA) and the dairy cow. In: Garnsworthy, P.C. and Wiseman, J. (eds) *Recent Advances in Animal Nutrition – 2001*. Nottingham University Press, Nottingham, pp. 221–250.

Butyrate A four-carbon saturated fatty acid, $CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$. It is produced in the fermentation of feedstuffs in the rumen and in the lower intestinal tract of both ruminant and non-ruminant animals. Together with the other steam-volatile fatty acids, acetate and propionate, it forms a major part of the energy supply of ruminants. (NJB)

Butyric acid: *see* Butyrate

By-product A product of plant or animal production that is incidental to the main product for which the plant or animal is intended. Plant by-products include those from the milling, brewing and distilling industries. Animal by-products include those from meat, fish, butter and cheese production. Many feeds (e.g. oilseed meals), formerly considered by-products, may be comparable in importance and value to the primary product. (MFF)

See also: Bagasse; Blood meal; Bone meal; Bran; Brewery by-products; Citrus products; Dairy products; Distillers' residues; Dried skim milk; Feather meal; Fish products; Hatchery waste; Meat products; Milling by-products; Poultry offal meal; Whey

C

Cabbage Cabbages (*Brassica* spp.) are members of the brassica family commonly grown for human consumption but also used as fodder for ruminants. The crude protein content of cabbages ranges from about 150 to 250 g kg^{-1} dry matter. The apparent metabolizable energy for ruminants is about 10–11 MJ kg^{-1} but is very low (< 1 MJ kg^{-1}) for pigs. Cabbages contain glucosinolates (about 20–30 μmol g^{-1} dry matter). Sheep fed cabbages perform well but tend to have elevated thyroid weights and increased incidence of Heinz bodies in their blood. (TA)

Cadaverine A bacterial decarboxylation product of L-lysine, $NH_2{\cdot}CH_2{\cdot}(CH_2)_3{\cdot}CH_2{\cdot}NH_2$. It is found in decomposing animal protein. (NJB)

Cadmium A mineral element (Cd) with an atomic mass of 112.411. It is found naturally in small amounts in rocks, soils and sea water. There is no known metabolic function for Cd and it is generally considered toxic. Certain edible plants may accumulate Cd from the soil. Although the amount accumulated may be small, animals or humans that consume the plant material may obtain enough Cd over time to cause kidney damage. Natural antagonists to the intestinal absorption and organ accumulation of Cd are other dietary minerals such as zinc, calcium, iron and copper. (PGR)

Caecectomy Surgical removal of the caecum or, in birds, usually both caeca. Following laparotomy under general anaesthesia, the caecum is ligated at two points no more than 8 mm apart and as close to the ileocaecal–colonic junction as possible. The caecum is then excised between the two ligatures and removed. The procedure is generally performed in birds to eliminate caecal fermentation (bacterial) in experiments involving estimation of digestibility based on measurements of nutrient contents of excreta (faeces + urine). The results of such studies have shown variable changes in digestibility, which is reduced for some nutrients. There is decreased uric acid excretion and improved nitrogen utilization. (MMit)
See also: Caecum; Digestibility

Caecum (or blind gut) A blind sac of the digestive tract located in the pig and ruminants at the ileocaecocolic junction of the small intestine and **colon**. In birds, two caeca are connected at this junction. In the horse the caecum is connected to the small intestine at the ileocaecal junction and is a large comma-shaped structure mainly located on the right side. The relative volume of the caecum varies significantly between species, being much larger in herbivores than in omnivores. Carnivorous animals have a very small caecum or (e.g. mink) none. The size (and capacity) of the caecum in omnivores is influenced by diet. Prolonged feeding of diets rich in fibre significantly increases both the size and volume of the caecum in the pig.

Together with the colon, the caecum acts as a site for the absorption of water and short-chain fatty acids produced in microbial fermentation. In the rabbit, specific pellets are produced in the caecum and recycled to the digestive tract after coprophagy, which allows the utilization of vitamins and amino acids produced by the microflora of the caecum. (SB)

Caeruloplasmin A glycoprotein found in the α_2-globulin fraction of mammalian plasma. It has a molecular mass of 150,000 kDa and a maximum of eight atoms of **copper** per molecule. It is synthesized in the liver and is the major carrier protein for copper in blood, comprising more than 70% of plasma copper. The concentration of caeruloplasmin in plasma varies with the nutritional copper status of an animal or human. It also has ferroxidase activity and is believed to function in iron metabolism by converting Fe^{2+} to Fe^{3+}. (PGR)

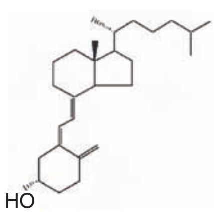
See also: Copper

Caesium A highly alkaline metal (Cs) with an atomic mass of 132.9. It occurs in the earth's crust at about 1 ppm. There is no known metabolic function for caesium. The metal is normally associated with radioactive fallout as ^{137}Cs from nuclear explosions and nuclear powerplant emissions. This radionuclide, which can accumulate in the tissues of plants, animals and humans, has a half-life of more than 30 years. (PGR)

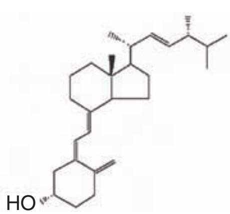
Caffeine 1,3,7-Trimethylxanthine. It is found in tea and coffee and their by-products. Caffeine stimulates lipolysis, which is activated by epinephrine and norepinephrine through adenylate cyclase by production of cAMP from ATP. Increased cAMP activates hormone-sensitive lipase and releases free fatty acids from stored lipids. The inhibition by caffeine of phosphodiesterase, which breaks down cAMP, results in less degradation of cAMP and maintenance of enhanced lipolysis and free fatty acids. (NJB)

Calbindin A protein, belonging to the superfamily of proteins containing a helix–loop–helix, that binds calcium tightly. (HFDeL)

Calciferol A general term signifying a compound possessing the ability to cure or prevent the disease rickets. Most often it refers to either vitamin D_2 or vitamin D_3 (see figure). (HFDeL



Vitamin D_3

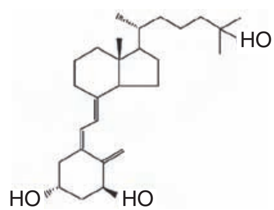


Vitamin D_2

Calcinosis A degenerative condition of a tissue or organ marked by deposition of calcium salts in either an unorganized fashion, or as nodules or plaques, most frequently in areas of tissue necrosis as seen in the degeneration of skeletal or cardiac muscle related to vitamin E or selenium deficiency. (DS)

Calcitonin A 32-amino-acid peptide hormone secreted by the 'c' or parafollicular cells of the thyroid gland in response to high serum calcium concentration. It reduces serum calcium by blocking bone resorption. (HFDeL)

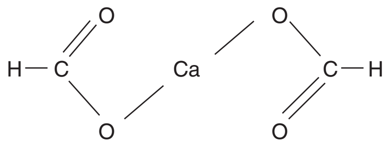
Calcitriol A trivial name for the hormonal form of vitamin D_3, 1α,25-dihydroxy vitamin D_3 (or 1,25-dihydroxy cholecalciferol). It functions in intestine, bone and kidney to elevate serum calcium concentration through a nuclear receptor mechanism.



(HFDeL)

Calcium A divalent metal with atomic mass 40.08. In its ionic form it is required for many functions in the plant and animal world. It is most critically needed for nerve and muscle function, for constructing the skeleton, for cellular integrity and cell-to-cell adhesion, but is required in many other life processes. (HFDeL)

Calcium formate The calcium salt of formic acid is an off-white crystalline powder that is recognized as a preservative in EU legislation. It is listed as 'E238, Calcium formate, $C_2H_2O_4Ca$, suitable for use in all feeding stuffs'. It is a neutral non-toxic substance, relatively safe and pleasant to handle. In the gut it reduces buffering capacity, selectively stimulates beneficial bacteria and improves gut wall health and absorptive efficiency, appearing particularly beneficial to newly weaned piglets. Calcium formate may also be used as an aid to making silage when its selective antimicrobial properties are exploited.



(CRL)

Calcium phosphate Various salts of calcium with phosphorus are used as mineral supplements for farm livestock. The main two are dibasic calcium phosphate, $CaHPO_4$ (usually anhydrous though the dihydrate is also available), and monobasic calcium phosphate monohydrate, $Ca(H_2PO_4)_2.H_2O$. Both the calcium and phosphorus from these compounds are readily available to animals. The choice depends upon the proportions of Ca and P required. Pure anhydrous 'dicalcium phosphate' contains just over 29 g Ca and almost 23 g P 100 g^{-1} but in practice, depending on the source and method of manufacture, the amounts are 25–27 g Ca and 17–20 g P. Actual levels of calcium and phosphorus supplied by 'monocalcium phosphorus' monohydrate are 15–17.5 g Ca 100 g^{-1} and 22–23 g P 100g^{-1}. (CRL)

See also: Dicalcium phosphate

Calf The young of any species of Bovidae (cattle) and of certain other species, such as deer. The term is usually applied from birth until the onset of puberty. This will occur at around 1 year of age, depending on season in some species and on plane of nutrition in all species. Within a few hours of birth, the bovine calf can walk and see and all of the adult organs are present, although the mammary glands of the female and the sexual organs in both sexes are not functional until puberty. In the female, the ovaries are present and contain all the ova that will ever be produced. In the male, the testes will usually have descended into the scrotal sac.

The newborn calf is almost entirely dependent on its mother's milk, not only for nutrition but also for disease immunity, since the bovine placenta does not permit the passage of maternal antibodies into the fetus. The rumen of the newborn calf is not developed and does not contain the microorganisms necessary for its function. A reflex induced by the action of suckling stimulates the oesophageal groove in the rumen to form a tube that delivers milk directly to the abomasum, where rennin causes coagulation as a prelude to digestion. If milk or milk substitute is ingested too fast, which is more likely under artificial rearing conditions, milk can spill from the oesophageal groove into the rumen. In the absence of the rumen microflora of the adult, harmful bacteria can feed on this and cause severe digestive upsets.

The calf would naturally suckle its mother's milk for the first few weeks of life, after which this is gradually replaced with solid food as the rumen develops. Calves in intensive milk pro-

The newborn calf depends on its mother's milk, not only for nutrition, but also for immunity.

duction systems are usually removed from their mothers within the first 2 days after birth and are fed milk or an artificial substitute until they are weaned on to solid food and water alone after 4–8 weeks. It is common for straw, or other roughage feed, to be made available to calves from a very early age in order to help to stimulate rumen development and function, but calves under intensive management would also receive concentrate feed. In the wild, calves may continue to suckle their mothers for many months, whilst gradually increasing their intake of solid food, which consists almost entirely of grazed or browsed material. The microorganisms needed for rumen function are picked up from the environment. The newborn calf is susceptible to cold but has relatively high levels of brown fat, which produces heat for thermoregulation.

(PJHB)

Calorie The heat required to increase the temperature of 1 g of water from 14.5 to 15.5°C. Kilocalorie (kcal) and megacalorie (Mcal) refer to 10^3 and 10^6 calories, respectively. Unfortunately, the use of the terms Calorie (with an initial capital) and CALORIE (both intended to mean kcal), which are to be found in older textbooks, is still widespread, especially in food packaging. This practice is confusing and strongly to be discouraged.

The calorie is not part of the Standard International (SI) system of units. The SI unit of energy is the joule, which is defined as the work done in moving a distance of 1 m against a force of 1 newton (N). The relationship 1 cal = 4.184 J is known as the mechanical equivalent of heat; it emphasizes the fact that heat, like work, is a form of energy. Even though technically out of date, the use of 'cal' and 'kcal' in the agriculture and food industries is still widespread. In this volume energy values are quoted in both joules and calories whenever needed to avoid confusion.

(JAMcL)

See also: Calorific factors; Energy units; Joule

Calorific factors Calorific factors express the energy per unit weight of a substance. It is important to distinguish between two types of calorific factors, namely heats of combustion and food energy values.

The heat of combustion, or gross energy, of a substance is the energy converted into heat when it is completely oxidized (i.e. burned) to carbon dioxide and water. It is a unique property of the substance, which can be measured precisely by use of a laboratory instrument called a **bomb calorimeter**. Although actual heats of combustion (J g^{-1}) vary considerably within each food category (carbohydrate, fat and protein), the heats produced per litre of oxygen consumed and per litre of carbon dioxide produced are remarkably consistent within each of the three. This makes it possible to estimate an animal's rate of metabolic heat production with high precision by measuring the respiratory gaseous exchange of oxygen and carbon dioxide (indirect calorimetry). The table gives heats of combustion (kJ g^{-1}) of some carbohydrates, fats and proteins.

Carbohydrate	
Monosaccharides (e.g. glucose, fructose)	15.6
Disaccharides (e.g. sucrose, lactose)	16.5
Polysaccharides (e.g. starch, cellulose)	17.5
Fats	34–40
Proteins	22–25

The food energy value of a substance is the **metabolizable energy**, or that part of the gross energy which is potentially useful to an animal and not discarded as the energy of waste products (i.e. faeces, urine and combustible gases). Food tables express the metabolizable energy per unit weight of substances. These are not unique properties of the food substance but depend on the digestive processes of the animal. Different food tables are appropriate for carnivores, herbivores and omnivores. Metabolizable energies of different food constituents are generally additive, allowing the overall value of a diet or ration to be assessed. (JAMcL)

Calorimeter: *see* Bomb calorimeter, Calorimetry; Direct calorimetry; Indirect calorimetry

Calorimetry The measurement of heat. A calorimeter is the instrument used for its measurement. The **bomb calorimeter**, a laboratory bench instrument, is used to measure the heats of chemical reactions, espe-

cially the heats of combustion of foods and individual food components. Animal calorimetry is the measurement of the heats produced by and given off from living animals and it has been used with animals ranging in size from mice to horses. Distinction must be made between **direct calorimetry**, which is the physical measurement of heat given off by the animal, and **indirect calorimetry**, in which the measurements are of the chemical quantities involved in metabolism; the heat generated is calculated from the heats of combustion of the end products. Indirect calorimetry thus measures heat production, whereas direct calorimetry measures heat loss by the animal to its environment. In the long term the two must agree, but over short periods there may be an imbalance between heat production and heat loss with a consequent change in body temperature. (JAMcL)
See also: Heat balance

Further reading

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Camelids The Camelidae (camels and llamas) belong to the suborder Tylopoda, closely related to, but distinct from, the Ruminantia. Today there are only six species. The two larger camels, the one-humped dromedary, *Camelus dromedarius,* and the two-humped bactrian camel, *C. bactrianus,* originated in Arabia and Iran–Turkestan, respectively. The four smaller species, the llama, *Lama glama,* the alpaca, *L. pacos,* the guanaco, *L. guanicoe*, and the vicuna, *Vicugna vicugna*, came from South America.

Only the guanaco and vicuna remain wild, although small feral populations of the other species may be found. The llama and alpaca have been domesticated for some 4000 years and the dromedary and bactrian camel for 3000 years (Clutton-Brock, 1981). They have all served as general farm stock and as pack and draught animals in the arid lands to which they are so well adapted. So successful was the dromedary as a pack animal in the desert that wheeled vehicles were seldom seen in North Africa until 200 years ago. They provide excellent meat and their milk resembles cow's milk in composition (see table). The milk is greatly prized by camel herders, who may rely on it for water and nourishment for many days on end. The animals are often shorn for their wool. The alpaca remains the chief provider of wool in Peru while the vicuna has an exceptionally fine and valuable coat. In Arabia the dromedary is bred and trained for racing, showing remarkable endurance, and this calls for special diets (Allen *et al.*, 1992).

Composition of milk of the dromedary compared with the dairy cow (g kg^{-1}) (Narjisse, 1989).

	Protein	Lactose	Fat	Ash	Total solids
Camel	40	42	43	8	134
Cow	38	49	44	7	138

There are some 17 million dromedaries and bactrian camels in the world; India, China and Ethiopia have about 1 million each. They may live for up to 40 years. Puberty is reached at 2–5 years, depending on health and nutrition. The gestation period is from 12 to 13 months and the interbirth interval 2 or 3 years. The shorter-lived South American camelids have an 11-month gestation period. They can interbreed and produce fertile hybrids. Much research has been done on the control and manipulation of reproduction and embryo transfer (Allen *et al.*, 1992).

The dromedary is particularly well adapted to dry savannah and scrubland pastures (Rutagwenda *et al.*, 1990). It takes forage from ground level to 3 m high and eats from a wide variety of plants. Its divided prehensile upper lip allows it to select green shoots from among thorny twigs and it also strips off leaves by pulling twigs through its mouth. Its long legs and ability to travel without water for some days give it a wide grazing radius around a water supply. It has wide footpads, not sharp hoofs, and so can walk easily over soft ground.

The camel's digestive system is functionally very similar to that of true ruminants, although anatomically distinct (Wilson, 1984). In place of the ruminant's upper dental pad, the camel has two incisors and one canine tooth. Rumination and the vigorous secretion of the parotid salivary glands resemble that of the ruminant. The forestomach is divided into three compartments, analogous to the rumen, reticulum and omasum but covered in a mucous non-papillated epithelium. This is followed by an acid-secreting fourth compartment resembling the abomasum. The forestomach shows a strong repetitive contraction at intervals, differing from the minute-by-minute contraction of the reticulorumen. Despite these differences in structure and motility, the camels ferment their food microbially in the forestomach, and produce and absorb volatile fatty acids as a result, in much the same manner as ruminants. Fibrous particles are selectively retained in compartments 1 and 2 for prolonged fermentation. A gutter-shaped structure running from the cardiac orifice of the oesophagus to the entrance to compartment 3, resembling the ruminoreticular groove, allows milk sucked by the calf to bypass the rumen.

The metabolism of water and salt by the dromedary has been thoroughly investigated (see Farid, 1989, for summary). The animal shows many adaptations to hot, dry conditions and tolerates long periods of water deprivation. Concentrated urine (up to 3 osmolar) and dry faeces (up to 60% dry matter) reduce excretion of water; heat storage by diurnal fluctuation of body temperature (37–40°C) reduces the need for evaporative heat loss; a furry coat protects against solar radiation; and appropriate behaviour reduces heat production by day. The camel appears to have a higher requirement for salt than sheep or cattle, 1% NaCl in drinking water being beneficial but 2% has a deleterious effect.

Much has been published on the management, feeding habits, nutrition and diseases of camels in books and in the proceedings of international conferences (see reading list). The nutritional requirements of camels under various conditions (work, lactation, etc.) and the composition of preferred camel browse plants are conveniently summarized by Wilson (1989a). (RNBK)

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Candida *Candida albicans* is a yeast-like fungus that is a normal inhabitant of the nasopharynx, digestive tract and external genitalia. Disruptions of mucosal integrity may result in *Candida* infections, most commonly in birds. Infection of the oral mucosa is called thrush. In poultry, lesions are most common in the crop. Thrush is common after use of therapeutic levels of antibiotics or unsanitary drinking facilities. (PC)

Cannula A tube introduced surgically into a duct or cavity of the body. A narrow cannula is more commonly called a catheter. Cannulation is performed in order to sample repeatedly body fluids such as digesta, blood or secretions or to introduce material into the body.

Cannulas in the digestive tract may be simple, by which only samples of digesta are obtained, or re-entrant, by which the entire flow is collected from the proximal cannula, measured, sampled and returned via the distal cannula. Because a simple T-cannula, although less invasive than a re-entrant cannula, allows only sampling with no estimate of total flow, it requires the inclusion in the diet of an indigestible **marker** which follows the flow of the nutrient. A further problem, common to both types, is that the cannula is relatively small and may give unrepresentative samples, especially with fibre-rich feeds. None the less, cannulation at the terminal ileum is routinely used for determining the ileal digestibility of one or more nutrients, in particular amino acids. A more advanced technique, the post-valvular T-cannula, has a large cannula placed in the caecum opposite the ileocaecal valve. Using a nylon cord it can be steered in such a way that, during a collection, virtually all the digesta passing through the ileocaecal valve is directed into the cannula. Ileal digesta can be collected without cannulation by slaughtering animals and sampling digesta post mortem or by a surgical modification such as ileostomy or ileorectal anastomosis. However, results indicate that the terminal ileum alters in its physiology and microbiology to assume some of the roles of the large intestine.

Cannulas (catheters) can be guided under X-ray into particular blood vessels via superficial veins or arteries. Cannulation of the cardiovascular system may be combined with flow measurement in order to quantify the flow of a component of interest. Cannulation of secretory ducts, e.g. those of the salivary glands, pancreas or gall bladder, may be used to follow changes during development and responses to feeding, diet composition, etc.

Cannulation may influence the composition or flow of the fluid being sampled; thus results need to be evaluated carefully. (SB)

Canola: *see* Rape

Canthaxanthin: *see* Carotenoids

Capric acid Decanoic acid, $CH_3{\cdot}(CH_2)_8{\cdot}COOH$, a saturated medium-chain fatty acid, shorthand designation 10:0. It is found in coconut and palm kernel oils.

(NJB)

Key reference

Babayan, V.K. (1987) Medium chain triglycerides and structured lipids. *Lipids* 22, 417–420.

Caproic acid Hexanoic acid, $CH_3{\cdot}(CH_2)_4{\cdot}COOH$, a saturated medium-chain fatty acid, shorthand designation 6:0. It is found in coconut and palm kernel oils.

(NJB)

Caprylic acid Octanoic acid, $CH_3{\cdot}(CH_2)_6{\cdot}COOH$, a saturated medium-chain fatty acid, shorthand designation 8:0. It is found in coconut and palm kernel oils.

(NJB)

Carbohydrates The most abundant group of organic compounds in the world. There are three classes: monosaccharides, oligosaccharides and polysaccharides. Plants produce carbohydrates by photosynthesis for their own needs, simultaneously providing a stored form of solar energy. Higher animals and microorganisms use carbohydrates as energy sources and as precursors of more complex compounds.

The term carbohydrate was originally coined because these molecules were believed to be hydrates of carbon, having the general formula $C_n(H_2O)_n$. Structural characteristics common to carbohydrates are: (i) the carbon skeleton is unbranched; (ii) all but one carbon bears a hydroxyl group; and (iii) one carbon exists as a carbonyl group which, if on a terminal carbon, gives rise to an aldehyde but if on an internal (centrally placed) carbon, typically carbon 2, it creates a ketone. These compounds are known as aldoses and ketoses, respectively. Sugars of five or more carbons in length have a strong propensity to form a ring structure through the reaction of a hydroxyl group on one carbon with the aldehyde or ketone to produce an internal hemiacetal or hemiketal and thereby a furanose or pyranose ring. In so doing, a new asymmetric or chiral centre is generated. This carbon is known as the anomeric carbon and the hydroxyl group generated may exist in an α or β configuration (Fig. 1).

The smallest molecules generally termed carbohydrates are glyceraldehyde and dihydroxyacetone, also the only possible three carbon sugars, or trioses. The most abundant naturally occurring carbohydrates are the five-carbon (arabinose, xylose and ribose) and six-carbon (glucose, fructose, mannose and galactose) monosaccharides (Fig. 2) and polymers of these. Monosaccharides have the general formula $(CH_2O)_n$.

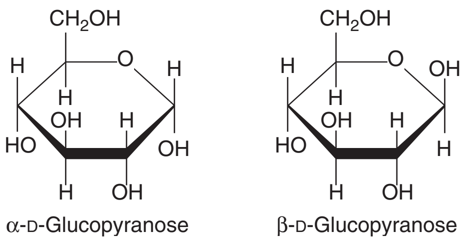


Fig. 1. Alpha and beta-D-glucose are anomers whose sole configurational difference resides in the sterid arrangement about carbon atom 1; this 'carbonyl' carbon is also called the anomeric carbon atom. The plane of the ring projecting from the plane of the paper are the thicken edges. In the alpha configuration, the hydroxyl goup on carbon atom 1 is below the plane of the ring and is so projected on a flat surface. In the beta configuration, the hydroxyl group on carbon atom 1 is above the plane of the ring and is so projected on a flat surface.

Natural sugars are optically active (i.e. rotate the plane of polarized light) because they contain one or more asymmetric carbon atoms, so that the number of stereoisomers can be considerable. Laevorotatory sugars are indicated by a small capital L or a minus (–) sign, and dextrorotatory sugars by a small capital D or plus (+) sign. Since the sign of rotation of plane-polarized light provides no information about the configuration or the centres of asymmetry of the molecule, a convention of nomenclature has been devised to indicate configurational properties. This consists of using D or L to indicate the centre of asymmetry most remote from the aldehydic end of the molecule. Further distinction is required to identify the asymmetry of carbon atom one, which is designated as α or β orientation. The linear and cyclic structures of sugars can be depicted in a variety of ways on a plane surface. The International Union of Pure and Applied Chemistry and the International Union of Biochemistry have recommended carbohydrate nomenclature that indicates structure, configuration and linkages, although many of the more common carbohydrates have deeply entrenched trivial names.

Monosaccharides are commonly joined together through a glycosidic linkage to produce di-, tri-, oligo- and polysaccharides. This is formed between the anomeric carbon atom of one monosaccharide and any hydroxyl group on another monosaccharide through formation of an acetal. A common linkage, which produces a linear chain, is between carbon 1 of one monosaccharide and carbon 3 of the adjacent monosaccharide, denoted as (1→3); a branch on this linear chain may be between carbon 1 of the branching monosaccharide and carbon 6 of the monosaccharide in the chain, indicated as (1→6). Several derived monosaccharides have very important metabolic functions. Reduction of the aldehyde groups of an aldose gives a polyhydric alcohol, or alditol. Sugars are phosphorylated as the first step in animal metabolism. Amino sugars have a hydroxyl group, usually on the carbon 2 atom, replaced by an amino group. Replacing a hydroxyl with a hydrogen, usually on carbon 2 or 6, produces deoxy sugars.

The α(1→4) and (1→6) links between glucoses, such as in starch, are hydrolysed in the small intestinal lumen of mammals by amylases. Disaccharides from the diet, e.g. sucrose, lactose and maltose, as well as maltose and isomaltose produced by the action of amylase on starch, are hydrolysed to constituent monosaccharides by specific disaccharidases in the mucosal brush border of the small intestine. Of the monosaccharide products, glucose is actively absorbed, whereas galactose and fructose are absorbed from the small intestine by facilitated diffusion.

None of the β-linked pentoses or hexoses are susceptible to the digestive enzymes of animals, nor certain α-linked polysaccharides such as fructans, but they can be degraded by microbial enzymes in the gut (*see* **Fermentation**). Fermentation of these carbohydrates, which are collectively known as dietary fibre, is an important source of energy for rumi-

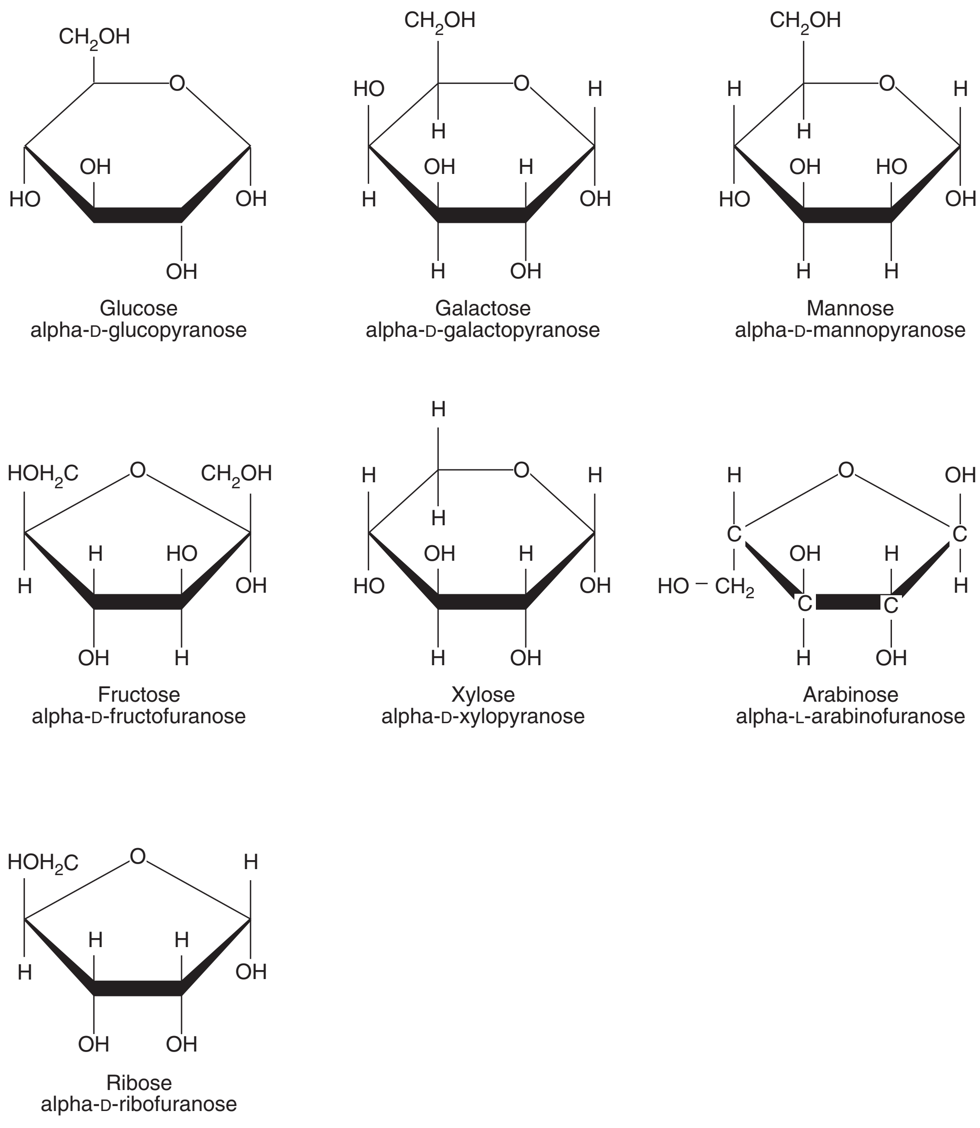


Fig. 2. Most abundant naturally occurring monosaccharides in their most common structural forms.

nants and a minor source for non-ruminant species. (JAM)

See also: Dietary fibre; Monosaccharides; Oligosaccharides; Starch; Storage polysaccharides; Structural polysaccharides

Carbon dioxide A diatomic gas, CO_2, that makes up ~0.033% by volume of air. In photosynthesis, plants use atmospheric CO_2 in the biosynthesis of all the organic components in their cells. In animals, carbon dioxide is an end-product of the catabolism of fatty acids, carbohydrates and amino acids. In solution in the body carbon dioxide becomes carbonic acid: this is rapidly converted enzymatically to bicarbonate which is part of the blood and tissue buffer system.

Metabolism can be likened to a slow burning in which fuel (food) is combined with oxygen to provide the energy for life processes together with the release of carbon dioxide and waste energy in the form of heat. The amount of carbon dioxide produced is similar though slightly less than the amount of oxygen consumed, being approximately 0.35–0.47 l for every kilojoule (kJ) of energy converted into heat. The table gives crude estimates of the carbon dioxide production (l day^{-1}) of growing farm animals at different body weights. For pregnant animals these estimates should be multiplied by approximately 1.5, for laying hens by 1.75 and for lactating animals by 2, or even 3 for a high-yielding cow. For maintenance conditions they should be reduced to about two-thirds.

Body weight	Chickens	Sheep	Pigs	Cattle
50 g	2			
100 g	4			
200 g	7			
500 g	10			
1 kg	16			
2 kg	27	50		
5 kg		70	60	
10 kg		100	120	
20 kg		180	220	200
50 kg		300	400	400
100 kg			600	650
200 kg			800	1000
500 kg				1600

(NJB, JAMcL)

Carbon–nitrogen balance Apart from fat, which can represent 5–40% of the total body mass of farmed animals, the remainder or 'fat-free body' consists of 20–23% protein, 70–75% water and small amounts of minerals and carbohydrate. Carbon and nitrogen balance is a technique for measuring energy retained in the body (as growth, milk, eggs etc.) by assuming that all retained energy is in the form of protein and fat. Energy retained as protein and as fat is the product of their masses retained and their heats of combustion. Since protein is 52% carbon and 16% nitrogen, whilst fat has 77% carbon and no nitrogen, the quantities of retained protein and fat can be calculated from the retained carbon and nitrogen. These in turn may be measured as the differences between the quantities of the two elements in the food consumed and in the faeces and urine excreted with allowance for the carbon lost in carbon dioxide and methane during respiration. The necessary calculations are encapsulated in the equation for retained energy (RE):

$$\text{RE (kJ)} = 51.83\%\ \text{C} + 19.4\%\ \text{N}$$

where C and N (g) are retained masses of the elements. To use the technique it is necessary to collect, weigh, sample and analyse all food, faeces and urine over at least one 24 h period, as well as measuring the quantities of carbon dioxide and methane expired.

(JAMcL)

See also: Indirect calorimetry; Respiration chamber

Carboxylases A group of enzymes involved in incorporation of carbon dioxide into metabolic intermediates involved specifically in **gluconeogenesis** (e.g. pyruvate carboxylase) and **lipogenesis** (e.g. acetyl-CoA carboxylase) and in the catabolism of leucine. In all these examples the vitamin biotin is involved as the enzyme co-factor. (NJB)

Carboxypeptidase An **exopeptidase**, hydrolysing peptide bonds from the C-terminus of proteins. Carboxypeptidase A (carboxypolypeptidase; peptidyl-L-amino acid hydrolase; EC 3.4.17.1) and carboxypeptidase B (protaminase; peptidyl-L-lysine [L-arginine] hydrolase; EC 3.4.17.2) are secreted as inactive procarboxypeptidases from the pancreas and activated in the duodenum by trypsin. The liberated products are free amino acids or di- or tripeptides. Carboxypeptidase A hydrolyses all linkages except those in which the terminal amino acid is arginine or lysine, whereas carboxypeptidase B only hydrolyses bonds with terminal arginine or lysine residues. (SB)

See also: Protein digestion

Carcass (or carcase) Although the term may be used to describe a dead animal, particularly in the wild, in animal production systems it normally refers to animals that have been prepared for human consumption. This usually implies the removal of the digestive tract and contents and sometimes other internal organs. However, the extent of preparation varies between animal species and is also affected by religious and cultural restrictions. Poultry, for example, may be sold intact, with feathers removed, eviscerated with head on, or (in most modern processing situations) plucked and eviscerated with head and legs removed; however, parts such as heart, liver, gizzard and neck may be returned to the eviscerated carcass (often in a separate plastic bag). Pigs are normally eviscerated and shaved; the head may be removed or left attached. Cattle and sheep are normally skinned and have the head and lower parts of the legs removed. Depending on consumer demand a variable amount of subcutaneous and visceral fat may be removed. In Europe, as a result of bovine spongiform encephalopathy, it is now necessary to remove all spinal cord material to minimize the risk of contamination.

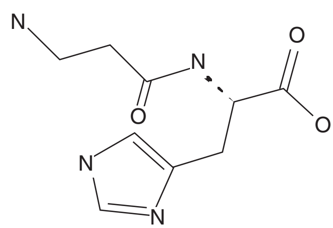
As a consequence of these different practices, the proportion of 'carcass weight' to pre-slaughter weight varies. This ratio, described as 'kill-out proportion', is also affected by the breed and stage of maturity of the animal and by pre-slaughter feeding or fasting. There is also a difference between 'hot carcass weight', i.e. weight at time of evisceration, and 'cold carcass weight', which is the weight after a period of hanging in a refrigerated room. Typical kill-out proportions are: broilers, 0.7–0.75; turkeys, 0.8–0.85; cattle, 0.5–0.6; pigs, 0.75–0.8; sheep, 0.5. (KJMcC)

See also: Meat production; Meat yield

Carcinogens Substances that cause cancer. Most carcinogens in feeds are secondary carcinogens, requiring metabolic activation by hepatic cytochrome P450 enzymes. Examples of carcinogens in feed include aflatoxin, fumonisins, pyrrolizidine alkaloids in *Senecio* spp. and ptaquilosides in bracken fern (*Pteridium aquilinum*). The commonest dietary cause of cancer in livestock is bracken fern, causing urinary tract cancer (enzootic haematuria) in cattle. This is a significant problem in parts of Western Europe (especially Britain), Asia, New Zealand and Central and South America. Bracken-induced tumours may also occur in the nasopharynx, oesophagus and forestomach of cattle. Infection with bovine papilloma virus type 4 is a predisposing factor. Rainbow trout are especially sensitive to aflatoxin-induced liver cancer, caused by dietary levels of as low as 1 ppb aflatoxin. (PC)

Carnitine Carnitine, $(CH_3)_3 \cdot N^+ \cdot CH_2 \cdot CH(OH) \cdot CH_2 \cdot COO^-$, is essential for the transport of long-chain fatty acids across the impermeable inner mitochondrial membrane.The role of carnitine palmitoyltransferase is to control the rate of mitochondrial fatty acid catabolism but medium-chain fatty acids (up to C-8) are thought not to require carnitine for entry to the mitochondrion and thus their rate of catabolism is not dependent on carnitine. The precursor of carnitine biosynthesis is trimethyllysine, produced by methylation of protein-bound lysine by *S*-adenosylmethionine. (NJB)

Carnosine A dipeptide, $C_9H_{14}N_4O_3$, of β-alanine and L-histidine (β-alanylhistidine). It is found in both brain and skeletal muscle. The enzyme carnosine synthetase is widely distributed in tissues. Tissue carnosine can be depleted in dietary histidine deficiency and this complicates studies on histidine requirements.

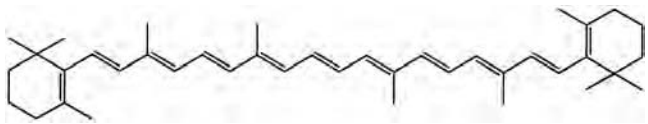


(NJB)

Carob Carob seeds are a product of the leguminous Mediterranean tree *Ceratonia siliqua*. The pods and seeds are sweet and palatable. The fat content is ~ 5 g kg^{-1} and the protein content 50–100 g kg^{-1}. The apparent metabolizable energy for poultry is 5–6 MJ kg^{-1} and 10–12 MJ kg^{-1} for ruminants. Although palatable due to the relatively high sugar content (about 200–300 g kg^{-1}), the meal tends to contain tannic acid which reduces nutrient digestibility and probably apparent metabolizable energy. Recommended concentrations in poultry diets are less than about 50 g kg^{-1} while adult ruminants may accept levels as high as 100 g kg^{-1}. (TA)

Carotenes: *see* Carotenoids

Carotenoids A group of plant pigments of which a small percentage give rise to vitamin A activity and thus are called provita-



Structure of all-*trans* β-carotene.

min A carotenoids. β-Carotene (see figure) is the most active provitamin A carotenoid. Provitamin A carotenoids such as α, β and γ carotenes are found in pasture grass, silage and hay as well as in lucerne and green and yellow vegetables such as carrot and sweet potato. Cryptoxanthin and β-zeacarotene, which contribute provitamin A activity, are also found in yellow maize. The common potato and white maize and other grains are virtually devoid of provitamin A activity. Although a number of carotenoids can serve as vitamin A precursors, they are not all bioequivalent. For example, β-cryptoxanthin and β-zeacarotene are reported to be 50–60% and 20–40% as biopotent as is β-carotene, respectively. In addition, not all carotenoid-like structures have provitamin A activity. For example, xanthophylls found in green leaves and lycopene found in tomatoes do not have provitamin A activity. The biopotency of provitamin A substances is also affected by a number of additional factors. The physical matrix in which the carotenoids exist within food plays a role in limiting their availability. Heating of plant foods prior to ingestion improves their bioavailability but may also lead to isomerization of the naturally occurring all-*trans* configuration to *cis* configurations, which can reduce their biological value. Appreciable amounts of carotene (and vitamin A) may be degraded in the reticulum and rumen of grazing ruminants. In addition, carotenoids are unstable to oxygen and light exposure. Loss in green forages may occur during field curing (up to 80%), and hay stored for 2 years is estimated to contain less than 10% of the original carotenoid content.

The digestion of fat substances (including carotenoids) in non-ruminant animals takes place largely in the small intestine. Once released from foods, carotenoids in bulk lipid droplets in the intestine are acted on by bile salts and pancreatic lipase, forming mixed lipid micelles. The capacity of micelles to incorporate carotenoids may be one factor that limits carotenoid absorption at higher intakes. Without micelle formation, carotenoids are poorly absorbed. Carotenoids are thought to be absorbed by intestinal mucosal cells by a mechanism involving passive diffusion. Once inside the intestinal enterocyte, the carotenoid may be converted to vitamin A or absorbed as such. There is variability in the ability of animals to absorb carotenoid unchanged into the body. For example, birds convert carotenes into vitamin A with only trace amounts of carotenoid passing unchanged into the tissues. Most species do not absorb carotenoids intact. Sheep, goats, pigs and rabbits contain virtually colourless body fat. In contrast, β-carotene can be found in the body fat of the cow, horse and human.

More is known about the metabolism of all-*trans* β-carotene than of any other carotenoid. Much of the conversion of β-carotene is presumed to occur in the enterocyte of the small intestine through the action of a dioxygenase which can cleave between the 15 and 15′ carbons yielding retinaldehyde as the primary product in a 1:2 ratio, respectively. Evidence has also been provided for the eccentric or non-central cleavage of β-carotene yielding β-apo-carotenals which are then oxidized to β-apo-carotenoic acids and retinoic acid. The extent of conversion of β-carotene to vitamin A is highly species dependent. The vitamin A activity (1 IU = 0.3 μg all-*trans* retinol) available from carotene is estimated at 1667 IU mg^{-1} in the chicken and at 400 IU mg^{-1} in horses and cattle. Swine may be even less efficient. High intakes of retinyl ester have been shown to reduce intestinal β-carotene cleavage activity, though the manner in which the conversion of β-carotene to vitamin A is regulated is unclear. Retinaldehyde resulting from β-carotene cleavage is reduced to retinol followed by esterification with long-chain fatty acids in the intestinal enterocyte. Retinyl esters are the major lymphatic product of β-carotene metabolism. Carotenoids (in a few species) and retinyl esters are transported by chylomicrons from the intestinal mucosa to the bloodstream via the lymphatics. Lipoprotein lipase acts on the chylomicron to release free fatty acids that are taken up by the liver and ultimately other tissues. (MC-D)

See also: Vitamin A; Retinyl palmitate

Carp: *see* Common carp; Grass carp

Carrageenan (Irish moss) A polysaccharide extracted from red algae in seaweed (*Rhodophyceae*) used as a thickener and vegetable gum. It is composed mainly of potassium, sodium, magnesium, calcium, sulphate esters and 3,6-anhydro-galactose copolymers. Commercial carrageenan is frequently standardized by dilution with sugars and mixed with salt to obtain food-grade gelling or thickening agents. (JKM)

Carrot Carrots (*Daucus carota*) are widely distributed throughout the north temperate zones. They are annual or biennial herbs of which the larger-rooted late varieties are used for stock feed. Surplus supply and reject carrots from the food industry are used to provide energy for livestock. Carrots contain β-carotene, vitamin A and phytochemicals. Their high vitamin A content makes carrots a particularly valuable supplement for hay and straw. Carrots can be fed to cattle, sheep and horses. They are low in protein but enhance forage intake levels. Prolonged use of carrots at high levels can produce a yellow colour in the milk fat of dairy cattle or carcass fat of beef cattle. Typical inclusion rates are 10–15 kg day^{-1} for cows, 5 kg 100 kg^{-1} body weight for beef cattle and up to 5% of the diet in ewes. Carrots are usually fed in their fresh state but may be dried and ground into a meal for inclusion in compound supplements. The dry matter (DM) content of carrots is 110–130 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is crude protein 92–95, crude fibre 110, ether extract 15–17, ash 70–75 and neutral detergent fibre 200–210, with ME 11.9–12.8 MJ kg^{-1} DM. (JKM)

Cartilage A type of non-vascular supporting connective tissue composed of chondrocytes and collagen fibres embedded in a firm chondrin matrix. Cartilage is elastic, translucent, bluish white and gelatinous in nature. Temporary cartilage present in the fetal skeleton is later replaced by bone but permanent cartilage remains unossified. (MMax)

Casein A group of proteins found in milk, which precipitate under acid conditions (pH < 4.6) to form a clot or curd. Casein constitutes about 80% of the total proteins in cows' milk and is the main ingredient of cheese. Casein is also precipitated by the action of rennin on milk, either in the animal's stomach or added during cheese manufacture; this curd is softer than that precipitated by acids.

The five major classes of casein found in milk are α_{s1}-, α_{s2}-, β, κ and γ, comprising 43, 10, 31, 11 and 5% of total casein on average. Most casein is aggregated with calcium phosphate in large micelles ranging in diameter from 30 to 300 nm; more than 90% of the calcium in milk is associated with casein micelles. Spray-dried milk powder can be reconstituted with water because the casein–calcium micelles retain their structure and redisperse. (PCG)

Cashmere goats Cashmere is one of the finest and most luxurious animal fibres and is the undercoat of a number of breeds of goats selected over many years for the production of this highly valued fibre. The name derives from Kashmir where, in former times, the fibre was traded. Like all domesticated goats (*Capra hircus*), cashmere goats are thought to be descended from the bezoar or Persian wild goat (*Capra aegagrus*). All are double-coated, carrying their fine cashmere undercoat, produced by the secondary hair follicles, beneath an outer coat of coarse guard hair that grows from the primary follicles. Both fibre types are found all over the body, except on the face and legs; the term 'undercoat' is frequently misinterpreted as meaning that the cashmere fibres are found only on the undersurface or belly of the goat. The main populations of cashmere goats are found in China and Mongolia and through the southern parts of Russia to Afghanistan and Iran. In recent decades small populations of cashmere goats have been established in the USA, Australasia and in Europe, the last being based on a new synthetic breed, the Scottish cashmere goat.

Cashmere goats are generally small: adult females (does) weigh some 40–50 kg and the males (bucks) about 60–70 kg. The fibre characteristics of the many breeds of cashmere goat have been reviewed by Millar (1986). Cashmere mean fibre diameters are in the range 13–18.5 microns (μm). Coarser mean diameters are not regarded by the textile industry as conforming to the generally accepted definition of cashmere. Within a fleece having a mean fibre diameter of, say, 15 μm, individual fibres may range in diameter from less than 8 to about 28 μm. The best quality cashmere has a mean fibre diameter of 14–15 μm; it is dull, with no lustre, and is highly crimped, i.e. the fibres have a tight spiral form. Cashmere is generally white, but grey, brown and fawn cashmere is also produced. In coloured goats the cashmere fibres are lighter in colour than the guard hair. The weight of cashmere produced per goat varies widely from about 150 g or less in animals producing the finest cashmere, to around 400 g or more in those with coarser fibre. Cashmere fibres are the goat's protection against cold winters and they grow seasonally. It is generally believed that growth is initiated by the shortening day length following the summer solstice and that it ceases at the winter solstice. There is evidence, however, that in some breeds the period of cashmere growth is longer than 6 months. The cashmere fibres are shed or moulted in the spring, at which time the cashmere is generally harvested by combing the goats.

Cashmere goats are seasonally polyoestrus. Does come into heat at 21-day intervals during the breeding season which, in the northern hemisphere, extends from about August to February. Gestation length averages about 150 days. (AJFR)

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Cassava (*Manihot esculenta* Crantz)

Also known as manioc, tapioca, Brazilian arrowroot and yuca, cassava is a herbaceous shrub up to 4 m high with fingerlike leaves. It can develop into a small tree. It is widely grown in the tropics and subtropics for its tuberous starch-filled roots. The mature cassava plant (12 months old) contains 6% leaves, 44% stem and 50% tubers. By-products of root processing are 8% peel and 17% pomace. The tubers contain a glycoside, linamarin, concentrated in the skin which is hydrolysed by linamarinase, an enzyme also present in the plant, to release hydrocyanic acid (HCN). Bruising the roots activates the enzyme. The HCN can be removed by heating, soaking or prolonged sun drying. Bitter varieties contain more than 0.02% HCN and require thorough processing before feeding. Most commercial varieties are sweet, with < 0.01% HCN, and can be used raw. Slicing, soaking and drying removes much of the HCN, as does cooking. Mortalities have been reported in animals drinking water used for soaking cassava.

Both fresh and dried cassava roots are fed to ruminants. Dried cassava roots can be used as a replacement for grain as an energy source in the rations of dairy cattle, fattening beef animals and lambs. Although an excellent source of energy, cassava is deficient in protein, fat, trace elements and vitamins. Cassava protein is particularly low in the sulphur-containing amino acids (lysine, methionine and cysteine). The inclusion of supplementary sulphur in the ration, along with a source of degradable protein or non-protein nitrogen, allows rumen microbes to manufacture the necessary balance of amino acids. This also assists in the detoxification of HCN in the rumen and liver. Replacement of maize, oats or barley by cassava in dairy rations has no effect on milk yield and can reduce production costs.

Grain in poultry rations can be partly replaced by cassava chips or root meal, with supplementary methionine (0.2–0.3%) for layers. Up to 20% inclusion in poultry rations allows satisfactory production levels. Cassava tubers, with a digestible dry matter (DDM) of 92%, can replace up to 75% of cereal in pig rations, provided that the final ration contains no more than 100 ppm HCN, producing leaner carcasses than grain-based diets. As with poultry rations, attention must be paid to balancing the energy:protein ratio in the ration.

Cassava leaves can also be used as feed, especially to provide undegradable protein (UDP) to ruminants. Unlike the roots, the leaves are a good source of protein, contain-

Table 1. Typical composition of cassava products (g kg^{-1} dry matter).

	DM(%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh leaves, 4 weeks	15.3	24.8	18.3	8.5	5.2	43.2	0.98	0.52
Fresh leaves, 8 weeks	16.1	24.1	26.0	8.0	5.0	39.9	0.99	0.56
Stem		10.9	22.6	8.9	9.7	47.9	0.31	0.34
Fresh roots	32.1	3.9	4.9	4.8	1.0	85.4	0.09	0.12
Fresh peel	27.9	5.3	21.0	5.9	1.2	66.6	0.31	0.13
Pomace	83.5	2.2	26.9	3.4	0.6	66.9	0.68	0.05

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Digestibility (%) and ME content of cassava.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminants					
Leaves	57.0	39.0	54.0	71.0	9.18
Tubers	–	53.0	51.0	90.0	12.23
Poultry					
Leaf meal	63.0				7.80
Pigs					
Leaf meal					9.70
Tubers	91.6				14.57

ing 25% crude protein (CP) and producing up to 6 t CP ha^{-1}. The CP content, and hence feeding value, decreases as the leaves become older (see Tables 1 and 2). Leaf protein has a high lysine content but is low in sulphur-containing amino acids. In labour-intensive production systems, leaf stripping can be practised to provide supplementary fodder for ruminants. However, removal of leaves can reduce root yields, and the use of leaves from bitter varieties can result in HCN toxicity. Sun drying of leaves may reduce the HCN content. Cassava foliage is usually used as a supplement to grass fodder to increase dietary protein levels. The use of 0.5% leaf in layer rations will provide carotene for enhanced yolk colour. Inclusion rates of up to 150 g kg^{-1}, and 300 g kg^{-1} for growing pigs, can be used with the addition of methionine and an energy source. Dried leaf meal is bulky, and pelleting is recommended for chick feed.

Silage can be made from the whole cassava plant. Cassava peel, a by-product from the processing of roots for human use, can also be used for animal feed. Peel is rarely fed fresh, because of high levels of cyanogenic glycosides, which are reduced by sun drying, ensiling and fermentation. Rumen DM degradability of dried or ensiled cassava peel is > 70% after 24 h. In rations, peel is offered primarily as an energy source with a protein supplement. Optimum value is obtained with a rapidly degradable protein to synchronize energy and nitrogen release.

Cassava pomace, the residue after extraction of starch from cassava roots, has a crude fibre (CF) content similar to leaves but is low in protein, fat and minerals. Although it can be used as a ruminant feed, it is more commonly fed to non-ruminants. (LR, JKM)

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Castor bean (*Ricinus communis* L.)

A variable species, appearing as an annual herb in temperate climates and, in tropical areas, as a perennial tree with leaves deeply divided into six fingers. Each spiny outer shell contains three seeds (beans) which can be removed after drying. The bean is the source of castor oil, with a mechanical extraction rate of around 66%. Approximately 60,000 t of castor bean meal are produced annually in India. Castor bean meal contains 0.22% ricin, a toxin, which can be deactivated by steam treatment (5 kg cm^{-2} for 15–30 min). Alternatively the meal can be boiled for 10 min in three times its own volume of water, the water discarded and the process repeated. The wet meal can be air dried at 70–80°C. Detoxified meal is a good source of protein and energy for ruminants, and can be included in concentrate mixtures for sheep at a level of 10%. Poultry appear to be less affected by ricin than mammals, and up to 40% of detoxified meal can be included in their rations. (LR)

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Castration Removal of the testes of a male animal by surgery or by chronic interruption of the vascular and nerve supply to the testes and scrotum. Rendering the testes dysfunctional by surgical or chemical means. (MMit)

See also: Sex differences

Catabolism Catabolism (sometimes katabolism) refers to cellular metabolic processes leading to the systematic enzymatic breakdown of molecules. These processes differ from the extracellular breakdown of molecules called digestion, which occurs in the intestinal tract. For example, the catabolism of amino acids in the liver leads to the recovery of amino acid nitrogen in urea, while the digestion of protein in the intestinal tract leads to free amino acids. (NJB)

Cataract A common degenerative condition of the ocular lens in which the crystalline lens becomes opaque to varying degrees. It commonly arises during diabetes or some forms of poisoning. Cataracts are defined relative to the portion of the lens that is opaque, aetiology, degree of change over time, degree of opacity and relationship to other intraocular pathological changes such as adhesions between the lens capsule and iris. Cataracts result from degeneration of the lens epithelium or changes in the osmotic status of the lens cortex allowing excess water to invade the lens crystal. (DS)

Catecholamines A group of neuroactive amines. Dopamine, norepinephrine and epinephrine are derived from tyrosine via its hydroxylation to L-dopa (L-dihydroxyphenylalanine). Further metabolism of L-dopa leads to the production of these three catecholamines. They are synthesized mainly in the adrenal medulla but norepinephrine, for example, is made in

Table 1. Typical composition of castor bean products (% dry matter).

	DM(%)	CP	CF	Ash	EE	NFE	Ca	P
Castor bean meal, mechanical extraction		34.8	33.2	10.4	10.6	32.2		
Castor bean meal, solvent extraction	92.0	38.5	32.3	7.1	1.0	21.1	0.76	0.87

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Digestibility (%) and ME content of castor bean.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminants					
Castor bean meal	80.8	8.9	92.9	43.4	7.75

other organs and in nerve endings. In Parkinson's disease there is a deficiency of dopamine synthesis. (NJB)

Catfish A rather large group of (principally) freshwater fishes characterized by a body with no scales, or else covered with bony plates, and a head with up to four pairs of barbels. Catfish of the families Ictaluridae and Clariidae are the major species established in aquaculture. The channel catfish (*Ictalurus punctatus*) is native to North America and has constituted a major aquacultural enterprise in the USA for over three decades. Walking catfish of the genus *Clarius*, which are native to Africa and Asia, have been cultured in these countries as well as in Europe.

The nutritional requirements of channel catfish have been extensively studied with as many as 40 nutrients in all of the major groups having been demonstrated to be necessary for normal metabolic functions. Currently there is less nutritional information available for *Clarius* catfish. Catfish in both genera are omnivorous in their feeding behaviour and will consume a variety of food organisms in nature. As such, these fish generally can thrive on prepared diets composed of plant-derived feedstuffs with relatively low protein concentrations ranging from 28 to 32% of diet for juvenile and subadult fish. These diets also typically contain relatively high levels of soluble carbohydrate from cereal grains and grain by-products. (DMG)

See also: Aquaculture; Freshwater fish

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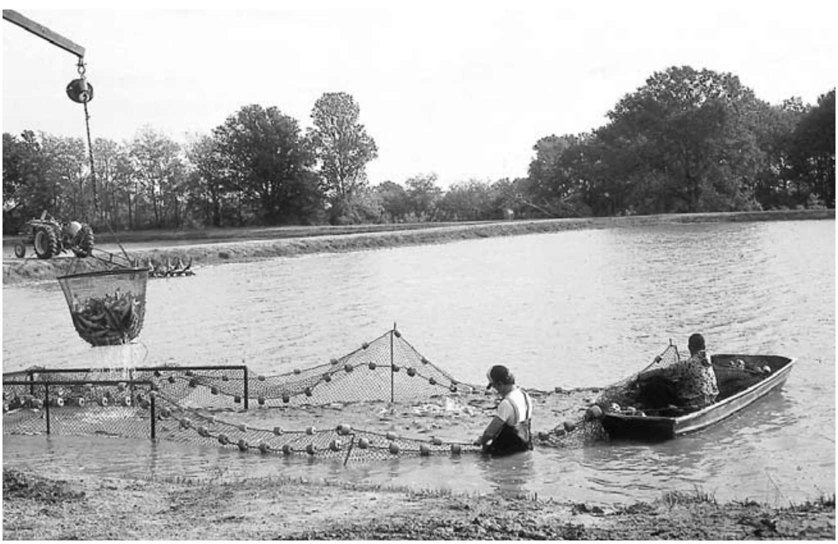
Catheter A tube introduced into a body cavity for the withdrawal of fluid or for the introduction of substances. A catheter is commonly placed in a vein to obtain repeated blood samples or in the bladder for the complete collection of urine. A larger tube introduced into the gut is normally called a cannula. (DS)

Cation: An ion with a positive charge. (NJB)
See also: Acid–base balance

Cattle Cattle belong to the order Artiodactyla (even-toed ungulates), suborder Ruminantia, family Bovidae, subfamily Bovinae and tribe Bovini. Bovinae are characterized by the presence of hollow horns and Bovini by their



Harvesting catfish from a freshwater pond.

large size. Commercially important species among the tribe Bovini are found in the genus *Bovina* (mainly *Bos* species). Humpless cattle (*Bos taurus*) predominate in northern temperate latitudes whereas humped cattle (*Bos indicus*) inhabit the more arid regions of the world. These two species can interbreed to produce fertile offspring. Other species in this genus include *Bos grunniens* (domestic yak), *Bos javanicus* (Bali cattle) and *Bos frontalis* (domesticated gayal), found in Asia.

Domestication of these species involved selection for functional traits such as docility, mature size, draught, milk production and muscularity, as well as type traits such as coat colour and polledness. Differential selection for such traits resulted in the formation of breeds, i.e. animals of common origin with certain distinguishing characteristics passed uniformly from one generation to the next. Adaptation to local environmental conditions through natural selection also occurred. For example, the N'Dama breed (*Bos taurus*), resident in West Africa, developed resistance to trypanosomiasis (sleeping sickness) spread by the tsetse fly.

In developed countries, particularly those in North America and Europe, cattle have been classified by utility, where selection has favoured the production of either meat or milk (Buchanan and Dolezal, 1999). Mature size can vary considerably within each class and this, together with the genetic potential for milk production, can have a significant bearing on the animal's metabolizable energy (ME) requirements for maintenance (0.40–0.55 MJ ME kg^{-1} $Wt^{0.75}$ for non-lactating beef cows; 0.50–0.65 MJ ME kg^{-1} $Wt^{0.75}$ for lactating beef cows; and up to 0.77 MJ ME kg^{-1} $Wt^{0.75}$ for lactating dairy cows), so determining their suitability to specific nutritional environments (Sinclair and Agabriel, 1998).

The rapid increase in milk yield during the first 4–8 weeks of lactation normally requires the cow to meet her metabolic requirements through a combination of dietary intake and body tissue mobilization. The metabolic demands during this period are carefully regulated through the combined effects of a number of homeorhetic and homeostatic hormones that collectively coordinate the processes of lactogenesis, voluntary feed intake and nutrient partitioning in support of galactopoiesis. Of these, growth hormone (somatotrophin) promotes milk production by diverting the products of digestion and intermediary metabolism away from tissue deposition and towards the mammary gland during periods of negative energy balance, characteristic of early lactation. This is achieved, in part, by inhibiting the insulin-mediated uptake of glucose by skeletal muscle, and by inhibiting the ability of insulin to stimulate lipogenesis. Exogenous bovine somatotrophin (bST) has been shown to result in a 12–35% increase in milk yield in high-yielding dairy cows (Zinn and Bravo-Ureta, 1996).

Voluntary feed intake in ruminants is highly variable and difficult to predict. Intake (per unit liveweight) is affected by a number of animal- and feed-related factors. The principal animal-related factors include genotype (generally dairy genotypes have a higher intake capacity than beef genotypes; and high-yielding cows eat more than low-yielding cows), body composition (thinner cows eat more than fatter cows) and physiological status (lactating cows eat more than non-lactating cows). Principal feed-related factors include the dry matter content of the feed, its particle size, cell wall content and rate of digestion, and a variety of factors that influence conditions within the rumen. All these factors interact during early lactation to limit nutrient intake and the products of rumen fermentation relative to the metabolic requirements of the cow, thus placing greater emphasis on the mobilization of body tissues. As a consequence, the high-yielding cow is very sensitive to a number of metabolic disorders, particularly during early lactation when demands placed on the animal's metabolism are at their greatest. For example, the excessive mobilization of body lipids during this period, combined with an inadequate dietary supply of glucogenic precursors, can result in the incomplete oxidation of fatty acids, causing an accumulation of ketone bodies in the blood that can ultimately lead to clinical ketosis. In time, the accumulation of fatty acid deposits in the liver can impair liver function, resulting in various disorders and culminating in fatty liver syndrome. Other common metabolic disorders in the periparturient cow include milk fever, the clinical manifestation of calcium deficiency. Calcium metabolism in mammals is tightly regulated and, whilst total bone calcium levels are high, only the most recently deposited fraction of bone calcium can be mobilized. Factors that predispose cows to milk fever include age (older cows are more prone than younger cows) and calcium supplementation during the immediate pre-partum period; restricted intake during this time can increase the efficiency of absorption following parturition.

The inability of the high-yielding cow to derive all the nutrients necessary to sustain her metabolic requirements during early lactation means that frequently she will benefit from dietary components that resist microbial fermentation in the rumen. These forms of starch, lipid and proteins are largely digested and absorbed in the lower gut. Young and rapidly growing cattle may also benefit from such supplements, particularly from protected sources of protein. In these circumstances, the efficiency of absorption of amino acids and the production response will depend on the biological value of the rumen-undegradable protein fraction of the supplement.

Production responses in growing stock to concentrate supplementation normally arise through alterations in the molar proportions of the principal volatile fatty acids within the rumen, high-grain diets resulting in increased propionate production from the rumen. With the possible exception of protected sources of starch, older and more slowly growing cattle seldom benefit from 'rumen-protected' supplements, the products of rumen fermentation normally being sufficient to meet their requirements for maintenance and growth. Further exceptions to this rule, however, arise when young cattle (particularly non-castrated males) undergo compensatory growth or have an abnormally high potential for lean tissue growth, e.g. the doubled-muscled breeds.

(KDS)

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Cattle feeding Digestion in cattle involves an initial microbial fermentation in the rumen followed by digestion of the microbial biomass and previously undigested feed by enzymes produced further down the gastrointestinal tract. The maintenance of effective rumen microbial function requires adequate fibre, energy, protein, minerals and vitamins in the diet. The nutrient requirements of high-yielding dairy cows cannot be met from microbial digestion of coarse fibre alone, and high quality supplements must be fed (*see* **Cow feeding**). Cattle for beef production do not have to be fed high quality diets, but the fast growth and rapid turnover that can be

Grazing is a central feature of many systems of cattle production.

achieved when supplements of energy and protein are fed may make this a more profitable system than low-input production. Cattle production systems range from extensive suckled calf production to intensive cereal-based beef production.

Suckler cows are usually kept on marginal land that cannot be used for the production of high value crops (e.g. mountainous or arid regions). The demands of the cows can be met from low-quality fodder, which is all that can be grown in such regions. In the UK, a medium-sized suckler cow has an energy requirement of about 100 MJ day^{-1} during winter. This is provided by about 8 t of silage for an autumn-calving cow, whereas the requirements of a spring-calving cow are likely to only be about two-thirds of this amount. This means that more land must be reserved for forage conservation for autumn-calving cows – perhaps 60% of the grassland area for two cuts, compared with perhaps 40% for a spring-calving herd. In many hill farms, setting such a high proportion of land aside for conservation, when the grass growing season is short anyway, is not possible due to constraints of the terrain and the need for grazing. The introduction of machinery for making and handling silage in big bales has assisted many farms in moving from making hay, with all its difficulties in wet areas, to conserving fodder as silage.

The suckled calves produced on marginal farms are usually sold for fattening to farms where better quality food can be grown. These 'store' cattle can be fed a variety of diets, but any change in diet should be introduced gradually. High quality forages, especially maize silage, root crops and cereals, are most likely to be included in the ration, but waste products from the vegetable industry, such as stock feed potatoes, can be included and reduce the cost of the ration. The skill of the farmer in buying low-cost feeds, and cattle, undoubtedly plays a part in the profitability of the store-finishing enterprise.

The cattle can be finished indoors in winter, in which case they are usually fed good quality forage and a limited amount of concentrates, perhaps 2–3 kg per head per day. Alternatively they can be finished at pasture. If the cattle are purchased in early or mid-winter, this will only be applicable to animals of late-maturing breeds. In this case they should not be fed a high quality ration in the winter or the cost of finishing will be too great; silage alone or clean straw and a small amount of concentrates (*c.* 1.5 kg per head per day) would be appropriate. They may only grow at about 0.5 kg day^{-1} during winter but they will compensate for this when they are at pasture. The grazing cattle can be sold when they are finished or, in an emergency, when the grass availability is very low.

In America there is a large supply of suckler cows on rangeland producing suckled calves for finishing. The feedlots usually finish the store cattle intensively over a 6-month period. Local arable farmers may be contracted to produce whole-crop barley silage with some chopped hay or straw and rolled barley for the final fattening period.

Calves from dairy herds are normally housed inside and fed conserved feed. High growth rates in housed cattle are best achieved by offering high quality forage *ad libitum*. If this is not available, whatever forage is available should be supplemented with a cereal, such as rolled barley, the quantity depending on the quality of forage fed. Sufficient concentrate must be fed to allow the cattle to finish indoors, if this is what was planned. If insufficient concentrate is fed on a daily basis early on in the winter, the farmer may actually end up providing more concentrates in total, because marketing of the cattle cannot start in the mid-winter period. The successful operator knows how fast the cattle are growing and feeds supplements accordingly, so that the cattle can be marketed at the right time and plans can be made for the next season's cattle. If cattle are reared over a longer period, such as a 24-month system that finishes the autumn-born cattle off pasture in their second summer, it must be ensured that not too much expensive food is fed during winter if the system is to be profitable.

Cattle may also be fed indoors throughout their life, mostly on conserved forages or cereal-based diets. Grass and maize silages are most common, or a mixture of the two, since the high protein concentration in grass will complement the high energy content of maize. Roots can be fed, but not usually at more than one-third of the diet. Calves are usually reared on hay initially and transferred to a silage diet at 8–10 weeks. Protein supplements can be kept at a constant level, so that as the cattle grow they consume more silage and the protein content of the ration is reduced. The system of feeding a predominantly cereal diet is common where the two main inputs, cereals and calves, are inexpensive relative to the finished product. The main feeding-related disorders that occur are rumen acidosis, bloat, liver abscesses and laminitis. (CJCP)

See also: Cow feeding

Cauliflower Cabbage flower (caulis), *Brassica oleracea*, of which there are many varieties, has a compact white head of fleshy flower stalks and is eaten by humans as a vegetable. Cauliflowers are available year-round and are particularly plentiful in spring and autumn. They have a very high vitamin C content and are rich in potassium, fibre and folate. Surplus production can be fed fresh to cattle and sheep. Cauliflower is a good source of protein, has no fat but contains high levels of natural sugar and dietary fibre. Typical dry matter (DM) content of cauliflower is 120–130 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is crude protein 230–240, crude fibre 120–125, ether extract 20–25, ash 115–120, neutral detergent fibre 290–295 and starch 5–8, with ME 11.5–12 MJ kg^{-1} DM. (JKM)

Celery Celery (*Apium graveolens* L.) is widely grown for human consumption. It has recently been introduced into the tropics for cultivation at higher altitudes. Surplus production may be available for use as animal feed. The leaves are rich in protein and carotene; they have been used up to a rate of 10% of the diet in chickens and can effectively replace lucerne meal. In Africa, the dry matter content of fresh leaves is 110 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 272, crude fibre 35, ash 190, ether extract 69, neutral detergent fibre 434, calcium 27 and phosphorus 17. (JKM)

Cell walls Heterogeneous macromolecular structures that are exterior to the plasma membrane and give rigidity and shape to the cell. Bacteria, fungi and plants have cell walls of different compositions. Plant cell walls are composed of a mixture of polysaccharides, protein, **lignin** and cutin. The cell walls of grasses also contains silica. The principal polysaccharides are **cellulose**, arabinoxylans and pectin, but there is large diversity in polysaccharide composition among plant species. Plant extensin is a fibrous protein associated with the deposition of the cell wall. Lignin is a polyphenolic compound that imparts rigidity to the cell wall. Cutin is composed of higher-molecular-weight alcohols and gives the surface of the cell wall a waxy appearance.

The compositions of the cell walls of grasses and legumes differ. In general, grasses usually have a higher percentage of cell wall in the above-ground biomass than legumes at a similar stage of maturity. However, legumes usually have a greater percentage of lignin in the cell wall than grasses. The polysaccharides in the cell walls of grasses are composed of approximately equal ratios of cellulose to arabinoxylans and other heteropolysaccharides, whereas in legumes the ratio of cellulose to other heteropolysaccharides is much higher. The composition of the cell wall also varies widely among specific plant parts and cell types within each cell tissue. Cells that are involved in photosynthesis have thin primary cell walls with little or no lignin. Cells that have a structural role have thickened secondary cell walls that are highly lignified.

At an early stage of development, the plant cell wall has a low content of lignin and the cell wall polysaccharides are highly degradable by microbial enzymes. As the plant cell matures, the contents of lignin, cutin and silica increase and the degradability of the cell wall polysaccharides decreases. These changes in the composition and degradability (digestion) of the cell wall are responsible for decreases in digestible energy as forages mature.

Mammals and other animals do not have enzymes that hydrolyse cell wall polysaccharides but obtain energy from cell walls through fermentation of polysaccharides by symbiotic, anaerobic microorganisms that reside mainly in sacculated organs of the digestive tract, such as the rumen, colon or caecum. These microbes possess a diversity of enzymes that break down the cell wall polysaccharides. The monosaccharides undergo fermentation to volatile fatty acids (VFAs) that are absorbed and used by the host for energy metabolism.

'Cell wall' and 'fibre' are often used as synonyms. This may lead to confusion: many non-fibrous polysaccharides that do not occur in plant cell walls are referred to as 'dietary fibre' in the human nutrition literature because they are not digestible by mammalian enzymes but require fermentation to yield energy. Therefore, caution is required in the use of the terms. (JDR)

Cellobiose A disaccharide, 4-*O*-β-D-glucopyranosyl-D-glucose, $C_{12}H_{22}O_{11}$, the basic structural unit of cellulose and a product of the hydrolysis of cellulose by cellulase. The stereochemistry of cellobiose allows the formation of two intramolecular hydrogen bonds. Cellobiose is often used as a substrate in microbiological tests for cellulase activity. (JDR)

Cellulase An enzyme that hydrolyses the β(1→4)-*O*-glycosidic linkages in cellulose. Cellulases occur in bacteria, fungi and plants but not in animals. In bacteria and fungi, cellulases degrade plant cellulose to glucose, cellobiose and oligoglucans to derive energy for growth and reproduction. Cellulase in bacteria is located in protuberances on the cell surface called cellulosomes. These structures are involved in the attachment of bacteria to plant cell walls and are required for normal cellulase activity. (JDR)

Cellulolytic microorganisms As no mammal secretes an enzyme complex capable of degrading cellulose, the symbiotic relationship between the enteric fibrolytic microflora and herbivores is vital to the utilization of fibrous plant material. Plant cell walls are degraded by a combination of bacteria, fungi and protozoa, the first two groups accounting for about 80% of the activity. The main cellulolytic bacteria are *Fibrobacter succinogenes*, *Ruminococcus albus*, *R. flavifaciens* and *Butyrivibrio fibrisolvens*. Among the fungal species are *Neocallimastix frontalis*, *N. patriciarum*, *Orpinomyces bovis* and *Piromyces communis*, while ciliate protozoa of the genera *Diplodinium* and *Eudiplodinium* degrade cellulosic material by engulfment (phagocytosis). In contrast to the weak opportunistic interaction of protozoa with plant material, the majority of cellulolytic bacteria and fungi form strongly associated colonies. This strategy allows the cellulolytic enzymes to be concentrated on the substrate, restricts access to the site of hydrolysis and end-products and protects the enzymes from ruminal proteases. Electron micrographs of fibrolytic bacteria and fungi adhering to plant cell walls show the material being gradually eroded. Considering the highly complex nature of the substrate involved, this implies that a range of specific fibrolytic enzymes are released simultaneously. In ruminants, the primary site of cellulolytic activity is the reticulorumen, followed by the caecum, while in horses and pigs this occurs in the enlarged colon. (FLM)

Cellulose A homopolysaccharide of glucose in which glucose residues are linked between carbon 1 of one glucose residue and carbon 4 of the adjacent glucose (β-D-glucopyranose–β-D-glucopyranoside linkages); this linkage is written as β(1→4). Cellulose is the main polysaccharide in the plant cell wall. It is the most abundant natural polymer on the earth's surface and, were it not degraded and converted to CO_2 by microorganisms, atmospheric CO_2 would be rapidly depleted by the fixation of CO_2 into cellulose by plants. The macromolecular structure of cellulose is formed by intramolecular and intermolecular hydrogen bonds that give cellulose its fibrous properties. Cellulose is organized into bundles of microfibrils that form a network around the plant cell. At early stages of growth this network is flexible and the cell structure is maintained by turgor pressure and the resistance of the network. After the cell has elongated and lignin is deposited in the cell wall, the shape of the cell may become fixed.

Animals do not have digestive enzymes that are capable of hydrolysing β(1→4)-glycosides (cellulases) but symbiotic microorganisms of the digestive tracts do have cellulases and degrade cellulose to volatile fatty acids. These acids are absorbed and metabolized by the host. The rate of degradation of cellulose is slow compared with other polysaccharides. Microbial attachment to the surface of the cellulose microfibrils is required for cellulose degradation to proceed. (JDR)

Cereals Those members of the *Gramineae* (grass) family that are cultivated for their grain, which is primarily used for human and animal food. The cereals most commonly cultivated are barley (*Hordeum sativum*), maize (*Zea mays*), oats (*Avena sativa*), wheat (*Triticum aestivum*), rice (*Oryza sativa*), rye (*Secale cereale*), triticale (hybrid of wheat and rye) and sorghum (*Sorghum bicolor*). Most of the proteins of cereal grains are found in the endosperm (e.g. 72% in wheat) and their overall content is influenced by a range of factors, including species, variety, fertilizer application, soil fertility and climate. Protein concentrations are typically 97–160 g kg^{-1} dry matter (DM) for barley and wheat but lower for maize and oats. Cereal proteins are generally deficient in essential amino acids, especially lysine. In all cereal species the starch-rich endosperm is the most important fraction, both nutritionally and economically. The starch comprises amylose and amylopectin and their ratio determines the quality of the starch. The cell wall content (as NDF) ranges from about 124 for wheat to 310 g kg^{-1} DM for oats. The animal feed industry represents a major market for cereal grains, which contribute a large proportion of the energy supply to pigs, poultry and young ruminants. Generally cereals make a lower contribution to the diets of ruminants. Cereal by-products arise from a number of industries, including milling, brewing, distilling and starch manufacture. Cereal by-products play an important role in the diets of ruminants owing to their greater capacity to degrade fibre. (ED)

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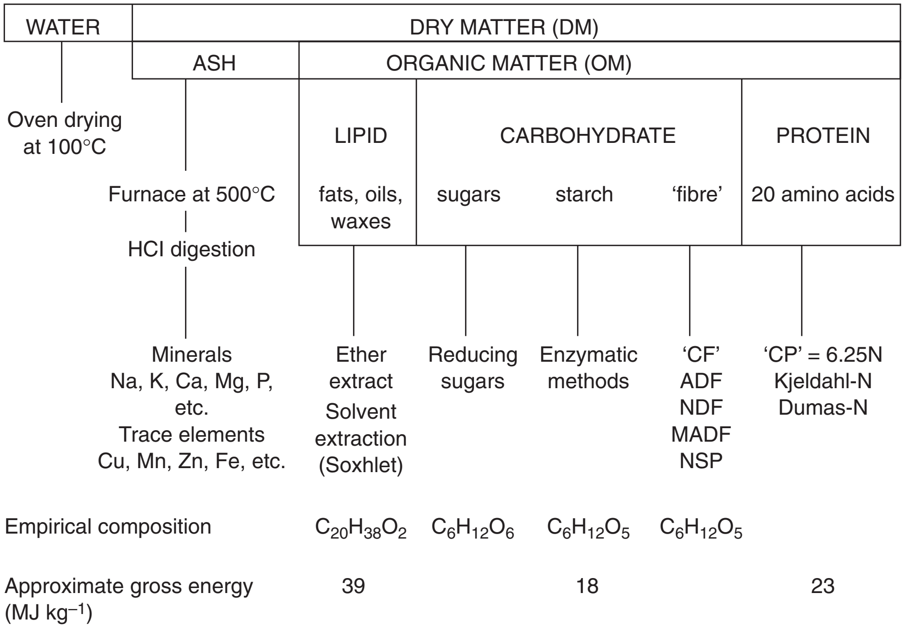
Ceruloplasmin The US spelling of **caeruloplasmin**.

Cetoleic acid *cis*-11-Docosenoic acid, $CH_3{\cdot}(CH_2)_9{\cdot}HC{=}CH{\cdot}(CH_2)_9{\cdot}COOH$, molecular weight 338.6, shorthand designation 22:1 n-11, a long-chain 22-carbon monounsaturated fatty acid found in the oils of cetaceans (whale and dolphins) and fish. (NJB)

Chelate An association of two or more independently existing molecules or ionic species to form a heterocyclic ring compound. The new compound formed by this association exhibits chemical and physical characteristics distinct from those of either parent compound or element. In biological systems chelates typically involve a metal cation such as iron, cobalt, copper, magnesium or zinc bound to an organic compound via oxygen, nitrogen or sulphur elements. Examples include chelates such as haemoglobin, chlorophyll and vitamin B_{12}. Ligand bonds vary from relatively stable covalent bonds to very unstable, highly ionic bonds between molecules. In animal nutrition, chelating compounds are used to sequester or stabilize metal ions. A common chelating agent is ethylenediaminetetraacetic acid (EDTA). (TDC)

Chemical composition Descriptions of the chemical composition of foods (and of plant and animal tissues) are largely based on the proximate analysis scheme introduced by Henneberg and Stohman at the Weende Institute in Germany in about 1840. In this scheme (see figure) food is considered to be composed of water and dry matter. The dry matter consists of an inorganic fraction (minerals and trace elements), represented practically as ash, and an organic matter fraction represented by the mass lost on combustion. The organic matter in turn is composed of three classes of chemical compounds: lipids, carbohydrates and proteins.

The lipid consists of fats, oils and waxes, which are mainly long-hydrocarbon-chain glycerol triesters $(\text{-}CH_2\text{-})_n$. They are hydrophobic and insoluble in water but soluble in non-polar organic solvents. Total lipid can be determined by a percolating extraction with solvent in a Soxhlet extractor. Originally, diethyl ether was used and total lipid was therefore described as ether extract (EE). The lipid components can be further characterized by determining individual fatty acids from gas chromatography of their methyl esters (FAME-GC: fatty acid methyl esters) or by high-pressure liquid chromatography (HPLC) of intact triglycerides.



The proximate analysis scheme for plant and animal tissues.

The protein content of foods can be estimated from the nitrogen content. Proteins contain, on average, 160 g N kg^{-1}; hence crude protein (CP) is defined as N × 6.25. Total nitrogen has traditionally been determined by the Kjeldahl procedure (1883) but the Dumas method is also used. Methods of estimating protein from nitrogen determination do not distinguish between protein and non-protein nitrogen (NPN). Amino acid composition can be determined on hydrolysates by ion exchange or HPLC methods.

The carbohydrate fraction of foods consists of soluble sugars (mainly monosaccharides and disaccharides), starch and non-starch polysaccharides (NSP), imperfectly described as 'fibre'. In the Weendes system the carbohydrate fraction was considered to consist of crude fibre and nitrogen-free extractives (mainly starch and simple sugars). The term 'fibre' is used for a complex range of plant cell wall constituents that may or may not include lignin, which is not a carbohydrate but a complex aromatic polymer of phenylpropane subunits. Many methods for determining and characterizing fibre have been developed from the original much-criticized acid–alkali crude fibre (CF) method. In forages the Van Soest scheme (acid detergent fibre, ADF; and neutral detergent fibre, NDF) has been developed to better characterize fibrous cell wall constituents fed to ruminants. In starchy foods the Englyst non-starch polysaccharide (NSP) enzymatic procedure is more appropriate for non-ruminant animals and humans. Enzymatic or chromatographic methods can be used to measure individual monosaccharides, disaccharides and starch.

Major minerals (Na, K, Ca, Mg, P) and trace elements (Fe, Cu, Mn, Zn, Co, Mo, etc.) can be determined by flame emission spectroscopy (FES), atomic absorption spectroscopy (AAS), or inductively coupled plasma spectroscopy (ICP) conducted on hydrochloric acid solutions of the ash from feeds. Modern ICP spectrometers can measure as many as 26 elements simultaneously on one ash solution.

The gross energy (GE) value of foods is determined by combustion in an adiabatic bomb calorimeter. It may also be approximated from the lipid, nitrogen and carbohydrate determination, using average heats of combustion of those components. It will be appreciated that a full characterization of the chemical composition of a food is a lengthy, complex and costly procedure that can never be complete. Gross composition is 'operationally defined' and overlap between the classes of lipid, carbohydrate and protein (e.g. glycolipids, lipoproteins) means that measured constituents may not sum to 100% in any given food.

Because of the many costly analyses required to determine the composition of foods, a newer method of analysis, near infrared spectroscopy (NIRS), attempts to characterize the composition of food from its spectral signature in the near infrared. Instrumental methods of food analysis have now largely replaced extractive wet chemical methods for food analysis. (IM)

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Chemical probiosis The control of the **gastrointestinal microflora**, especially of bacterial pathogens, by dietary substances that interfere with microbial adhesion. Many bacterial pathogens adhere to the gut surface by the binding of their fimbriae to sugar moieties on the epithelial surface. The fimbriae contain specific **lectins** called adhesins: this binding mechanism is essential for adhesion and infection by many pathogenic bacteria that need to resist peristalsis in the intestine in order to colonize it.

Lectins are proteins capable of specific and reversible binding to sugar moieties. Suitable lectins for inhibition of bacterial adhesion can be isolated from bacteria, e.g. from those pathogenic bacteria that cause infections. Certain plant lectins have similar affinities to those of the specific bacterial lectins involved in adhesion of the bacteria to intestinal epithelial cells and these can also be isolated and used to inhibit bacterial adhesion. On the other hand, lectins themselves may have a major influence on the turnover of the intestinal cells and the effect of lectins in relation to infection by pathogenic bacteria depends on the specificity of the lectin as well as its concentration. Thus, dietary lectins can both enhance and reduce colonization by pathogenic bacteria.

In an alternative form of chemical probiosis, bacterial adhesion is inhibited by feeding simple or complex carbohydrates that have a terminal structure that closely mimics the carbohydrate side chains of the bacterial receptors on the gut wall. While dietary lectins actually occupy the same sites as the bacterial adhesins, the complementary saccharides act by competing with them.

Chemical probiosis is an alternative to probiosis by the addition of live bacteria (called probiotics) which also function by a competitive exclusion of pathogenic bacteria. Thus, both methods may help to maintain normal commensal flora (the resident non-pathogenic flora). (SB)

See also: Prebiotic; Probiotics

Chemical score An evaluation system used to assess the relative value of a single protein or mixture of proteins (and amino acids) to be used in a diet. A value is obtained by assessing the amino acid pattern (usually mg amino acid g^{-1} N) of the protein(s) in relation to an established reference amino acid pattern. This pattern may be developed from the estimated amino acid requirements of the animal in question, or from the pattern of high quality protein, such as egg protein. The value of a protein is not constant, because amino acid requirements vary with species and with purpose (maintenance, growth, milk or egg production). The score is calculated by dividing the amount of each indispensable amino acid in the diet by the amount of the same amino acid in the reference pattern: the score is the lowest of these ratios. For example, if the lowest score is for lysine (making it the first limiting amino acid) and the amount of lysine (mg g^{-1} N) in the diet is 80% of that in the reference pattern, the chemical score is 80%. This protein evaluation scheme assumes accurate estimates of the amino acid content of the proteins involved and that dispensable amino acid nitrogen is not limiting. (NJB)

Chemical treatment of feeds Straws, high-moisture grains and forages may be chemically treated when making hay, silage or alkalage to ensure preservation without deterioration, to improve nutritive value, or both.

Alkali treatment in the form of sodium hydroxide, ammonia or urea has been used on a number of low-quality forages, including straws, husks and hays. It is carried out in an enclosed container and results in an end-product with a pH of 10–11. Alkali reduces the number of ester linkages between lignin and cell wall carbohydrates and increases the digestibility from *c*. 55% before to 65% after treatment. Urea is also used in the production of alkalage from whole-crop cereals. This product is akin to silage with the exception that it is alkaline and not acidic. The urea preserves the crop by releasing ammonia, which inhibits the activity of undesirable microorganisms within the clamp.

Hydrochloric, sulphuric and formic acids are used in the preservation of green crops as silage. These inhibit microbial activity within the silo, preserving the forage by direct acidification.

Recently the longer-chain organic acids propionic, caproic and acrylic have been included in acid mixtures to inhibit yeasts and moulds associated with the aerobic spoilage of silage. Propionic acid is used in the storage of high-moisture cereal grains (moisture content 20–30%) for the same purpose. Sodium benzoate is used in the preservation of a variety of feeds for its anti-microbial activity. Sulphites and bisulphites are also used in the preservation of silages. These generate sulphur dioxide, which is toxic to many spoilage microorganisms. (DD)

Chestnut The reddish brown edible nut of sweet chestnut (*Castanea sativa*), primarily harvested for human consumption. When used as animal feed, chestnuts may be ground or crushed and made into meals or occasionally pellets. They can be fed to most species of livestock but the level of inclusion for ruminants is limited by the high oil content. Like all nut products, they can be contaminated with aflatoxins and are therefore subject to feed regulations. Treatment may be required to remove such contamination. The typical dry matter (DM) content of chestnuts is 920–930 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 12–16, neutral detergent fibre 180, lignin 41, acid detergent fibre 146, ether extract 70, WSC 95 and starch 53, with ME 13.7 and gross energy 20.6 MJ kg^{-1} DM. (JKM)

Chick A young bird, especially one that has recently hatched. The term is frequently used to describe young birds that are still covered by down and have not yet developed a complete feather cover. (SPR)
See also: Broiler chickens

Chicken Domestic fowl bred for either their meat or eggs. The modern commercial layer falls into two main categories: white breeds and brown breeds. Most of the eggs consumed worldwide are white. This is because the white layer is a more efficient and prolific genotype. Most modern breeds produce in excess of 20 kg of egg mass by 76 weeks of age with a feed conversion ratio (FCR) of just over 2.0. Brown hens can also produce about 20 kg of egg mass output, over the same time period, but require more food to do so. They are typically heavier birds and therefore have a higher **maintenance** requirement. The other consequence of being heavier is that they lay larger eggs; but, as the total mass of egg they lay is similar to that of white birds, they lay fewer eggs. Today's laying hen can lay 329 eggs in 392 days, which is almost 85% lay, or the equivalent of laying 6 days out of every 7, throughout the bird's life. Brown hens lay eggs of an average weight of 63 g on an average 115 g of feed per day.

With increased commercialization has come greater intensification, leading to large units with environmentally controlled houses. Due to disease problems such as coccidiosis in extensive systems, hens were transferred into cages where they could be spatially separated from their faeces. This was done on the basis of bird welfare. Today, birds are being returned to the range because cages raise concerns about the birds' welfare. Modern medicines and vaccines mean that birds can be kept in large colonies, out of doors and on the same pastureland in successive years. Hens are also kept indoors on the floor in what have become known as 'barn' or 'deep litter' systems. This allows full environmental control as with a cage system but enables the hens to display their natural pecking order, roam, perch and dust-bathe.

Hens kept on extensive production systems, such as free-range or barn, consume greater quantities of food for the same egg mass output compared with caged birds, due to a greater maintenance requirement because of higher activity levels and a greater energy need for thermoregulation. This can range from 10% to 20% extra feed. Since feed represents about 65% of the cost of egg production, this is a very significant increase.

Nutrient requirements of the modern layer have not changed significantly with time. While the egg mass output has increased dramatically, the feed efficiency has also improved, compensating for the extra output. Each breed company, of which there are about ten major ones worldwide, produces its own tables of nutrient requirements for the particular strain but these hardly differ at all.

The most important aspect of commercial egg production is the rearing phase. If a pullet is grown to the right body weight (a guide to its body composition) and stimulated into lay with an increasing-light pattern, its performance can be predicted with a high degree of accuracy. Most problems experienced by the industry are due to stimulating immature pullets that do not have the body reserves to cope with the stress of early lay. For the first few weeks of lay the hen will be in a net energy deficit, because her appetite is insufficient to replenish her daily output of an egg. With time, nutrient intake from feed will exceed egg mass output, on a daily basis, enabling the bird to regain lost body condition.

The modern broiler chicken grew out of the egg industry. Instead of destroying useless males after hatching commercial layers, they were reared for meat. Since the Second World War, as the demand for meat has increased, selective breeding for meat traits has taken place. Family selection for characteristics such as weight for age, feed efficiency and carcass yield have led to the development of the today's meat breeds. Historically there were both heavy and light broiler breeder strains. The heavy breeds were used by integrated units, where one company owned the breeding and broiler growing operations. In these organizations the benefits of yield and growth characteristics outweighed those of broiler numbers. However, independent hatcheries preferred the light breeds that laid more eggs and hence gave more chicks for them to sell. Also in certain markets around the world people buy a chicken irrespective of its conformation or yield features. In these markets bird numbers are of greatest importance.

At time of writing some 85% of the chickens in the world are from one of four breeds. All of these are heavy breeds, and are all very similar in conformation. Their growth patterns differ, as do their feed efficiencies and mortality, but overall no one breed predominates.

Almost all of the worlds' broiler chickens are kept in barns, where they can roam on the floor. However, as a consequence of appetite selection, the birds are not very active. Their average life expectancy is about 40 days, by which time they will be expected to be in excess of 2.2 kg liveweight. To achieve this weight they will have consumed about 3.75 kg of feed, depending on the feed cost per unit of energy, which equates to an FCR of 1.7.

Genetic improvement appears to progress unabated. Each year broiler weight at 42 days increases by about 50 g, equivalent to achieving the same body weight 1 day sooner each year. This saves maintenance, making the bird more feed efficient. It is also physiologically younger, which means its growth is more efficient. The consequence of both these factors, coupled with the intensive selection for feed efficiency by appetite, means that FCR improves by about 2 points per year as well. As a consequence of these improvements, the nutrient requirements of the modern broiler chicken are constantly changing. Trying to get the extra nutrients required for additional growth into a decreasing feed intake cannot be balanced by the greater efficiency of the birds, therefore the nutrient density of the feed has to increase year on year.

In an attempt to meet more accurately the bird's nutrient requirement on any given day, standard feeds (which were historically fed for 10–14 days each) are now formulated as a concentrate. They are then diluted with an increasing daily percentage of whole wheat so that the nutrient intake is different and exact every day. The use of whole wheat as an on-

farm ingredient has the added benefit, over compound feed, of enabling development of gizzard function. The feed is more effectively ground and the pH rapidly lowered, immediately following ingestion. This has the effect of reducing the bacterial load on the bird, thereby reducing mortality and morbidity, leading to greater feed efficiency. (KF)
See also: Broiler chickens; Domestic fowl

Chickpea A legume, *Cicer ariatinum*, grown primarily for human consumption. The seed varies considerably in colour (from black to beige or white), shape and composition, depending on the cultivar. Chickpeas have been fed to pigs and poultry: they contain about 200 g protein kg^{-1}, about 300 g starch kg^{-1} and about the same quantity of non-starch polysaccharides. They contain small amounts of trypsin inhibitors. They also contain tannins, at low concentrations in the light-coloured varieties; black cultivars contain about 2 g kg^{-1}. Such low levels would be unlikely to cause detrimental effects in animals. The apparent metabolizable energy for poultry is about 12 MJ kg^{-1} and that for ruminants about 14 MJ kg^{-1}. Chickpeas are reported to contain phyto-oestrogens. (TA)

Chicory A Mediterranean herb (*Cichorium intybus*) of the family *Asteraceae*. It is a hardy plant, the roots of which are used in coffee substitutes and blends. The curled dandelion-like greens are used as potherbs, and true endive (*C. endivia*) is grown for salad. Forage chicory is grown in New Zealand and more recently in the USA for feeding to ruminants. Forage chicory is a perennial plant, producing leafy growth, which is higher in nutrient and mineral contents than lucerne (alfalfa) or temperate grasses. Having a taproot it is drought tolerant but it can be damaged by overgrazing and frost. Chicory pastures have a lifespan of 5–7 years and yield 7.5–15 t ha^{-1} under rotational grazing, provided that they are maintained with a minimum stubble height of 38–50 mm and given rest periods of 25–30 days. The digestibility of forage chicory leaves is 90–95% with a protein level of between 100 and 320 g kg^{-1} dry matter, depending on plant maturity. (JKM)

Chinese cabbage *Brassica rapa* (*Pekinensis* and *Chinensis* group) is also known as celery cabbage, pak-choi, pe-tsai and wong bok. It has a mild flavour similar to that of celery. Chinese cabbage is more closely related to turnip and swede than to other varieties of cabbage, its leaves being thinner and more delicate than cabbage leaves. Cultivation practices are the same as for regular cabbage but Chinese cabbage matures faster and may be ready in as little as 60–65 days after sowing. It is used fresh in salads or cooked like regular cabbage and may become available for animal feed due to either oversupply or inferior quality. It is suitable for ruminants and can be fed to dairy and beef cattle at 30% and to ewes at 20% of their total diets. The dry matter (DM) content of Chinese cabbage is 90–110 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 210–230, crude fibre 100–120, ether extract 17–20, ash 105–115 and neutral detergent fibre 275–285, with MER 11.5 MJ kg^{-1}. (JKM)

Chitin A linear polysaccharide chain of β(1→4)-linked *N*-acetyl-D-glucosamine $(C_8H_{13}NO_5)_n$ units. It is the principal component of the exoskeleton of crustaceans (crabs, lobsters, etc.), insects and spiders and is also found in some fungi, algae and yeasts. It is similar in structure to cellulose but the C-2 hydroxyl group is replaced with an acetylated amino group. Upon acid hydrolysis, chitin yields glucosamine and acetic acid. It is insoluble in water, dilute acids or bases and is resistant to bacterial hydrolysis. (TDC)

Chitinase An enzyme that liberates *N*-acetyl-D-glucosamine from **chitin**. Chitinase is produced in the gastric mucosa as well as by the enteric microflora. An industrial preparation of chitinase (chitodextrinase; poly(1→4-α-(2-acetamido-2-deoxy-D-glucoside)) glycanohydrolase; EC 3.2.1.14) is purified from *Streptomyces griseus*. (SB)

Chitosan Deacetylated chitin, i.e. a polymer of D-glucosamine rather than of *N*-acetyl-D-glucosamine. In feed ingredient analysis, chitosan is classified as dietary fibre, isolated with the acid detergent fibre fraction. In the digesta it is positively charged and mimics cholestryamine in sequestering cholesterol and other bile acids. (TDC)

Key reference

PDR for Nutritional Supplements (1st edn). Medical Economics Co. Inc., Thomson Healthcare, Montvale, New Jersey, pp. 84–86.

Chlorella A single-celled freshwater blue alga, which ranges from 2 to 8 μm in diameter with an unusually high content of chlorophyll. *Chlorella* completes its reproductive cycle in 17–24 h and is rich in protein, vitamins, minerals and other bioactive substances including compounds referred to as 'chlorella growth factor'. It is used as a feed for larval fish and in nutritional supplements for humans. (SPL)

Chloride The ion of the inorganic element chlorine. It is required by living systems, and in metabolism is usually found as a counter anion to the cations sodium and potassium. The distribution of chloride between extracellular and intracellular fluid varies with the tissue. For example, the extracellular concentration relative to the intracellular concentration in neurons is 13, in skeletal muscle 31, but in cerebrospinal fluid only 1.14. In regard to plasma osmotic pressure (290 mosm), chloride is the major anion to counter sodium. The other significant anion is bicarbonate. In renal function, the reabsorption of sodium and chloride plays a major role in body electrolyte and water metabolism. Laboratory animals fed chloride-deficient diets respond within hours by markedly reducing urinary excretion of chloride. Poor growth and reduced efficiency of feed utilization (gain/feed) is seen within weeks of feeding a deficient diet. However, a chloride deficiency is not expected under normal feeding conditions. (NJB)

Chlorophyll A generic name applied to plant pigments involved in photosynthesis. The chlorophylls trap light energy and direct it through chemical reactions to the production of ATP. Chlorophyll-*a* is a magnesium-containing porphyrin and is the major chlorophyll in algae and higher plants: it absorbs light at wavelengths from 400 to 450 nm and 640 to 680 nm. Chlorophyll-*b* absorbs light at wavelengths from 430 to 500 nm and 640 to 700 nm. Both absorb essentially no light at wavelengths from 450 to 600 nm. Thus, green light passes through the tissue, giving plants their characteristic colour. (NJB)

Choice feeding The provision of two or more types of food, either simultaneously or sequentially, can be made in order to determine feeding preferences or specific appetites, or allow self-adjustment of **nutrient** intake to meet specific requirements of individual animals. If there is no nutritional advantage of one food over the other(s), the animal will prefer that which has the more pleasant flavour. If one is toxic, then, no matter how initially pleasant its taste, the animal will soon learn to avoid it in favour of a balanced food, even if that food has a flavour that is initially unpleasant.

Pigs and chickens, when given a choice between two foods, one containing more and the other less of a nutrient than the optimum, will, within a few days, be choosing a mixture that provides a more-or-less balanced diet. This has been demonstrated for protein on numerous occasions and is also true for some individual amino acids, minerals and vitamins. Such specific appetites depend on the animal learning to associate the sensory properties of each food with the metabolic consequences of eating that food; few, if any, specific appetites are truly innate.

Ruminants can also exhibit nutritionally wise choice between high- and low-protein foods, which is surprising in view of the fact that the digesta from many meals are mixed together in the rumen and there is a long separation in time between eating a meal and experiencing the metabolic consequences. It is not yet clear the extent to which ruminants are making selections for dietary nitrogen to support optimal rumen microbial activity, as compared with selection to optimize the supply of amino acids to their own bodies.

Choice trials need to be designed carefully, with adequate sample sizes, for the following reasons:

1. *Individual variation.* Unless a preference or avoidance is very marked (for example, rejection of food or water tainted with a bitter substance such as quinine), there is great individual variation in preference. Hence, large numbers of animals are needed to demonstrate a difference.

2. *Positional preference.* Animals can learn to associate differences in food composition with the position in their pen of the food containers. The position of foods offered should be represented equally in all positions, and positions should not be switched for any particular animal even if the foods are easily distinguished by other means, e.g. colour or flavour. To allow for social influences on choice, animals should be far enough apart for a neighbour's presence not to interfere with the subject's choice.

3. *Colour and flavour preference.* An obvious way to enhance a food's identity is to flavour or colour it uniquely. Although some animals have inherent flavour or colour preferences, these are easily overridden by the relative nutritional value of the foods. However, if the food preference itself is weak and if novel flavours or colours are aversive to some animals (because of neophobia) more than others, it is important to use colours that are easily distinguished by the subjects, for which there are no marked preference or avoidance, and to distribute the colours equally among the foods being offered. Generally speaking, mammals learn to use food flavours more readily than colours as cues to nutritive value, while with birds the reverse is true.

4. *Feeding preferences.* Animals demonstrate neophobia – a fear of new things – and this applies to foods. Preference or avoidance of particular foods may be apparent in the short term, perhaps because of some novelty effect, without being so in the longer term. Just because one food is eaten in greater quantities than the other does not mean that the second is less palatable, simply that to make a balanced diet the animal should eat less of the second. The term 'palatability' is frequently, but wrongly, taken to be a property of a food, when in fact it is a property of the food, the animal, and the animal's previous experience of eating this, or similar, foods.

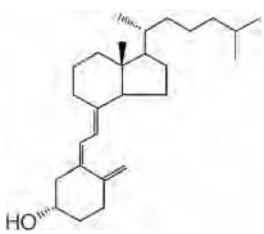
Specific appetites

Under natural conditions, herbivorous and omnivorous animals usually select their (balanced) diets from potential food supplies that vary greatly in terms of their nutritional contents. Such selection involves meeting specific requirements for particular nutrients, based on 'specific appetites' for those nutrients. Evidence for specific appetites can be obtained in a two-choice situation, either by offering the nutrient concerned in one position and an otherwise balanced diet that is lacking that nutrient in another position, or by offering two versions of the same diet that are sufficient and deficient in the nutrient concerned. Alternatively, soluble nutrients can be provided in drinking water, and subjects eating a diet deficient in such a nutrient can be given a choice between water with and without that nutrient. Specific appetites may be in response to a short-term demand, as for example the demand for dietary calcium for eggshell formation when an egg enters the shell gland of a laying hen. This has been demonstrated by offering hens a choice between a low-calcium diet and a separate calcium source such as oyster shell. Other specific appetites, however, may be in response to a long-term demand, as for example when physiological requirements change prior to an annual breeding season, or when an animal is suffering from a long-term deficiency in a particular nutrient. Thus, some specific appetites have been demonstrated experimentally by feeding subjects on a diet deficient in the nutrient concerned for a week or so before the choice trial. Most appetites are learned and it may take many days for subjects to arrive at a balance between the foods on offer that is sufficient to meet the requirement. In domestic fowls, specific appetites have been demonstrated for three minerals (calcium, zinc and phosphorus), one vitamin (thiamine), protein in general and two specific amino acids (methionine and lysine). In addition, heat-stressed fowls have been shown to develop an apparent (learned) specific appetite for vitamin C, which is known to alleviate the consequences of heat stress. In other words, these birds learned that they felt better when they ate more of the vitamin C-supplemented food.

Self-selection from compound feed and whole grain is increasingly allowed in commercial poultry production. This saves money by not having to mill the grain and assumes that an individual's production of eggs or rate of growth is a cause, rather than a consequence, of its level of nutrient intake, and that birds are capable of adjusting their protein and energy intakes precisely to meet their needs. In broilers, the proportion of whole wheat in the diet is typically increased gradually from 5% at 2 or 3 weeks of age to 20% or more in the final week. All this wheat is eaten and it does not appear to cause greater variation in body weight gain.

For pigs and ruminants, studies of ability to select a balanced diet have been largely confined to protein. (JSav, JMF)

Cholecalciferol A specific form of vitamin D, namely vitamin D_3. This form of vitamin D possess the cholesterol side-chain, hence the prefix 'chole' on calciferol. It has the structure:



It is the form of vitamin D manufactured in skin by ultraviolet irradiation and is thus considered the natural form of vitamin D. Cholecalciferol is biologically inactive until it is hydroxylated in the liver to 25-hydroxyvitamin D_3, producing the blood form of vitamin D_3. This compound must then be further hydroxylated in the 1α-position in the kidney to produce the final vitamin D hormone, 1α,25-dihydroxycholecalciferol (trivial name: calcitriol). This hormone derived from vitamin D stimulates the enterocytes of the small intestine to absorb calcium and phosphorus into the plasma from the intestine. Together with parathyroid hormone it causes the mobilization of calcium from bone and together with parathyroid hormone causes renal reabsorption of calcium in the distal tubules of the kidney, resulting in a rise in serum calcium in the blood to normal levels. Cholecalciferol, therefore, is the building block from which the vitamin D endocrine system is constructed. Production of the 1α,25-dihydroxycholecalciferol in the kidney is dictated by either a drop in serum calcium or a drop in serum phosphorus. The drop in serum calcium triggers the parathyroid gland to secrete parathyroid hormone that turns on the enzyme in the kidney to produce the active hormone from vitamin D, i.e. 1α,25-dihydroxycholecalciferol. This major hormone causes the elevation of plasma calcium and phosphorus to normal levels that then suppress further production of parathyroid hormone.

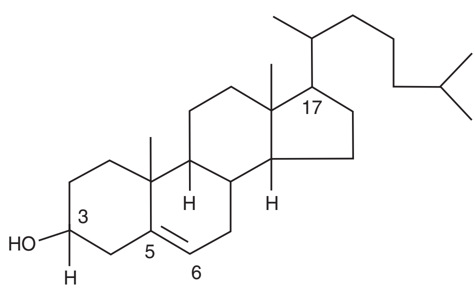
The daily requirement of cholecalciferol for humans is 10 μg or 400 IU. This amount can be produced by 10 min of ultraviolet irradiation of hands and face by summer sunlight in northern hemispheres. A similar production of vitamin D_3 in farm animals can be expected. However, in modern production methods, exposure to sunlight is limited and supplementation is recommended. It is necessary to supplement the diets of poultry with 10–20 μg kg^{-1} of diet to prevent a deficiency of vitamin D and supplementation of diets for cattle, pigs and sheep is also recommended.

Through its active hormonal form, vitamin D has many functions beyond the elevation of plasma calcium and phosphorus. It is believed to function in the immune system, in the islet cells of the pancreas, in the parathyroid glands to suppress the parathyroid gene, and parathyroid gland proliferation. It also is believed to function in the keratinocytes of skin and should, therefore, be considered more broadly than simply a substance that prevents rickets in children and osteomalacia in the adult. A deficiency of vitamin D results in low plasma calcium and low plasma phosphorus. In children it causes the disease rickets, which is characterized by failure of calcification of the organic matrix of bone, resulting in deformities characteristic of the disease. In adults, the deficiency disease is called osteomalacia. (HFDeL)

Cholecalciferol derivatives Compounds that possess the basic structure of vitamin D_3 but have chemical modifications such as an acetate on carbon 3 (cholecalciferol 3-acetate) or a hydroxyl group on the 25-carbon (25-hydroxycholecalciferol) or a hydroxyl on carbon 1 and a hydroxyl on carbon 25 (1α,25-dihydroxycholecalciferol). The acetate increases lipid solubility and stability. The hydroxyl groups increase biological activity. (HFDeL)

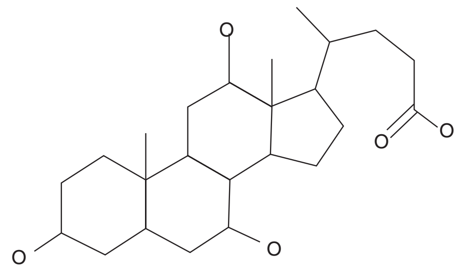
Cholecystokinin (CCK) A polypeptide hormone that stimulates enzyme secretion from the pancreas. CCK is produced in endocrine cells in the small intestine, mainly in the duodenum, where arriving peptides and lipids stimulate its secretion into the blood, which in turn stimulates the pancreatic secretion of proteases and lipases. (SB)

Cholesterol A neutral lipid, $C_{27}H_{45}OH$, and the principal sterol of higher animals. It is found in all body tissues, associated with lipids and membranes, in the plasma membrane as well as in intracellular membranes such as those of the Golgi and mitochondria of cells. It is synthesized in the body entirely from acetyl-CoA and is the precursor of all other steroids in the body, e.g. corticosteroids, sex hormones, bile acids and vitamin D. In the liver, cholesterol synthesis is responsive to dietary cholesterol such that synthesis is decreased when dietary levels are elevated. Cholesterol is in low-density (LDL), intermediate-density, high-density (HDL) and very low-density lipoprotein particles. It is delivered to tissues by LDL and removed from tissues by HDL. Cholesterol is excreted from the liver in bile as cholesterol and as the bile salts taurocholic acid and glycocholic acid.



(NJB)

Cholic acid A primary bile acid, $C_{24}H_{40}O_5$, usually conjugated with glycine or taurine. It is synthesized in the liver from cholesterol in a vitamin C-dependent step. Because bile is usually alkaline, the carboxyl carbon is negatively charged and cholate is found in bile as the sodium or potassium salt.



(NJB)

Choline An organic base, $(CH_3)_3 \cdot N^+ \cdot CH_2 \cdot COH$. A major source of choline is the phospholipid fraction of seed oils, eggs and animal fat. In metabolism it can be directly incorporated into diacylglycerol to form phosphatidylcholine (lecithin) as cytidine diphosphate choline. Phosphatidylcholine can also be formed by methylation of phosphatidylethanolamine, three methyl groups being added by *S*-adenosylmethionine. Phosphatidylcholine is a critical constituent of cellular and subcellular membranes. When both fatty acids of phosphatidylcholine are palmitic acid, it is a surfactant and plays an important role in the development of neonatal lung function. As acetylcholine, it is involved in nerve transmission. Choline can be oxidized to betaine aldehyde and then to betaine and is thus a source of the methyl group used in the methylation of L-homocysteine to form L-methionine. The other two methyl carbons of betaine become one-carbon sources (potential methyl sources) via the folate system. (NJB)

Cholinergic mechanisms The actions of one portion of the autonomic nervous system. Cholinergic neurons innervate sweat glands, blood vessels and skeletal muscles. Stimulation of these nerves results in vasodilation. In general, cholinergic mechanisms are counteracted by the noradrenergic system which releases catecholamines. (NJB)

Chondrocyte A mature, differentiated chondroblast cell embedded in a cartilaginous matrix, similar to the osteocyte (mature osteoblast cell). In the epiphyseal cartilage of growth plates, chondroblasts hypertrophy and calcify the matrix before apoptosis, reabsorption and replacement by trabecular bone as a normal sequence of longitudinal bone growth by endochondral ossification. In articular cartilage, cartilage matrix is not calcified and chondrocytes maintain the extracellular matrix.

(TDC)

Chopping Forage ensiled in clamps, towers or 'sausages' is generally chopped prior to packing. Chopping increases the rate of release of cell nutrients, particularly water-soluble carbohydrate: this stimulates the growth of lactic acid bacteria and fuels the lactic acid fermentation. It improves compaction, which, by excluding oxygen from the silo, increases the speed of fermentation and improves silage quality. Increased compaction also improves the aerobic stability of silage at feed-out.

A range of forage harvesters have been developed that chop forage to varying degrees. *Flails* harvest a standing crop or previously mown material with limited chopping; forage is ensiled in long lengths. Machines that harvest previously mown forage include: (i) the *forage wagon*, which has either no chopping or a limited cutting action (forage is ensiled in long lengths); (ii) the *double chop*, which cuts each forage plant in two places (the forage is still ensiled in relatively long lengths but this method is an improvement on the flail and the forage wagon); and (iii) the *'precision' chop* or *metered-feed*, which can chop forage to lengths of 25 mm or less, offering the optimum chop length for ensilage.

Traditionally balers did not carry out any chopping of the forage. More modern balers have double-cut or 'opticut' actions which enable limited chopping action for baled silage. Immediately prior to feeding, baled silage can be chopped in bale choppers which reduce the particle length to *c.* 50 mm. Such post-ensiling forage processing has shown benefits in terms of forage digestibility and intake and overall animal performance. (RJ)

Chromatography A very powerful method used in the separation of complex, multicomponent samples and for the separation of an analyte from potential interferences. It includes a diverse and important group of methods that permit the physical separation of closely related components of complex mixtures. The components to be separated are selectively distributed between two immiscible phases, a mobile and a stationary phase. All separations involve the sample being transported in a mobile phase that may be a gas, liquid or supercritical fluid, through an immiscible stationary phase that is fixed in place in a column or on a solid surface. The phases are selected so that components of the sample distribute themselves with repeated sorption/desorption steps during the movement of the analyte along the stationary phase. Those components that are retained strongly by the stationary phase move slowly with the flow of the mobile phase, whereas weakly held components travel rapidly. Due to these differences in mobility and distribution coefficients of the individual analytes in the sample, components separate into discrete bands or zones that can be qualitatively or quantitatively analysed.

Chromatographic methods can be categorized either by the physical means by which the phases come into contact, i.e. column chromatography in which the stationary phase is held in a narrow tube, or by the types of phases and kinds of equilibria involved in the transfer of solutes between the phases. Three general categories of chromatography are liquid chromatography (LC), gas chromatography (GC) and supercritical-fluid chromatography (SFC), in which the mobile phases in the techniques are liquids, gases and supercritical fluids, respectively. A detector placed at the end of the column can respond to an eluting analyte, and plotting of its signal as a function of time produces a series of peaks. The plot, known as a chromatogram, can be used to identify components of the sample based upon the position of the peak or, from the area under the peak, give a quantitative measure of the amount of each component.

In LC separations, normal-phase (NP) chromatography involves a polar stationary phase, such as silica gel or alumina, and a non-polar mobile phase such as hexane, chloroform or dichloromethane. It is used for the analysis of relatively non-polar compounds; however, retention characteristics of silica gel are strongly influenced by trace amounts of water. In reversed-phase (RP) chromatography, there is a non-polar stationary phase and polar mobile phase. It is ideal for the analysis of polar analytes. HPLC (high-pressure liquid chromatography) is a variation of LC in which the mobile phase is forced along under high pressure to allow for a greater efficiency of separation. If an LC mobile phase consists of only one solvent used for the analysis, the chromatography is called isocratic. Alternatively, if the chromatography starts with one solvent or a mixture of solvents and gradually changes to a different mix of solvents as the analysis proceeds, it is said to be a gradient elution. Common LC applications include the analyses of substances such as drugs, drug metabolites, antibiotics, steroids, food additives, antioxidants, amino acids, proteins, carbohydrates, lipids, pesticides, herbicides, PCBs etc.

GC is used for the separation of volatile components. For GC, the mobile phase (a gas) is usually helium or nitrogen but can also be hydrogen. Components of a mixture have a different affinity for the stationary phase and thus can be separated. Common GC applications include the analysis of hydrocarbons, PCBs, steroids, drugs, pesticides, fatty acids, amino acids, alcohols, ethers, chlorinated aromatics, glycols etc. (JEM)

See also: Gas–liquid chromatography

Chromic oxide An inorganic compound, Cr_2O_3, which is not absorbed in the digestive tract and is the **marker** most commonly used in digestibility studies. However, its passage does not correspond well to that of either the solid or liquid phase of the digesta and it is therefore not a perfect marker. It may be used to mordant straw or cellulose: in this form it follows more closely the movement of solid digesta. (SB)

Chromium A transition metal (Cr) with an atomic mass of 51.996. It exists in nature in three oxidation states as +2, +3, or +6, with +3 being the most stable. Chromium is purported to be involved in glucose metabolism in animals and humans through its influence on insulin action. A Cr-containing oligopeptide that activates insulin receptor tyrosine kinase activity has been isolated from bovine liver. A covalent complex of Cr and picolinic acid has been reported to enhance glucose tolerance and insulin sensitivity in Type II diabetics. This complex also has been shown to cause chromosomal damage in Chinese hamster ovary cells. Although the US National Research Council does not list recommended amounts of Cr for any of the major farm species, the recommended intake for small laboratory animals is between 1 and 2 mg kg^{-1} diet. (PGR)

Further reading

National Research Council (1997) *The Role of Chromium in Animal Nutrition*. National Academy Press, Washington, DC.

Stoecker, B. (1996) Chromium. In: Ziegler, E.E. and Filer, L.J. Jr (eds) *Present Knowledge in Nutrition*. ILSI Press, Washington, DC, pp. 344–352.

Chromium picolinate The chromium (Cr) salt of picolinic acid. Chromium picolinate is one of many dietary Cr supplements. Chromium appears to have a positive effect on insulin action and glucose metabolism. Although positive effects have been reported in diabetics, there do not seem to be anabolic responses in animals. (NJB)

Key reference

Lukaski, H.C. (1999) Chromium as a supplement. *Annual Review of Nutrition* 19, 279–302.

Chylomicron A lipoprotein particle found in lymph and blood. It is made in the intestinal cells from the hydrolysis products of dietary triacylglycerols (fat), monoacylglycerols and fatty acids, which are combined with a protein. These particles are secreted into the lymphatic system. The particles ultimately enter the general circulation as chylomicrons. Specific apolipoproteins bind to the chylomicron. Lipoprotein lipase in the inner wall of blood capillaries releases the fatty acids for tissue uptake. (NJB)

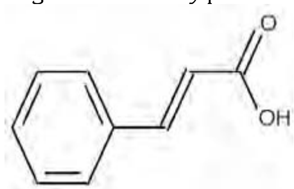
Chyme Intestinal contents, i.e. **digesta**, consisting of undigested food, endogenous secretions, desquamated mucosal cells and microbes. (SB)

Chymotrypsin The active form of chymotrypsin (α-chymotrypsin; EC 3.4.21.1) is an **endopeptidase** that hydrolyses primarily those peptide bonds whose carbonyl groups are contributed by aromatic amino acids, i.e. tryptophan, phenylalanine or tyrosine and, to a lesser extent, by leucine and methionine. It is secreted from the **pancreas** into the duodenum as its inactive precursor, chymotrypsinogen, which is activated in the duodenum after excision of two internal dipeptides by trypsin. (SB)

See also: Pancreatic juice

Cimaterol A phenethanolamine β_2-adrenergic agonist ($C_{12}H_{18}N_3O$, molecular weight 220). These compounds lack the catechol nucleus of the catecholamines whose action they mimic and are therefore not susceptible to degradation by the enzyme catechol-*o*-methyltransferase, thus exhibiting prolonged action. Originally developed for use as a bronchodilator in humans, but employed as a leanness-enhancing repartitioning agent in livestock, cimaterol acts by redirecting nutrients from adipose tissue to skeletal muscle. It is closely related to clenbuterol. (MMit)
See also: Beta agonists; Clenbuterol

Cinnamic acid $C_9H_8O_2$, molecular weight 148. A phenylpropane derivative and the basic building block for many phenolic acids.



Cinnamic acid derivatives (phenolic acids) occur in the cell walls of many forages and are involved in cross-linking fibre. The phenolic acids are antimicrobials and hence may inhibit digestibility of cell wall materials. The phenolic compounds are metabolized by rumen microbes and are conjugated with glycine as a mechanism of detoxification. Phenolic compounds form complexes with proteins and other nutrients and therefore have antinutritional activity, especially in animals on low protein diets. (DRG)

Circadian rhythm A circadian (*circa*, about; *dies*, a day) rhythm is a biological cycle whose period length under constant conditions (continuous illumination or total darkness, constant temperature and random servicing and noise levels) is still close to, though not necessarily equal to, 24 h. In poultry, deep body temperature, locomotor activity and pre-ovulatory luteinizing hormone release are examples of biological functions that operate with a circadian rhythm. Under 24 h conditions, most rhythms are principally regulated by dawn, dusk or both signals, and oscillate at 24 h intervals. However, not every rhythm that oscillates every 24 h under a 24 h light/dark cycle is a circadian oscillator – only those that tend to persist under constant conditions. It is likely that the activity of serotonin *N*-acetyltransferase, the main hormone involved in the control of melatonin synthesis in the pineal gland, is responsible for the regulation of circadian rhythms in birds, whilst a circadian pacemaker in the suprachiasmatic nucleus has been identified in mammals. (PDL, CLA)

Cirrhosis A disease in which functional liver tissue is replaced by scar tissue (fibrosis). Causes include alcoholism, infections (hepatitis), nutritional deficiencies (e.g. vitamin E, selenium) and dietary hepatotoxins (e.g. pyrrolizidine alkaloids). In advanced stages, liver cirrhosis is irreversible. (PC)

***cis*-Fatty acids** Unsaturated fatty acids in which the double bonds are in the *cis* configuration, making the carbon chain twist and lowering the melting point. In the *cis* configuration, the single hydrogens on the carbons of the double bond are on the same side of the chain, whereas in the *trans* configuration they are on opposite sides. (NJB)

Citric acid A six-carbon tricarboxylic acid, molecular structure $HOOC{\cdot}CH_2{\cdot}C(OH)(COOH){\cdot}CH_2{\cdot}COOH$. It is produced in the mitochondrion by the combination of oxaloacetic acid and acetyl-CoA produced in the catabolism of carbohydrates, fatty acids and some amino acids. This reaction forms part of the tricarboxylic acid cycle or Krebs cycle. With the exception of erythrocytes, citric acid is thought to be produced in all cells. Citric acid can also leave the mitochondrion and provide the two-carbon acetyl-CoA units required for fatty acid biosynthesis. (NJB)

Citrulline An amino acid ($C_6H_{13}N_3O_3$, molecular weight 175.2) not found in protein. It is a metabolite in the urea cycle that is synthesized primarily in liver mitochondria from carbamoyl phosphate and ornithine. Orally ingested citrulline, either as free citrulline or that in animal products, can be converted to arginine in the kidney. (DHB)
See also: Non-protein amino acids; Urea cycle

Citrus products Citrus pulp is the solid residue remaining after the extraction of juice or segments from citrus fruits. It typically represents 50–70% of the original fresh weight. It comprises peel, rag (internal tissue) and seed in proportions of approximately 60–65, 30–35 and 0–10%, respectively. The pulp, predominantly from oranges, is usually dried. Calcium oxide, added to reduce the hydrophilic effect of the pectins, ensures that citrus pulp is a good source of calcium (2.2%); however, it is low in phosphorus (0.2%). In composition and nutritive value, citrus pulp is similar to sugarbeet pulp. Although the pectin and neutral detergent fibre contents comprise 50% of the pulp, both are highly degradable. Protein and ash contents are low. Fresh pulp has a pH of 4.0 but the buffering capacity is only one-fifth that of grass silage. The pulp stores well in the absence of air and produces a high quality silage when combined with grass, the low pH and residual sugars having an immediate impact on the ensiling process. The pulp also has an absorptive action, restricting the loss of effluent and associated nutrients. To some extent the high fibre content limits its use in non-ruminants and if large quantities of seeds are present their limonin content could render the pulp toxic to non-ruminants.

Citrus molasses is the syrup produced by concentration of the juice released from citrus peel. It has a typical dry matter content of 70%, of which 60–65% is sugar, but is low in protein. The material is highly viscous and requires to be stirred regularly. It is highly acceptable to cattle but pigs require a few days to become accustomed to the flavour. In both cases it can replace up to 50% of the starchy concentrate in the diet of fattening animals. (FLM)

Claws Present in some animals and all birds, claws are formed from the terminal phalanges and are composed of closely packed, renewable layers of keratinized cells producing horny pointed nails. In birds, claws are adapted for grasping, perching and preening. In very young birds claws can be clipped to obtain blood samples. (MMax)

Clenbuterol A phenethanolamine β_2-adrenergic agonist ($C_{12}H_{18}Cl_2N_2O$, molecular weight 277). These compounds lack the catechol nucleus of the catecholamines whose action they mimic, and are therefore not susceptible to degradation by the enzyme catechol-ortho-methyltransferase, thus exhibiting prolonged action. Originally developed for use as a bronchodilator in humans but employed as a leanness-enhancing repartitioning agent in livestock, clenbuterol acts by redirecting nutrients from adipose tissue to skeletal muscle. It is shown to promote growth and leanness in broiler chickens, an effect that is markedly influenced by dietary protein content. Clenbuterol is closely related to cimaterol. (MMit)

See also: Beta agonists; Cimaterol

Climate Climate describes the usual weather conditions of a location, whereas weather refers to the actual conditions (temperature, humidity, wind, precipitation and barometric pressure) at a given time. Both affect the performance and productivity of animals in a variety of ways. Heat produced by metabolism has to be dissipated to the environment as it is produced, requiring a balance between heat production and heat loss. Heat losses to the environment can be influenced either reflexly or voluntarily by the animal, but only within limits set by the physical laws that govern conductive, convective, radiative and evaporative exchanges, each of which is determined by climatic factors. Thus Newton's Law of Cooling (a physical law) states that the rate of convective and radiative heat loss from a surface is proportional to the temperature difference between it and its surroundings; nothing the animal does can alter this truism, but the slope of the relationship (temperature difference per unit heat loss, i.e. insulation) can be altered by the animal. Dilation and contraction of peripheral blood vessels and erection of the hair or ruffling of the feathers are short-term reflex actions that alter insulation; huddling and seeking shelter are voluntary short-term actions. Long-term adaptations to climate include laying down of body fat and growth of the coat, both of which increase insulation.

Evaporation from the body surface is proportional to the vapour-pressure difference between the surface and the surrounding air (a physical law), the rate constant being dependent on the rate of air movement over the surface. The animal can adjust the availability of moisture at the skin surface by sweating and so increase the surface vapour-pressure, and it can increase air movement over the respiratory passages by panting, but no amount of reflex action by the animal can overcome the final limit set by air humidity. If the absolute humidity of environmental air exceeds the saturation vapour pressure corresponding to deep body temperature, evaporative heat loss is impossible.

Solar radiation can impose a large additional heat load on an animal, even exceeding its normal rate of heat production. This is beneficial in cold environments, but in hot climates shade is essential to avoid it.

At air temperatures below a certain level (the lower critical temperature), heat balance can only be maintained if the animal increases its heat production. This can be done reflexly by shivering or voluntarily by exercise or by increasing food consumption. Increased heat production of stall-fed animals is wasteful if it involves extra feeding. So long as windbreaks are available, the lower critical temperature is unlikely to be reached by grazing mature sheep or cattle even in the very cold winter conditions of North America, but their young require maternal warmth and protection. Deep snow is not of itself a serious cold hazard for sheep, but proves fatal if it prevents them from finding food. Heavy rain reduces the coat insulation of many species, but does not penetrate the fleece of sheep.

At high air temperatures, an upper critical temperature is reached when an animal's productivity falls. This is usually due to a reduction in food intake, either because herbage is sparse in hot climates or because the animal becomes unwilling to make the necessary effort to find and eat enough food. This is particularly true of high-producing cows. (JAMcL)

See also: Environmental temperature; Evaporative heat loss

Cloaca In birds and reptiles, the most posterior section of the alimentary canal, also receiving the terminal portions of the urinary and reproductive ducts. In birds the cloaca is divided by folds of mucous membrane into three compartments: proctodeum, urodeum and coprodeum. (MMax)

Clover silage Two types of clover are commonly used in silage production: white (*Trifolium repens*) and red (*Trifolium pratense*). Clover is usually ensiled as part of a mixture with grasses. Clover contains low concentrations of water-soluble carbohydrates but high concentrations of protein. The protein is of good feed value but its buffering capacity makes the crop more difficult to ensile. This problem is exacerbated by the low concentrations of water-soluble carbohydrate available for lactic acid production during fermentation, thus an additive is essential. (DD)

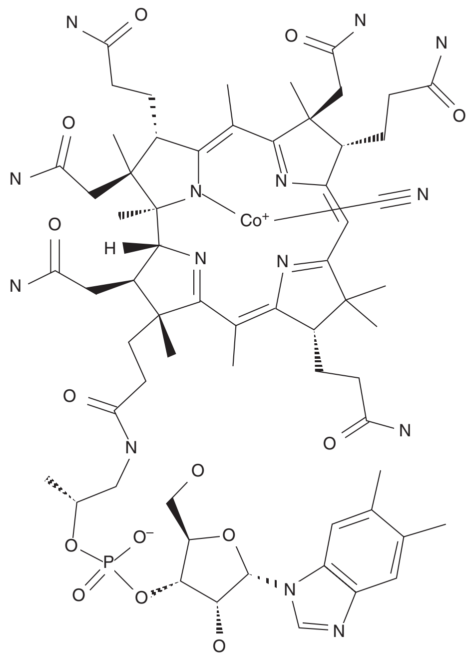
See also: Silage

Coating Some feed materials may be coated to protect their chemical structure and hence nutritional value in extreme environmental situations. For example, vitamin premixes are normally coated with gelatin, which minimizes the risk of the inherently unstable vitamins becoming denatured by heat during feed manufacture.

Some feed ingredients may be protected to ensure maximum absorption in specific parts of the gastrointestinal tract. This is particularly pertinent for ruminant animals, as many materials are digested in the rumen and utilized by the resident microflora, the direct benefits to the host animal being lost. Proteins, specific amino acids and fats may be treated in order to protect them from rumen degradation so that they are absorbed in the abomasum or small intestine. It may be of benefit to coat specific mineral elements with either a protein or a polypeptide to maximize absorption. This is not only nutritionally valuable but also reduces environmental pollution from the excretion of elements such as copper.

Pelleted compound feeds may be coated with flavours, medications or fats to improve palatability or for particular veterinary or nutritional reasons. (MG)

Cobalamin Vitamin B_{12}, $C_{63}H_{88}CoN_{14}O_{14}P$, contains a corrin ring (similar to a porphyrin ring) with a cobalt ion at its centre. It is exclusively synthesized by microorganisms and is not found in plants unless they are contaminated by bacteria. In liver it is found as methylcobalamin, adenosylcobalamin and hydroxycobalamin. It can be provided as a vitamin as cyanocobalamin. In ruminants, B_{12} analogues are synthesized by rumen microorganisms and a dietary supply is generally unnecessary. Cobalamin is absorbed from the intestine by a complex system involving specific binding protein (intrinsic factor), acid and proteolytic enzymes and is taken up in the lower small intestine by specific transporters. In the blood it is transported by transcobalamine II. Once in the cell it can be converted to methylcobalamin in the cytoplasm. In this form cobalamin participates in a reaction in which L-homocysteine is methylated by *N*-5-methyltetrahydrofolate to form L-methionine and tetrahydrofolate. This is a critical metabolic role for vitamin B_{12} in methyl group and one-carbon metabolism. A deficiency of vitamin B_{12} results in a deficiency of folate and elevated blood homocysteine. Animals deficient in vitamin B_{12} have elevated blood levels of homocysteine and ultimately will show signs of a folic acid deficiency. The reason for a folic acid involvement is that the release of tetrahydrofolate in the transmethylation reaction provides tetrahydrofolate to be used in other folate-dependent reactions.Without the transmethylation reaction, folate one-carbon units are 'trapped' as *N*-5-methyltetrahydrofolate. As the *N*-5-methyltetrahydrofolate pool builds up, the tissue becomes deficient in tetrahydrofolate and metabolic reactions requiring tetrahydrofolate as a co-factor slow or cease. This limits the flow of one-carbon units from serine, glycine, betaine, histidine, formate and formaldehyde into the folate system. One product excreted in the urine and representative of a folate deficiency is an intermediate in histidine catabolism, *N*-formiminoglutamate (figlu). This limitation in one-carbon units decreases the ability of cells to produce purines because fewer one-carbon units as *N*-10-formyltetrahydrofolate and *N*-5,*N*-10-methenyltetrahydrofolate are available for the nucleic acid (purine) synthesis. The result is a megaloblastic anaemia due to the impaired DNA synthesis limiting cell division in the developing erythrocytes. B_{12} is transported by transcobalamine II and once in a cell it can be converted in the mitochondrion to adenosylcobalamin, which is required as a vitamin co-factor in propionate metabolism. Propionate can be produced from the catabolism of threonine and methionine and from anaerobic intestinal fermentation. Propionate, as propionyl-CoA, must be carboxylated by a biotin-dependent step to produce methylmalonyl-CoA which, with the aid of the vitamin B_{12} co-factor adenosylcobalamin, is ultimately converted to succinyl-CoA, which can be used in metabolism. A decrease in the participation of B_{12} in this reaction leads to the urinary excretion of methylmalonate. Elevated excretion of homocysteine and methylmalonate, while being signs of a deficiency of vitamin B_{12}, can also be apparent in response to a series of inherited disorders.



(NJB)

Key reference

Seetharam, B. (1999) Receptor-mediated endocytosis of cobalamin (vitamin B_{12}). *Annual Review of Nutrition* 19, 173–195.

Cobalt A mineral element (Co) with an atomic mass of 58.93. It is an essential trace element for most animal species but, unlike most other minerals, not in ionic form but as a vital part of vitamin B_{12}, or cobalamin, which is involved in methyl group transfer reactions. A deficiency of the vitamin leads to anaemia. The minimal requirement of Co for ruminant animals is about 0.1 mg kg^{-1} diet for sufficient microbial synthesis of vitamin B_{12} for the animal to utilize. Cobalt itself is non-toxic but 4–10 mg kg^{-1} body weight could cause loss of appetite and reduced weight gain. Ionic Co is readily absorbed from the gut and shares a common pathway with iron. Co is excreted primarily in the urine.

(PGR)

Further reading

Smith, R.M. (1987) Cobalt. In: Mertz, W. (ed.) *Trace Elements in Human and Animal Nutrition*, 5th edn. Academic Press, Harcourt Brace Jovanovich, New York, pp. 143–183.

Stabler, S.P. (2001) Vitamin B-12. In: Bowman, B.A. and Russell, R.M. (eds) *Present Knowledge in Nutrition*. ILSI Press, Washington, DC, pp. 230–240.

Coccidiosis Parasitism by protozoa of the genera *Eimeria*, *Isospora*, *Cystoisospora* or *Cryptosporidu*. Nearly all animals are susceptible. Infection generally results in the invasion and destruction of the intestinal mucosa with subsequent diarrhoea and productive losses. Severity of the disease is directly related to the dose (number of oocysts ingested) and the immune and nutritional status of the host. Both improved management to prevent oral exposure to infective oocysts and treatment with coccidiostats are effective in control. (BLS)

Cockerel A young male domestic fowl. Mature birds are described as cocks or roosters. (KJMcC)

Cocoa bean (*Theobroma cacao* L.) The cocoa tree is indigenous to South America, but the main centre for cocoa bean production is tropical West Africa. Cocoa beans are found in large yellow or orange pods which grow directly on the stems or branches of the tree. Beans are removed from the pod and fermented with its encasing white mucilage, and dried for processing into cocoa powder and cocoa oil. Pods contain a high concentration of potassium. Cocoa shells, the main residue from processing, contain a toxic alkaloid, theobromine, which is poisonous to animals, but only traces of this are found in cocoa pods.

Although cocoa bean shells have a high protein level (16%; see table), the digestibility of the protein is low (6.6%). Cocoa pods can be used in a maintenance ration for small ruminants, comprising up to 25% of the diet. Up to 7 kg day^{-1} has been fed to dairy cattle without adverse effects. Dried and ground pods can be included in concentrate mixtures at up to 20% without deleterious effects on production levels. (LR)

Nutrient composition (% dry matter).

	CP	CF	Ash	EE	NFE
Cocoa pods	7.8	35.1	10.4	2.3	47.6
Cocoa bean shells	16.0	17.4	10.8	3.2	

CF, crude fibre; CP, crude protein; EE, ether extract; NFE, nitrogen-free extract.

Further reading

Devendra, C. (1988) *Non-conventional Feed Resources and Fibrous Agricultural Resources*. IDRC/Indian Council for Agricultural Research, Ottawa, Canada.

Gohl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series, No. 12. FAO, Rome.

Coconut (*Cocos nucifera* L.) Nuts are produced on the coconut palm tree, which can grow in poor sandy conditions. The nut consists of a hard shell covered by a fibrous outer layer, with an edible kernel inside. The nut must be split and the kernel dried for storage. Coconut water contained inside the nut is usually discarded. Oil can be extracted from copra, the dried kernel. The fibrous outer layer has no feed value. Ruminants can graze coconut orchards once the trees have reached 5–6 years old.

Copra is too valuable to use as a livestock feed, but coconut meal (the residue after oil has been extracted) is used as an animal feed. The oil content of coconut meal varies widely according to the efficiency of the extraction method. Coconut meal is rich in energy and protein (Table 1) and can be used for lactating animals. It becomes rancid as it ages, as a result of oxidation of residual oil, and can

Table 1. Typical composition of coconut products (% dry matter).

	DM(%)	CP	CF	Ash	EE	NFE	Ca	P
Coconut meal, mechanical extraction	88.7	19.5	8.5	5.4	18.4	48.2		
Coconut meal, solvent extraction	93.4	20.5	26.1	7.0	0.4	46.0		
Coconut meal, expeller	88.8	25.2	10.8	6.0	5.2	52.8	0.08	0.67
Copra	50.0	9.7	4.3	2.9	64.4	18.7	0.03	0.26

CF, crude fibre; CP, crude protein; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Digestibility (%) and ME content of coconut meal.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Coconut meal, expeller	91.0	35.0	95.0	80.0	13.16
Pigs					
Coconut meal, expeller	70.0				13.08

cause diarrhoea. The meal is low in lysine, isoleucine and methionine but has a high fibre content (Table 2). The maximum safe amount in dairy cow rations is < 2 kg day^{-1} because it leads to a harder butterfat. Beef cattle can consume higher levels without adversely affecting carcass fat. Coconut meal should be introduced gradually into livestock rations.

Because livestock can eat young coconut leaves, which damages tree development, grazing in coconut plantations is restricted until trees are too high for the animals to reach the leaves. (LR)

Further reading

Devendra, C. (1988) *Non-conventional Feed Resources and Fibrous Agricultural Resources*. IDRC/Indian Council for Agricultural Research, Ottawa, Canada.

Gohl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series, No. 12. FAO, Rome.

Cod Atlantic cod (*Gadus morhua*, L.) occurs naturally on both sides of the North Atlantic from Iceland and Spitsbergen to the Baltic Sea and Bay of Biscay in the eastern Atlantic, and from Greenland to Cape Hatteras, North Carolina, in the western Atlantic. Cod, haddock and pollock belong to the Gadidae, a family of physoclistous, soft-rayed fishes featuring thoracic pelvic fins and, frequently, a barbel on the lower jaw. The aquaculture production cost of cod is relatively high due to slow growth and early sexual maturation problems, which may be reduced by photoperiod manipulation.

There is small-scale cod hatchery production and grow-out in Newfoundland and, more recently, the New England states have initiated a successful early rearing programme. Atlantic cod eggs are buoyant, 1.2–1.6 mm in diameter and have no oil globule. Hatching occurs in 14–40 days at 6 and 0°C, respectively. Newly hatched larvae are 4.0–4.5 mm long and are pelagic until a length of 25–50 mm. Larvae can be successfully reared to metamorphosis on a sequential diet of microalgae, live food organisms such as rotifers and artemia, and microparticulate weaning feeds. (RHP)

Cod liver oil Oil obtained from the livers of cod and other fish from the Gadidae family. It is used as a source of unsaturated fatty acids (oleic, docosahexaenoic and eicosapentanoic) and fat-soluble vitamins. The nutrient composition is 38 MJ energy kg^{-1}, 1,000,000 IU vitamin A and 100,000 IU vitamin D kg^{-1}, with 226 g saturated, 467 g monounsaturated and 225 g polyunsaturated fatty acids kg^{-1} and 5700 mg cholesterol kg^{-1}. (JKM)

Coenzymes Metabolically essential compounds derived from B vitamins. The vitamins themselves are not able to participate as enzyme **co-factors** in metabolism. For example, thiamine is metabolically converted to its mono-, di- and triphosphate forms. It functions as a vitamin co-factor only as thiamine diphosphate. (NJB)

Coffee Coffee production for human consumption gives rise to a number of by-products that may be used as ruminant feeds. These include leaves, pulp from the bean, coffee residues, coffee meal and spent coffee grounds. The fresh fruit consists of 45% pulp, 10% mucilage, 5% skin and 40% bean. To produce coffee the fruit is processed to free the bean from the pulp, which accumulates in large quantities and is used in some areas as roughage for cattle. The fruit can be processed by either a dry method or by a wet soaking method. The pulp from the dry method is fibrous and rather poor roughage (see table), whereas that from wet processing has much greater feed value. Coffee pulp from the wet method can be fed to lactating dairy cattle at levels below 20% of the diet without affecting milk production. Digestibility of pulp (dry method) in sheep is crude protein 10.3%, crude fibre 27.9%, ether extract 53.2% and NFE 50.2%, with ME 1.33 MJ kg^{-1}.

Coffee meal is a dark brown to black residue produced when coffee seeds are removed from the outer coating, dried and then roasted. Coffee meal is high in fibre and has a very low energy value. It is a bitter product that inhibits food intake and will reduce overall feed intake if fed at levels greater than 2–4% of the total diet. It has a strong diuretic effect, which encourages urinary nitrogen and sodium losses, making it unsuitable for feeding to horses. Coffee meal can contain high oil levels which interfere with fibre digestion in ruminants at high inclusion levels. In addition, the oil content may cause the product to become rancid in storage. Coffee meal can be fed to dairy cows, beef cows and ewes, but not at an inclusion level greater than 4%.

Dried coffee leaves have a relatively low nutritional quality but they can be included in concentrates. The high tannin content of the coffee leaves reduces the digestibility of proteins and possibly of other dietary components. Spent coffee grounds, or cherko, are the waste product from instant coffee production. These are unpalatable and contain diuretics including caffeine, and tannins that reduce protein digestibility; inclusion rates should not exceed 2.5%. The nutritional composition of spent coffee grounds can be improved by solid fermentation (*see* **Solid-state fermentation**). (JKM)

Typical composition of coffee products (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	EE	NFE
Dried leaves	936	99	187	130	59	525
Residue/meal	910	120	440	17	25	398
Pulp, wet method	230	128	241	95	28	508
Pulp, dry method	900	97	326	73	18	486
Skins, Columbia	900	24	952	4	6	214
Coffee ground	197	133	624	5	196	42
Coffee oil meal	898	174	270	55	18	483

EE, ether extract; NFE, nitrogen-free extract.

Cold environment In a cold environment an animal is forced to raise its metabolism above the normal level in order to keep warm. This occurs at the so-called lower critical temperature, which in still air can be as low as −40°C for a fully fleeced sheep and as high as 34°C for a newly hatched chicken.

Wind causes a decrease and solar radiation an increase in the critical temperature. (JAMcL)
See also: Climate; Environmental temperature

Colestyramine A synthetic strong basic anion-exchange resin. It has quaternary ammonium functional groups attached to a polystyrene polymer. It can bind bile salts and if consumed in sufficient amounts may alter the excretion of cholesterol-based substances. (NJB)

Colic Severe and sudden attack of abdominal pain, often caused by indigestion. Caused in horses by the presence of gas, impaction of the colon, or a variety of other gastrointestinal disorders. It may also be caused by large numbers of parasitic worms, urinary calculi or nephritis. (JMF)

Colitis Inflammation of the colon, often accompanied by haemorrhage and ulceration. Symptoms are abdominal pain, fever, watery diarrhoea, dehydration, hypovolaemia, toxaemia, leucopenia, decreased serum Cl, Na and K levels and metabolic acidosis. The disturbances of mineral balance arise from damage to the epithelial tissue of the colon. The aetiological agents are many and include *Escherichia coli*, *Salmonella* spp., *Clostridium* spp., *Ehrlichia risticii*, Cyathostomes, fungi, various antibiotics, drugs and toxins. All farm animal species are potentially affected and can transmit the infection to humans. (CJCP)

Collagen A fibrous protein that makes up the major portion of white fibres in connective tissues. It is found in skin, tendons and bones and contributes approximately 25% of body protein in mammals. Collagen is converted to gelatin by boiling in water. At least 19 types of collagen, at least 35 mammalian collagen genes and at least 30 separate polypeptide chains have been identified. The characteristic molecular structure of collagen can be described as a three-stranded rope with strands winding around each other with a 1.5 nm right-handed twist. The polypeptide chains that make each strand have a left-handed twist composed of 18 amino acid residues for each turn in the helix. The three polypeptide chains of mature collagen type 1 are made of approximately 1000 amino acids. The three polypeptide chains have a unique amino acid sequence. A structural requirement for the triple helix assembly is a glycine residue in every third amino acid position. Two other amino acids found in high frequency are proline and hydroxyproline. Hydroxyproline is formed by post-translational modification of proline during collagen synthesis. Hydroxyproline accounts for 13–14% of the total amino acid content of collagen. These two amino acids make the structure more rigid. Another structurally important amino acid found in collagen fibrils is lysine. A post-translational modification of the ϵ-amino group of lysine involves conversion to a hydroxyl group to form hydroxylysine. Hydroxylysine can bind covalently to hydroxylysine in adjoining polypeptide chains to form cross-links, making a more rigid structure. The enzymes involved in forming hydroxyproline (prolyl hydroxylase) and hydroxylysine (lysyl hydroxylase) both require ascorbic acid (vitamin C) as a co-factor. This requirement may explain the bleeding gums and poor wound healing seen in scurvy (vitamin C deficiency) in humans, other primates and some birds.

As a nutrient source, collagen is an incomplete protein with regard to the amino acid pattern required by simple-stomached animals, as it is devoid of the indispensable amino acid tryptophan. Collagen has less than one-half the required concentrations (1 g amino acid 16 g^{-1} nitrogen) of eight of the nine indispensable amino acids; it also has excessive concentrations of the dispensable amino acids glycine, proline and hydroxyproline, which make up 47% of the total amino acids. Hydroxyproline cannot be used as an amino acid in protein synthesis, as it is only produced from proline during collagen synthesis. (TDC)

Colon That part of the digestive tract that lies between the caecum and the rectum (or, in those species lacking a **caecum**, between the ileum and the rectum). The colon is the main site for the resorption of water and sodium. It is also important for microbial activity and production of **short-chain fatty acids** (SCFA), particularly in non-ruminant herbivores, such as the horse, in which up to 70% of absorbed energy is from SCFA produced in the colon. (SB)

Colonization: *see* Gastrointestinal microflora; Rumen microorganisms

Colostomy Surgical removal of the large intestine with the creation of a fistula for the outlet of digesta from the distal ileum.

(SB)

See also: Cannula

Colostral immunity This passive immunity is of potentially enormous benefit to the young animal. It can provide protection against species-specific and environmental pathogens to which the dam, or colostrum provider, was exposed before parturition. This passive protection may be systemic, from colostral antibodies absorbed in the first 24–48 h of life, or by local action in the gut subsequent to this. (EM)

See also: Immunity

Colostrum The milk formed before and around the time of parturition. It may differ in consistency (thicker) and colour (cream/beige/yellow) from subsequent milk production.

Colostrum is the major source of passive immunity for most domestic animals (in contrast to humans, rabbits and guinea pigs) and is also a rich source of nutrients. Lipids and proteins (primarily caseins and albumins) are present in relatively high concentration, around 20%, but lactose levels are lower than in subsequent milk production. Vitamin content is high, particularly vitamin A, which is important in pigs and calves as placental transfer is limited. Colostrum acts as a natural laxative in the neonate, aiding passage of the meconium, the accumulated fetal faecal material.

Immunoglobulins in colostrum protect the neonates in two ways. IgA acts locally in the gut lumen and IgG is absorbed into the neonate's circulation, providing short- to medium-term protection to specific diseases. In many mammals IgG is the major immunoglobulin in colostrum, though IgA is present in milk for longer.

Immunoglobulin A (IgA) is produced in the mammary gland by plasma cells that have migrated from gut-associated lymphoid tissue of the dam, where they are stimulated by the gut flora. This IgA is not absorbed into the blood of the neonate but remains in the gut to act to protect the gut wall against infection.

Immunoglobulin G (IgG) is transported and concentrated from the dam's sera into colostrum by mammary acinar cells. Thus if circulating IgG is present at a high concentration in response to a specific antigen in the dam's sera, it should also be at a high concentration in the colostrum. This type of antibody is specifically transported across the neonate's intestinal epithelium (optimally in the lower jejunum in the calf) and into the circulation, provided that the neonate is less than 36 h old. Absorption of antibody is reduced after the neonate is 12 h old. Unless infected as a fetus, neonates of most farm species are born without gamma globulins in their circulation. Measurement of serum IgG in the neonate can thus indicate whether a satisfactory amount of colostrum has been consumed and antibody absorbed. Calves with less than 10 mg IgG_1 ml^{-1} are considered hypogammaglobulinaemic.

It is generally accepted the neonate should consume 10% of its body weight in colostrum in the first 24 h and if possible half of that in the first 6 h of life. Colostrum contains trypsin inhibitors to help to prevent breakdown of the antibody proteins. Antimicrobial factors such as lysosomes, lactoperoxidases and lactoferrins are also present.

Antibody levels in colostrum drop rapidly over the first few days of lactation. By day 3, globulin levels are less than 10% of those in the first colostrums to be produced.

If the dam has no colostrum, donor colostrum or frozen stored colostrum can be used. Commercial colostrum substitutes are also available. (EM)

See also: Immunity

Common carp (*Cyprinus carpio*) A freshwater fish of the family Cyprinidae, probably the most abundant domesticated fish species. It has four subspecies: *C. c. carpio* of the European–Transcaucasian area; *C. c. aralensis* of the mid-Asian region; *C. c. haematopterus* of the Amur–Chinese or Far Eastern region; and *C. c. viridivio-laceus* of North Vietnam; and a large number of strains are known. The original natural distribution of common carp was probably restricted to a narrow belt in central Asia but it has been introduced into so many parts of the world that it now enjoys the status of a virtually global fish and its culture is very widespread. Common carp are omnivorous fish and can be polycultured with other freshwater species. Carp dig and burrow into pond embankments and sides in search of organic matter. They gulp in mud, from which digestible matter is sieved and the rest rejected – a habit that often makes pondwater turbid. In the wild, adult common carp thrive on decayed vegetable matter containing bottom-dwelling organisms, notably tubificids, molluscs, chironomids, etc. In some countries the common carp is considered a nuisance species.

Although common carp have been farmed since ancient times, scientific studies of their nutrition is of relatively recent origin (mid 1960s) and most of the work is conducted on small fish under laboratory conditions and on post-juvenile stages in net-cage culture with practical diets. The protein requirement is 30–38% crude protein in the diet. Common carp can effectively utilize both carbohydrate and lipid as dietary energy sources. For growth of carp, the optimum ratio of digestible protein (mg) to energy (kcal) is 97:116. Common carp have no stomach and it is better to feed them frequently, about four times a day. (RMG)

Comparative slaughter The sacrifice of research animals for the purpose of measuring changes in the composition of the whole body or in the mass or composition of a tissue. The whole animal or the part of interest may be analysed for some biochemical or chemical analyte. Animals in an initial control group are slaughtered at the beginning of the experiment to provide a baseline against which changes can be assessed. (JSA)

Compensatory growth The accelerated growth that occurs when previously undernourished animals are well fed. They then appear to grow faster and more efficiently than similar animals that have been continuously fed. Compensatory growth occurs in ruminants and non-ruminants. It is sometimes referred to as 'catch-up growth', particularly in humans where it can be observed after a period of prolonged infection and poor food intake. In the agricultural context, it is characteristically associated with the spurt of growth that occurs when ruminants fed on low-quality conserved roughage are turned out to fresh grass in the spring or when the poor forage of a dry season is replaced by lush growth when the rains return.

Undernutrition may be either *quantitative*, with less feed consumed per unit of time, or *qualitative*, with reduced concentrations of usable energy or specific nutrients in the diet. The extent to which compensatory growth occurs depends on the severity of the undernutrition, the stage of growth during which it is imposed and the length of time for which undernutrition continues.

The precise scientific explanation of compensatory growth is fraught with many difficulties. Experiments purporting to demonstrate compensatory growth require great clarity of thought for proper elucidation. The growth rates of all animals slow down as they approach maturity, so when they are compared with ones that are physiologically younger, the latter will appear to be growing more rapidly. Compensatory growth in some circumstances may merely be a reflection of a rehabilitated animal rejoining its normal growth curve at a younger physiological age than its contemporaries. For this reason it is helpful to compare animals of similar physiological age (or weight range) rather than those of similar chronological age.

Many publications refer only to an acceleration of observed liveweight gain. This does not allow a distinction to be made between the growth of bone and muscle and the relatively simple changes resulting from a sudden increase in gut-fill (very significant in ruminants) or the rapid responses of the accessory organs of digestion such as the intestines and liver. Only in experiments where there has been a degree of carcass evaluation or measurement of chemical changes can tissue differences be confidently affirmed.

Apparent changes in efficiency have been variously explained as a carry-over of adaptive responses to undernutrition, including a reduced maintenance requirement and reduced energy costs of tissue deposition. Early feed restriction in broilers has been shown to reduce abdominal fat but not overall body weight, leading to an improvement in efficiency. This has been attributed to impaired hyperplasia of adipocytes in the restricted groups.

Many experiments show an enhanced daily intake per kilogram body weight in the compensating group, as for example in pigs (Ratcliffe and Fowler, 1980). Another key feature of the apparent improvement in efficiency is due to tissues with a relatively low energy density being deposited in the gain of the compensating group. This is due to a preferential growth of muscles and organs rather than the growth of adipose tissues (Blaxter, 1989; Lawrence and Fowler, 2002). In many agricultural situations, compensatory growth is a corollary of circumstances in which the growth curve is necessarily interrupted by a seasonal food shortage. Examples of deliberate exploitation of the phenomenon are rare, although Auckland *et al*. (1969) claimed that a 'low–high' pattern of protein concentration in the diet gave a greater efficiency of protein utilization in turkeys than did feeding them continuously with a high concentration. Deliberately slowing growth may be of benefit in the context of metabolic diseases such as ascites and bone disorders in poultry and this may be more acceptable if the period of retardation is followed by a period of compensatory growth. (VRF)

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Competition Animals in a group may compete with each other for access to food or water when availability of these resources is limiting relative to demand. This can occur if there is insufficient space at feeders or drinkers (especially nipples), or if the food or water supply is intermittent. Demand for food is greatest when animals are subjected to restricted feeding programmes, and demand for water increases when ambient temperature rises. Animals in a group tend to feed and drink synchronously, due to social facilitation, and competition at feeders and drinkers can lead to aggression, fights and injury, as dominant animals displace subordinate ones. (JSav)

Complementation The positive result of mixing one or more proteins to achieve a more favourable dietary amino acid pattern. When the amino acid pattern of one protein or mixture of proteins provides amino acids that are limiting in the pattern of another protein,

Animals in a group compete for access to food if there is insufficient space at feeders.

the process of mixing the proteins in a specified ratio yields a mixture of amino acids that meet the animal's needs for a specific process (e.g. growth, milk production) at a lower total nitrogen intake. Thus, the amino acid pattern of one protein complements that of another. (NJB)

Complete feed A mixture of dietary ingredients designed to meet all the nutrient requirements of an animal. The mixture is normally mixed to a uniform blend so that the animal cannot select individual ingredients.

For pigs and poultry, complete feeds are usually blended from cereals and protein sources, with added oil, minerals and vitamins to meet requirements. For ruminants, complete feeds (often referred to as total mixed rations) contain a mixture of forages, by-products, cereals, protein sources, fats, minerals and vitamins.

Complete feeds are normally designed to be fed *ad libitum*, which requires an estimation of potential voluntary feed intake. Where less productive stock are offered complete feeds (e.g. sows in early pregnancy), the metabolizable energy content of the complete feed is normally reduced, by inclusion of high-fibre sources, so as to limit energy intake and prevent excessive deposition of body fat. In ruminants, voluntary feed intake is usually greater when forages and concentrates are mixed as a complete feed than when offered separately. This is because the microbial population of the rumen reaches a stable equilibrium that enhances the digestibility of the forage components. Complete feeds also allow utilization of less-palatable feed ingredients that would otherwise be rejected when fed separately. (PCG)

Composition: *see* Body composition; Botanical composition; Chemical composition; Feed composition; Meat composition

Compound feed A mixture of different dietary ingredients blended together to form a complete feed for non-ruminants, or a supplementary feed to complement forage for ruminants. Compound feeds contain carbohydrate sources such as cereals and protein sources such as oilseeds or fish meal, with mineral and vitamin supplements. The ingredients are usually milled to reduce particle size and aid mixing. Most compound feeds are pelleted for ease of handling and use on farms. The energy content of pelleted compound feeds is often increased by spraying oil on to the pellets during the final phase of manufacture. Compound feeds are colloquially referred to as concentrates. (PCG)

Computed tomography (CT) Also called computed axial tomography (CAT), a specialized form of X-ray technique that acquires cross-sectional images of the body. The X-ray source and scanner rotate around the body measuring the transmission of the X-ray beam from which cross-sectional images are generated by computer. The image has dark and light areas corresponding to specific tissues. Computed tomography is used in animal nutrition studies to detect and measure adipose tissue, muscle and bone. CAT scanning is widely used in clinical practice. (SPL)

Computer software Programs, or series of instructions, performed by a computer to fulfil a task or application. For example, a word processor, database, spreadsheet or feed formulation utility. (RG)

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Concentrate A generic term to describe any non-forage dietary ingredient, usually for herbivores. Concentrates include compound feeds, protein concentrates, single raw materials (also called straights) and supplements. The concentrate:forage ratio of a ration is the sum of these ingredients divided by the total forage content of the ration, though some classes of stock may be fed on 100% concentrates, with no forage component.

Concentrates generally have greater concentrations of energy and protein than forages. They are also fermented more rapidly in the rumen. Rapid consumption of starchy concentrates in large quantities can upset rumen fermentation. Starch is rapidly fermented in the rumen, leading to a drop in rumen pH and build-up of lactic acid (acidosis). When rumen pH fall below 6.0, cellulolytic bacteria cannot digest the forage component of the ration and rumination becomes less frequent. The buffering action of saliva is reduced, exacerbating the drop in rumen pH. Acute cases of acidosis arise when animals accidentally gorge themselves on concentrates, often resulting in death within hours. Mild acidosis occurs in dairy cows or beef cattle given a high-concentrate diet and may be associated with reduced forage digestion, low milk fat content and laminitis.

Cattle fed on an all-forage diet normally have volatile fatty acid concentrations in the rumen of approximately 70% acetate, 20% propionate, 8% butyrate and 2% others. Feeding concentrates increases the proportion of propionate in rumen fluid, since this volatile fatty acid is an end-product of starch digestion. Propionate is a major precursor of glucose and so increased propionate production from concentrates results in increased circulating levels of insulin and greater body fat deposition. Concentrates are therefore useful for fattening animals and for lactating animals in early lactation that would otherwise be unable to consume sufficient energy to meet the requirements of milk production. Concentrates are also the major source of undegradable protein in ruminant diets which, for high-producing animals, is an essential supplement to microbial protein produced in the rumen.

Concentrates are usually fed at a restricted rate in order to avoid disrupting rumen function and also because they are more expensive than forages. Large allowances of concentrates should be divided into two or more separate meals. Traditionally, concentrates were allocated to dairy cows during milking. The greater milk yields achieved today require higher concentrate allowances, and faster milking routines mean that it is not possible for cows to consume all of their concentrate allowance in the milking parlour. Electronic concentrate dispensers are available for allocating concentrates to individual cows in small quantities and frequent meals throughout the day. Alternatively, a proportion of the concentrate allocation can be mixed with forage to form a basal ration that is supplemented on an individual cow basis with the remaining concentrates, or the whole concentrate allowance can be mixed with forage to form a complete feed. If concentrates and forage are fed separately, the concentrate allowance may be varied according to individual milk yield (e.g. 0.4 kg l^{-1}), or on a flat rate to all cows. Research results suggest that total milk yield is determined by the total allowance of concentrates throughout the year, rather than pattern of allocation. (PCG)

Conception rate Strictly defined as the number of animals conceiving, expressed as a percentage of the total number mated or inseminated. It is not normally possible to detect that an animal has conceived until some time after the event so that, in practice, conception rate is often synonymous with pregnancy rate. It may be expressed as the non-return rate, which is the percentage of animals not seen to return to oestrus within a defined period after mating or insemination.

Conception rate depends on the proportion of females that ovulate close to the time of insemination and on the proportion of ovulating females whose ova are fertilized. This in turn depends on the viability of the ova, the uterine environment and the number and viability of available spermatozoa.

Provided that females are not malnourished, nutritional levels tend to affect the number of ovulations, rather than the occurrence of ovulation. Severe underfeeding is likely to suppress cycling and oestrous behaviour. The female is thus less likely to be mated, and there will be no effect on conception rate per se.

Specific nutritional imbalances may affect the reproductive tract environment. High levels of dietary protein have been associated with low pregnancy rates in cows, for example. (PJHB)

Conditioning The mechanical treatment of crops at the time of mowing. The aim is to provide a rapid rate of moisture loss from the crop with minimal loss of dry matter. Conditioners are an integral part of the mower and can range from a simple mechanical tine that lacerates the crop, to a more complex mechanism with rubber or metal rollers. (RJ)

Connective tissue A tough sheet of fibrous tissue found as the outer membrane of organs (liver, kidney, muscle or skin) or the tough cord-like tissue that connects muscles to bones (tendons) or the tough fibrous tissue that connects bones to cartilage, muscle or other bones (ligaments). Connective tissues are comprised primarily of extracellular collagen fibres that appear white. Another abundant protein in some connective tissue is elastin, which is yellow. (TDC)

Contamination The presence of substances not intentionally added and usually of an undesirable nature. Common examples include: toxic elements occurring naturally or picked up during transport next to inappropriate substances or in dirty containers; pesticide residues from incorrect use; fruits or seeds of poisonous plants; or toxic fungal bodies such as ergot. Aflatoxins may develop in poor storage conditions and microbial pathogens such as salmonella may contaminate feeds. Lack of care in the feedmill may lead to one feed being contaminated by another. It is particularly important to avoid contaminating a non-medicated feed with one containing a medicine. (CRL)

Convulsions Electrolyte imbalances, especially magnesium deficiency, can upset the electrical potential of brain neurones, causing them to be hyperexcitable. This can cause uncontrolled motor neurone excitation, leading to irregular and spastic muscle contraction due to excessive excitation of neurones within the brain. (JPG)
See also: Hypomagnesaemia

Cooking: *see* Heat treatment

Copper Copper (Cu) is a mineral element with an atomic mass of 63.546. It is an essential dietary component for all farm animals. Copper is a transition element and has two redox states, Cu^{+} and Cu^{2+}. It is one of the most biologically active mineral elements and is an indispensable part of many enzyme systems involved in electron transfer and oxidation–reduction reactions in mammalian systems. Some of these Cu enzymes have antioxidant activity and are involved in the metabolism of reactive oxygen species such as superoxide and hydrogen peroxide. Others have ferroxidase activity, oxidizing Fe^{2+} to Fe^{3+}.

In most non-ruminant mammals, ingested Cu is absorbed primarily from the duodenum. The mechanisms of absorption involve transport proteins that are located in the plasma membranes of the enterocytes. These include CTR1 for Cu influx and ATP7a for Cu efflux. A genetic aberration in the gene for ATP7a produces a dysfunctional transporter allowing Cu to accumulate in the enterocyte, with little transferred to the blood. Although the mechanisms of Cu absorption in farm animals have not been studied to this extent, they are probably similar. After Cu is transferred to the blood, it is transported to the liver and other organs bound to serum albumin. Similar transport proteins as found in the intestine probably effect Cu uptake into the liver and other tissues; however, the efflux transporter in liver is ATP7b. Aberrations in this gene cause Cu accumulation in the liver.

Copper concentration in the serum or plasma is around 15 μmol l^{-1}, but slightly higher in females than males. During low intakes of dietary Cu in young animals, the Cu concentration in plasma can decrease to one-half the normal value within a few weeks. Adult animals are more resistant to Cu deprivation than the young. If the deficiency is allowed to progress, the animals can die of an aortic dissecting aneurysm, caused by the reduction of the Cu-dependent enzyme lysyl oxidase that cross-links collagen and elastin fibres.

The outward signs of Cu deficiency in mammals are less evident than with other mineral deficiencies. Food intake and weight gain are not affected to a great extent but the animals will develop anaemia. Copper-containing enzymes will be reduced in activity and can result in increased susceptibility to oxygen stress. Large blood vessels can weaken and lead to aneurysms. Copper deficiency *in utero* can lead to neurological damage in the offspring that is irreversible. High zinc concentrations in the diet can interfere with Cu absorption and lead to signs of Cu deficiency. Ruminant animals that consume diets modestly high in molybdenum and sulphur are susceptible to Cu deficiency because of the *in vivo* formation of thiomolybdate that binds Cu and renders it unavailable for absorption.

According to the US National Research Council, the Cu requirement of most farm species, including dairy and beef cattle, and horses, is approximately 10 mg kg^{-1} diet for all age groups. The requirement for pigs can range from 3 to 6 mg kg^{-1} diet, with the young animal requiring more than the adult. The Cu requirement for poultry ranges from 4 to 5 mg kg^{-1}; the young chick requires more than the adult.

Farm animals are rather susceptible to Cu toxicity. Hepatic necrosis has been observed in calves fed 45 mg Cu kg^{-1} diet for 13 weeks; however, adult cattle seem to show no adverse effects after consuming 200 mg daily for up to 15 weeks. Sheep, on the other hand, develop toxicity signs when exposed to as little as 30–80 mg Cu kg^{-1} diet for 20 weeks, but when dietary sulphur and molybdenum are low, Cu toxicity signs can develop with as little as 11 mg dietary Cu kg^{-1}. Young swine can show toxicity signs when fed Cu in excess of 250 mg kg^{-1} diet but Cu fed at levels of 100–250 mg kg^{-1} can promote growth in weanling pigs. Toxicity signs manifest themselves mostly as reductions in growth rates and/or haemolytic responses. (PGR)

See also: Absorption; Availability; Iron; Molybdenum; Thiomolybdates; Zinc

Further reading

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Copra: *see* Coconut

Coprophagy The consumption of faeces, generally implying the animal's own faeces. Nutritional benefits include the consumption of B-complex vitamins and bacterial proteins synthesized by microbes in the hindgut. In some animals, such as the **rabbit**, the process is more correctly referred to as caecotrophy and the ingested material referred to as caecotropes. Small herbivores such as rabbits and guinea pigs selectively excrete fibre and retain non-fibre components in the caecum, where they are fermented. At intervals, the caecotropes (night faeces, soft faeces) are consumed. Coprophagy and caecotrophy increase the digestibility of feeds, because of enhanced caecal fermentation and a second transit of ingesta through the digestive tract. (PC)

Cori cycle A metabolic cycle in which lactate produced from glucose by anaerobic metabolism in muscle is recycled to the liver and converted back into glucose. Anaerobic glycolysis in muscle produces pyruvate, which is reduced to lactate by the NADH produced in glycolysis. (NJB)

Corn Any growing cereal crop or harvested grain may be referred to as 'corn', especially the predominant crop of a particular area (such as wheat in England, oats in Scotland or maize in the USA). (ED)

Corrinoids Compounds containing the basic octadehydrocorrin ring structure of vitamin B_{12} and related compounds. Similar structures are the iron porphyrin ring of haem in haemoglobin and the magnesium-containing porphyrin of chlorophyll. (NJB)

Corticoids: *see* Adrenal

Corticosterone: *see* Adrenal

Cortisol: *see* Adrenal

Cottonseed The seed of cotton (*Gossypium* spp.) is obtained as a by-product of cotton fibre production, about 2 t of seed for each tonne of fibre. The seeds contain about 200 g kg^{-1} of oil, which contains a high proportion of unsaturated fatty acids. The oil is often extracted by compression and the fibrous husk is pressed with the seed kernel. The resultant cake is known as undecorticated cake and has a crude fibre content of around 300 g kg^{-1}; the decorticated cake has about 90 g kg^{-1}. This difference in fibre considerably affects the nutritive value of cottonseed, especially for non-ruminants.

Decorticated meal has a protein content of 400–500 g kg^{-1}, the undecorticated meal 200–250 g kg^{-1}. The protein is first limiting in lysine. Undecorticated cottonseed meal has an apparent metabolizable energy for poultry of about 8 MJ kg^{-1} while for ruminants it is about 12 MJ kg^{-1}. Cottonseed meal is rarely included in the diets of poultry or at levels of more than about 100 g kg^{-1} for mature ruminants because it may cause digestive problems. Cottonseed and the meal contain condensed tannins, a polyphenolic aldehyde, gossypol and two cyclopropenoid fatty acids (malvalic and sterculic acids). The tannins are present in small quantities (less than about 30 g kg^{-1}) and may reduce nutrient utilization slightly. The older varieties of cotton can contain up to about 20 g kg^{-1} but the newer cultivars have much lower concentrations in the seed.

Like tannins, gossypol chelates mineral elements and may reduce their absorption. Iron salts are sometimes added to chelate the gossypol and thus reduce the effects in animals. Processing the seed may cause reaction of gossypol with lysine, reducing its availability. Gossypol has an adverse effect on rumen microbes and is also associated with reduced reproductive capacity in animals. Feeding cottonseed to sheep has been shown to reduce protozoal numbers but it is uncertain if this was due to the effects of the gossypol or of the oil. Other adverse effects of gossypol include coloration of egg yolks in hens' eggs due to chelation of minerals. The cyclopropenoid fatty acids disturb lipid metabolism in animals and reduce performance. (TA)

Coumarin: *see* Dicoumarol

Cow The mature female of any species of Bovidae (**cattle**). The term is usually applied after the animal has delivered her first calf. Before that she is called a heifer. (PJHB)

Cow feeding The dairy cow has been selectively bred to produce considerably more milk than is required by any calf and so lactation, particularly at the beginning, requires a much greater intake of nutrients than the traditional high-fibre diet of cattle. Preparation for lactation is important and normally cows do not lactate for 7–10 weeks before calving. During this time farmers usually feed a high-fibre ration for the first 4–7 weeks and increase the energy content just for the last 3 weeks. The amount of concentrates fed near to calving depends on the condition of the cow and the desired milk output, but would typically be 2–4 kg day^{-1}. Feeding a high nutrient-density diet before lactation prepares the cow for milk production by, firstly, supporting growth of the rumen papillae, which takes about 5 weeks of exposure to cereals, and, secondly, by allowing the cow to lay down additional body reserves that can be used in early lactation, when voluntary feed intake is insufficient to supply the nutrient requirements for milk production. However, cows that are fat at calving consume less feed *post partum* than cows that are thin. They rely more on catabolizing body tissue for their energy and, to some extent, protein requirements. A large negative energy balance in the first 100 days of lactation increases the time to first ovulation and reduces progesterone secretion, leading to a longer calving index.

Calcium intake requires careful management before and immediately after calving. During early lactation the output of calcium increases considerably, because of milk production, and this may be more than the cow can provide from body stores in the bone tissue. Calcium absorption and excretion are regulated by the production of parathyroid hormone. If it is possible to restrict calcium intake before calving to approximately 3 g kg^{-1} dry matter (DM), increased activity of parathyroid hormone increases the absorption of calcium from the gastrointestinal tract.

In early lactation, feed intake does not increase as rapidly as milk production, creating a deficit in the nutrients required for maximum milk production. It is normally not until mid lactation that energy balance is restored. The deficit is met by the mobilization of body fat reserves and to some extent body protein and mineral stores. A high-energy diet accelerates the return to maximum intake, which is one advantage of allocating more concentrates to the early lactation period. An excessive weight loss during early lactation reduces milk yield, lessens the chance of conceiving and maintaining a viable embryo and increases the risk of acidosis. If cows have a low level of body reserves, it is less likely that they will be able to endure a period of underfeeding without milk yield being reduced. If forage has to be restricted towards the end of winter because of inadequate supplies, both the expected duration and the severity of the restriction should be taken into consideration when deciding whether to purchase additional feeds.

Milk fat is produced both by the synthesis of fatty acids in the mammary gland and by the absorption and secretion into milk of dietary fatty acids. In microbial digestion, the fatty acid profile of the feed is modified. Acetic acid is the main precursor for milk fat synthesis and, as the acetogenic bacteria digest plant cell wall, the fibre content of the diet is the most important determinant of the fat content of the milk. The ratio of lipogenic nutrients (acetic acid, butyric acid and long-chain fatty acids) to glucogenic nutrients (propionic acid, glucose and some amino acids) therefore determines milk fat content, in particular the ratio of acetate to propionate. Fibre digestion is impaired if the rumen pH is less than 6.3, and feeding large quantities of concentrates that are rapidly fermented in the rumen to acid end-products should be avoided. Rumen pH can be maintained by feeding alkali-treated forage or grain, or by stimulating the production of saliva, which contains buffers based on both sodium and potassium. The incorporation of unsaturated fatty acids into milk is possible if fats are protected from rumen fermentation. Normally no more than about 6% of unprotected fat should be included in the diet, as it has adverse effects on rumen digestion.

Milk protein is mainly casein (about 70%), the remaining 30% comprising β-lactoglobulin, α-lactalbumin and immunoglobulins. Variations in milk protein concentration in response to changes in nutrition are less than those of milk fat, but there is a clear relationship between the energy supply to the cow and milk protein content. The response of milk protein content is mainly due to the reduced use of amino acids to supply energy. Cows that are catabolizing body lipids to provide for their energy requirements, therefore, tend to have low concentrations of milk protein, as some of the feed protein will be utilized for energy. The optimization of the amino acid content of the diet could become more important if the control of nitrogen emissions from cattle should become more urgent.

Milk is likely to acquire taints from feeds when it is exposed to the environment, particularly if it is collected into cans in the feeding or living area of the cowshed and transferred to churns. For example, brassicas and beets may produce a taint if fed within 3 h of milking and so should preferably be fed after milking.

In most countries grass, or other feeds for grazing, cannot grow all year and so farmers conserve surpluses from times when growing conditions are good so that they can be fed to the cattle during the winter months, when it is too cold for grass to grow, or in the dry season, when there is insufficient moisture. In temperate countries fodder is mainly conserved as silage, which is cut at a younger stage of growth than hay and, therefore, tends to be more nutritious. In the humid tropics, making good quality silage is more difficult because the high temperature and humidity make controlling the fermentation more difficult. It also requires more equipment and facilities than haymaking. Maize silage is popular with cattle farmers because it has several advantages over grass silage. Silage can be fed either directly from a clamp, so-called self-feeding, or it can be extracted from the clamp by machine and fed along a passageway or in a circular feeder. If the silage is fed in a passageway, cows should be restrained behind a barrier that allows them to put their heads through to feed, but not to walk on the silage or pull their heads back through the barrier while they are still eating silage.

Hay relies on preserving grass by removing the moisture that microorganisms require for survival. Energy losses from the grass plant are often very high during haymaking, due to continued plant respiration. However, if the same grass could be used to make either hay or silage, the protein value of the hay would usually be greater than that of silage, because there is less protein denaturation during the conservation process.

In many parts of the world, straw and other crop residues, such as maize stover, are an important feed for cattle. Their available energy content is low, as most of the energy is locked up in the form of cellulose and other structural carbohydrates that are lignified. Cows will not consume much straw, because its rate of breakdown in the rumen is slow. The protein content of straw is much less than that required by most cows, often only 40 g kg^{-1} DM. The concentrations of minerals and vitamins are also low. Thus for high-yielding cows straw has little nutritional value but it helps to maintain rumen function and animal health. Straw can be upgraded by treating it with sodium hydroxide or ammonia, which reduce the lignification of the structural carbohydrate. It can also be harvested together with the cereal grain in the form of 'whole-crop' or arable silage.

Concentrated feeds, or concentrates, are based on cereals, or other feed high in energy and protein. They are usually made into a pellet, or compound, with the addition of a binding agent, most often sugarcane molasses. A dairy cow can give yields of 7000 l per lactation on high-quality forage alone, but in most situations farmers get an economic response to providing at least a low level of supplementary concentrates. In developing countries, less concentrate supplements are fed than in the industrialized countries and they are often of lower quality, because cereals are relatively expensive and are reserved mainly for feeding to humans. The allocation of concentrates to dairy cows should take account of their physiological state, i.e. whether they are lactating, pregnant or neither. Dairy farmers generally prefer to feed most concentrates to those cows giving the most milk, whatever their forage feeding system, but loose-housed cows fed high-quality forage *ad libitum* respond similarly whatever their milk yield. Feeding all the cows their concentrates at a flat rate through the winter period has the advantage of simplicity and it can be fed on top of or mixed in with their forage, rather than through individual feeders in the parlour or cow housing. The risk of upsetting rumen digestion with high-concentrate diets and causing low milk-fat concentrations or acidosis has led to such diets being based on digestible fibre, e.g. from beets, rather than starch from cereals. The starch in compound pellets is exposed to rapid degradation by the rumen bacteria.

Dairy cows can be given a complete diet – usually a mixture of silage and concentrates mixed up in a portable feeding wagon. An advantage of complete diets is that inexpensive by-product feeds can be incorporated into a mix, and feeds with low palatability can be masked by the strong taste of silage. Typical diet formulations for early, mid and late lactation or dry cows are given in the table.

Diet formulations for early, mid and late lactation cows.

	Early	Mid	Late/dry
Yield level (kg per cow day^{-1})	30–40	20	10
Forage DM as proportion of total DM	0.3	0.5	0.7
Energy density (MJ kg^{-1} DM)	12	11	10
Crude protein (g kg^{-1} DM)	17	14	12
Modified acid-detergent fibre (g kg^{-1} DM)	16	25	30
Calcium (g kg^{-1} DM)	8	6	5
Phosphorus (g kg^{-1} DM)	4.5	3.5	3.0
Magnesium (g kg^{-1} DM)	1.8	1.5	1.5
Sodium (g kg^{-1} DM)	1.8	1.5	1.5

(CJCP)

Cow lactation The lactation of the cow commences at calving. Milk production increases progressively in the first 2–3 months of lactation, and peak lactation normally occurs between week 8 and week 12 after calving. Thereafter, milk yield declines until the cow is dried off 2 months before she is due to produce her next calf. Thus, the usual total length of the cow lactation is 305 days and the dry or transition period is normally 60 days in length.

Lactation is normally considered in three phases: early lactation, the first 100 days after calving; mid lactation, days 100–200 of lactation; late lactation, days 200–305 of lactation. The pattern of voluntary food intake is similar to that of milk production but maximum food intake is not normally achieved until the fourth month of lactation. The rise in food intake is therefore slower than the increase in milk yield, particularly in the first 2 months of lactation. As a result the cow's requirement for energy often exceeds her intake of energy; she is in negative energy balance and loses body weight in early lactation. This loss in weight is normally replaced in the final 3 months of lactation, when milk yield is relatively lower than in mid and early lactation. The target for feeding the dairy cow should be to achieve a similar body weight and condition score at the end of the lactation as at its start.

The feeding strategy to meet the high nutrient requirements of the cow in early lactation is to maximize voluntary intake as soon as possible. The transition from the dry period to early lactation should be smooth, and the cow is often introduced to a lactation diet in the final

21 days of the dry period to allow the rumen microflora to adapt to the change in dietary ingredients from the dry-cow diet to the lactation diet. The energy density of the diet is increased in early lactation in an attempt to minimize the deficiency in energy intake at this time. The early lactation diet often comprises a higher proportion of rapidly digested concentrated feeds, including starch and lipids, and a lower proportion of slowly digested forages than the mid and late lactation diets. The concentration of metabolizable protein is also higher in early lactation diets than in diets formulated for mid and late lactation.

In mid lactation, the nutritional strategy is aimed at minimizing the rate of decline in milk yield, which can often be as much as 2.5% per week. Ideally, the milk yield of the cow should remain as close to peak yield as possible during the second 100 days of lactation, though the onset of pregnancy, with associated changes in the hormonal balance of the animal, is reflected in a change in the partition of nutrients from lactation to the growth of the placenta and fetus. Thus, if milk yield decreases substantially in mid lactation and the diet is not reformulated to take account of the reduction in nutrient requirements, the cow is liable to gain weight during this period.

Late lactation is the period when the voluntary intake of nutrients is most likely to exceed requirements for milk production, and as a result the cow normally gains weight during this phase of the lactation. Slowly digested forages should comprise the majority of the animal's nutrient supply. Supplementary protein may be required if the forage is deficient. The supply of essential mineral elements should be checked and any deficiencies rectified. Straw is often used at this stage of lactation as a way of reducing the energy density of the diet.

Cows are usually dried off at least 60 days before the predicted date of calving, to allow the udder to recover from the previous lactation and to condition the cow for the next lactation. Drying off is achieved by stopping milking abruptly. This can cause problems if the cow is still yielding a relatively large quantity of milk, and for this reason some very high-yielding cows have extended lactations, especially if they are not due to calve for a further 80–100 days after their normal 305-day lactation, because of delayed conception.

Lactating cows are normally milked twice daily, though where *Bos indicus* cattle predominate, the calf must be present to stimulate the release of oxytocin and milk ejaculation by the cow. *Bos indicus* cattle may only be milked once daily, and their milk yield may be reduced if the calf is allowed to suckle before the cow is milked. In contrast, herds *of Bos taurus* cows may be milked three times daily. This practice increases milk output by about 15%. In high-yielding herds the additional expense of the extra milking may be offset by the value of the increased milk yield.

A recent innovation is the introduction of automatic milking systems in which the cow is allowed to choose when she is milked. Most cows opt to be milked four to five times daily, usually with a reward of a meal of food following each milking. This system of rewarding cows for entering the automatic milking parlour includes recording cows' entry so that any cow not presenting itself can be checked for signs of ill-health.

The composition of milk changes during lactation. At calving the first milk, colostrum, is particularly rich in fat, protein, immunoglobulins, minerals and vitamins. In early lactation, when the volume of liquid produced is at its greatest, the concentration of solids in milk is usually at its lowest. The concentrations of milk fat and protein increase progressively as the volume of milk secreted is reduced later in the lactation.

Metabolic disorders are most likely to occur in early lactation. The major risks are hypocalcaemia (milk fever), hypomagnesaemia (lactation tetany or grass tetany) and acetonaemia or ketosis (twin lamb disease). Hypocalcaemia is most likely to occur soon after calving, when the output of calcium in milk is suddenly increased and the animal cannot absorb sufficient dietary calcium or mobilize sufficient reserves of calcium from body stores to meet the increased requirement. Immediate treatment with a readily available source of calcium, coupled with supplementary calcium in the diet, usually alleviates the condition. Careful management of the mineral nutrition of the cow during the dry period can reduce the risk and incidence of milk fever. Hypomagnesaemia can also occur soon after calving and is often associated with the start of the grazing season, when the animal is presented with herbage of lower magnesium concentration than the previous winter diet. The condition can also occur following a short period of inappetence, when magnesium intake is suddenly reduced. Hypomagnesaemia is prevented by supplementing the diet with magnesium. Acetonaemia is caused by a deficiency of energy in the diet and may be triggered by a period of inappetence caused by an infectious disease or sudden deprivation of food, or by a chronic deficiency of energy in the diet itself. Prevention of acetonaemia is by ensuring that the animal's appetite is maintained at all times, and that the early-lactation diet is relatively high in readily digested sources of energy. (JMW)

Cow pregnancy Pregnancy in the cow lasts from the time of fertilization of an ovum or ova in the oviduct until the resulting conceptus leaves the uterus. In a successful pregnancy a live calf, with its associated placenta, is born approximately 9 months after fertilization. The average length of gestation is typically 280–285 days but depends to some extent on the breed, particularly of the sire. For example, when used to inseminate Friesian cows, bulls of such large breeds as the Charolais, Simmental or Chianina tend to produce longer gestation periods than Friesian or Hereford bulls.

A cow normally ovulates one ovum at each oestrous period. Occasionally two or more are ovulated (*see* **Twinning**). More rarely, a fertilized embryo may divide to form identical twins.

Immediately after fertilization, the ovum begins to divide, forming a solid cluster of cells or blastomeres known as a morula (mulberry shape). This process takes 5 or 6 days, during which the embryo continues its passage down the oviduct and enters the uterus. From about day 6 after fertilization, the ovum hollows out to become a blastocyst, which consists of a single spherical layer of cells, the trophoblast, with a hollow centre and an inner cell mass at one edge. The inner cell mass is destined to form the embryo, whilst the trophoblast provides it with nutrients and will form the fetal component of the placenta. At about day 8 the blastocyst 'hatches' from its shell (the zona pellucida) and begins to elongate rapidly. From about day 14 the development of the so-called germ layers begins within the inner cell mass. These are termed the ectoderm, mesoderm and endoderm. The ectoderm gives rise to the external structures such as skin, hair, hooves and mammary glands and also the nervous system. The heart, muscles and bones are eventually formed from the mesoderm whereas the other internal organs are derived from the endoderm layer. By day 45, formation of the primitive organs is complete.

The embryo is able to exist for a short time by absorbing nutrients from its own tissues and from the uterine fluids, but it ultimately becomes attached to the endometrium by means of its membranes through which nutrients and metabolites are transferred from mother to fetus and vice versa. In the cow, antibodies cannot pass the placental barrier and the calf is thus dependent on the first milk (colostrum) produced by its mother at parturition to acquire immunity from her. The attachment process is known as implantation and may begin as early as day 20, although definitive placentation does not occur until days 40–45. If the cow is carrying twins, the placentae and their blood supplies tend to grow together. Thus, sex hormones from a male which is co-twin to a female are likely to interfere with the development of her sexual organs, resulting in a sterile female called a freemartin. The male may be affected to a lesser extent by hormones from the female. Twin calves are somewhat less likely to survive than singles, especially if they are developing in the same uterine horn.

Fetal growth is exponential throughout gestation, the rate increasing as pregnancy progresses. Thus, fetal requirements for energy, protein and minerals increase rapidly, especially during the last third of gestation (see table).

Deposition of nutrients and energy in the uterus of the cow. (Source: McDonald *et al.,* 1995.)

	Deposited in uterus (per day)			
Days after conception	Energy (kcal)	Protein (g)	Calcium (g)	Phosphorus (g)
100	40	5	–	–
150	100	14	0.1	–
200	235	34	0.7	7
250	560	83	3.2	22
280	940	144	8.0	44
Maintenance[a]	7000	300	8.0	12

[a] Approximate net daily maintenance requirement of a 450 kg cow.

Uptake of nutrients by the uterus and its contents is less efficient than for the cow's body in general, so that nutritional requirements to meet the demands of pregnancy in the cow are actually higher than the amounts deposited in the uterus. Furthermore, fasting metabolism during pregnancy is higher than that in non-pregnancy, because of a higher basal metabolism in the mother herself rather than the heat produced by the fetus. This may be a response to changes in hormone levels during pregnancy and it increases throughout pregnancy. This, together with the liveweight increase that should occur, leads to a gradual rise in the maintenance energy requirement. Thus, the requirement for energy in pregnancy is increased by far more than would be deduced from the storage of energy in the fetus. Nevertheless, in early pregnancy, nutritional requirements for pregnancy per se are small, especially in relation to the requirements for maintenance and for milk production in the mid-lactation cow. It is only in the last 3 months of pregnancy that special dietary provision has to be made for the growth of the fetus. At this stage, net requirements for protein and minerals such as calcium and phosphorus are quite substantial. Additionally, in the last 2 weeks, when mammary growth is fastest, a relatively modest 45 g protein day^{-1} is deposited in the udder. Net energy requirements are still quite small in relation to maintenance requirements. Furthermore, in the dairy cow, there will be no energy demands for lactation in the last 2 months or so of pregnancy. Dry pregnant dairy cattle normally have a dry-matter appetite in excess of their requirements. It is thus relatively easy for a cow to gain weight during this period and it is usually necessary to restrict energy intake at this time to avoid the cow calving at too high a condition. The latter can lead to calving difficulties and subsequent metabolic disorders, such as fatty liver syndrome, which can seriously affect production and reproductive performance. Intake can be restricted by feeding a single forage, such as grazed grass or silage, or by including chopped cereal straw in the diet to raise its cell wall content. (PJHB)

Reference and further reading

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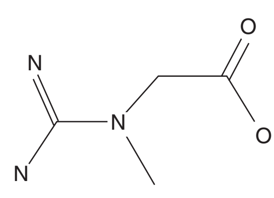
Cowpea A leguminous plant (*Vigna unguiculata*) grown in the semi-arid and sub-humid tropics, primarily for their seeds. These contain 200–300 g crude protein kg^{-1} and have an apparent metabolizable energy of about 14 MJ kg^{-1} for both sheep and poultry. The proteins are relatively low in sulphur amino acids. The seeds contain protease inhibitors: this limits the usefulness of raw seeds. The protease inhibitors can be inactivated by heat treatment. Cowpeas may be used as a green or dried fodder with a protein content of about 120 g kg^{-1}. (TA)

Crambe An annual of the *Brassica* group, native to the Mediterranean area and cultivated in North and Central America. *Crambe abyssinica* is grown for its oil, which is used in industry and contains 50–60% erucic acid. The residual crambe seed meal has value as a supplement in livestock and poultry feeds because of its high protein content (300–400 g kg^{-1}) and well-balanced amino acid content. However, the seeds contain anti-metabolites including goitrogens, and unprocessed meal is limited to 5% inclusion in diets for adult ruminants and is unsuitable for inclusion in non-ruminant feeds. (JKM)

Crazy chick disease (encephalomalacia): *see* Vitamin E

Creatine $HN{=}C(NH_2){\cdot}N{\cdot}(CH_3){\cdot}CH_2{\cdot}COOH$. Creatine is produced in a number of steps, first in the kidney and then in the liver, from arginine, glycine and methionine. It is converted to creatine phosphate in muscle (ATP + creatine ⇌ creatine phosphate + ADP), where it serves as an energy reserve to convert ADP to ATP during times of high ATP use. Creatine is oxidized and then excreted in the urine as creatinine.



(NJB)

See also: Adenosine triphosphate

Creatinine The anhydride of creatine and the end-product of creatine breakdown (by loss of H_2O and P_i) in muscle followed by total excretion by the kidney. Creatinine excretion is related to muscle mass and thought to be constant over 24 h. For this reason it is used in clinical settings as a basis to calculate total 24 h urine excretion from a single urine sample. (NJB)

Creep feeding The feeding of supplementary diet to suckling animals, most commonly applied to piglets. This practice allows piglets to compensate for any deficiencies in sow milk production and become gradually accustomed to eating solid food; it also induces development of the digestive enzymes necessary for breakdown of complex carbohydrates on which they will be dependent for energy after weaning. Because of the high nutritional quality of sow milk, piglets generally consume very little solid food before 3 weeks of age. However, if weaned later than this, creep feed will be consumed increasingly as milk supply declines and becomes inadequate. Thus, whilst creep feeding of piglets weaned at 3 weeks of age or younger is generally of little benefit, piglets weaned at later ages will show increased growth rate both before and after weaning.

There are large and unexplained differences, both within and between litters, in the quantity of creep feed consumed. To achieve good intake, it is necessary to feed a highly digestible and palatable diet containing a high proportion of milk products. Intake is further encouraged by freshness of feed, achieved by feeding little and often, and by presentation in a feeder in which the diet is easily visible and accessible. (SAE)
See also: Piglets

Crop Synonymous with ingluvies, a thin-walled extension of the oesophagus of birds, located to the right side of the neck. When full of food, the crop is easily palpated. Its function is to store ingested food when the gizzard is full. Movement of its muscular walls allows the food to soften and swell before chemical digestion in the proventriculus. The crops of well-fed birds are rarely empty. (MMax)

Crop fractionation: see Fractionation, green-crop

Crop residues: see Stover; Straw; Winemaking residues. *See also:* individual crop

Cruciferae **Cabbage** (*Brassica*) family, consisting of some 300 genera and 3000 species, including cabbage, sea cabbage, **kale**, Brussels sprouts, **cauliflower**, broccoli, **kohlrabi**, **oilseed rape**, **mustard**, radish, **crambe** and related weeds and herbs. (JKM)

Crude fibre A collective term for complex carbohydrates, mainly celluloses and lignin, that are insoluble in water, dilute acid and dilute alkali. There are various ways of estimating fibre, each of which defines a somewhat different fraction. In the proximate analysis of foods (the Weende system) crude fibre is measured by digesting a feed sample successively with dilute acid (1.25% sulphuric acid) and dilute alkali (1.25% sodium hydroxide). Soluble components such as sugars, starch, fat and protein are thereby removed, leaving an insoluble residue. The weight loss on ignition of this dried residue represents crude fibre. Other methods for examining complex, insoluble carbohydrate in feeds have involved the use of a neutral detergent that removes soluble material and leaves behind cellulose, hemicellulose and lignin (neutral detergent fibre). Subsequent boiling with an acid detergent hydrolyses the hemicellulose, leaving behind cellulose and lignin (acid detergent fibre). Oxidation of lignin with potassium permanganate leaves cellulose and ash. Ignition of this residue gives a value for cellulose. (CBC)

Crude protein The crude protein content of a feed, or other biological material, is defined as its N content multiplied by the factor 6.25. The value of this factor is based on the observation that N occurs in different proteins in a fairly constant proportion, 16% on average. In determining the crude protein content of a material its N content is measured, usually by a Kjeldahl procedure. Crude protein is not an exact measure of the protein content of a material, because different proteins have different proportions of amino acids and their N content may thus vary a little from 16%,

and also because not all the N present in biological materials is in the form of protein. Compounds, other than protein, that contain N are generally classed as non-protein N. These compounds are diverse in structure and function; they include free amino acids, amines, amides, purines, pyrimidines and nitrogenous lipids. The level of non-protein N in most animal feeds and tissues is very small compared with the level of protein N. In addition, much of the non-protein N in feeds may be utilized by animals for the synthesis of non-essential amino acids or, in the case of ruminants especially, for the synthesis of microbial protein. Although the use of an average conversion factor of 6.25 does not lead to an exact value, the protein content of feeds and the protein requirements of farm animals are invariably expressed in this way. (CBC)
See also: Kjeldahl; True protein

Crushing Crushing usually refers to the pressing of oilseeds in order to extract their oil. Oil-rich vegetable seeds, such as **soybean** (20% oil), **oilseed rape** (46%) and **linseed** (39%), are first dehulled and then crushed between rollers or in a screw press. The resultant oil is collected, further purified and used for other purposes. The remaining meal is known as expeller or cake and still contains approximately 10% oil. This can either be used as an animal feed or, more commonly, it undergoes further chemical treatment to extract the remaining oil.

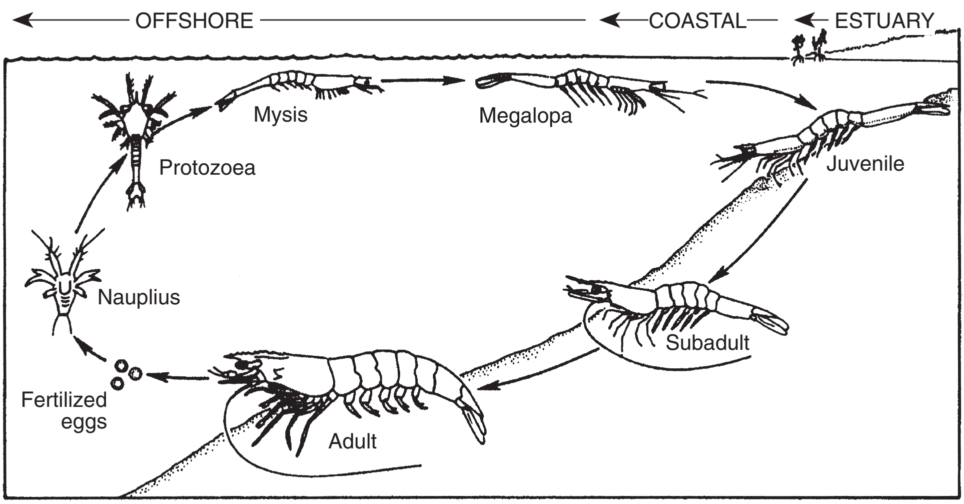
Crushing can also refer to rolling, especially of cereals such as oats and barley, to prepare them for feeding. This is also known as 'bruising'. (MG)

Crustacean feeding Fisheries biologists have always had some interest in the type of food needed by large crustaceans such as lobster, shrimp or prawn. These animals were known to thrive on a variety of molluscs, worms and other invertebrates found in aquatic environments. Aquaculturists interested in culturing crustaceans used this knowledge to maintain crustaceans in the laboratory and, in the case of shrimp and the prawn, to produce limited numbers in ponds where abundant supplies of natural feeds were present. However, in the 1970s as culturists became interested in intensifying the production of crustaceans, natural feeds quickly became a limiting factor. The lack of suitable formulated feeds and, more importantly, the paucity of information on what was needed to make formulated diets for crustaceans, stimulated research interests in aquaculture centres throughout the world.

The initial flurry of nutritional research encompassed a fairly diverse group of crustaceans, including lobster, shrimp, the freshwater prawn and crayfish but today this has narrowed to focus primarily on marine shrimp. Commercial pond production of marine shrimp grew exponentially during the 1980s to become a significant industry in a number of tropical countries. Early culturists almost always used an extensive approach that depended on enriching the natural productivity of the pond ecosystems to provide food for the shrimp. However, intensification in response to continuing market demand necessitated the direct addition of feeds to increase production per pond area. As a consequence, crustacean nutritional studies became centred on providing information applicable to marine shrimp and the need to formulate artificial feeds for their culture.

Culturing of marine shrimp and many other crustaceans is made more difficult by the fact that they have complicated life cycles, with each stage requiring a distinct type of feed.

Such a life cycle is not unusual for crustaceans of aquaculture interest. The nauplius sustains itself on stored yolk but the rest of the hatchery (sub-juvenile) stages have distinctive requirements. Protozoea feed exclusively on algae or other similar-sized microscopic feedstuffs. Increasingly, specific species of algae are cultured to provide an optimum feed for the protozoea stage. After a few days the protozoea stage moults into a mysis stage that requires zooplankton rather than phytoplankton for continuing growth. The shrimp industry is heavily dependent on feeding brine-shrimp nauplii that have been freshly hatched from cysts to support mysis production. Finally, as the mysis stage moults into the megalopa (or post-larva as the industry refers to it) larger types of zooplankton are needed. It is only at this last stage that formulated rations are exclusively used.



Life cycle of a typical marine shrimp species.

Most crustaceans require ten essential amino acids, essential fatty acids (EFA), vitamins and minerals for their growth, survival, reproduction and health. Unlike fish and other terrestrial animals, they require sterols and phospholipids, particularly phosphatidyl choline, as indispensable nutrients. Cholesterol is more effective in promoting growth and development of crustaceans including lobster and penaeid shrimps. Juvenile *Penaeus japonicus* require 1% eicosapentaenoic acid (20:5 n-3) and docosahexaenoic acid (22:6 n-3) in their diet. Several crustaceans (*P. japonicus*, *Penaeus orientalis*, *Macrobrachium rosenbergii* and *Palemon paucidence*) have limited ability to convert linolenic acid (18:3 n-3) to 20:5 n-3 and 22:6 n-3. The recommended dietary phospholipid concentration for various penaeids ranges from 0.84% for *Penaeus chinensis* to 1.25% for *Penaeus penicillatus* and *Penaeus monodon*. Recommended lipid levels for commercial shrimp feeds range from 6% to 7.5% and the level should not exceed 10% of the diet.

Protein is an important component of crustacean diets. The optimum protein level for growth of penaeid shrimps ranges from 28 to 57%. Wide variations in these values among and within species in various studies have been due to the differences in species, size, protein quality, utilization of non-protein nitrogen for energy, stability of pellet, feeding rate, water quality and the contribution of natural food organisms in the pond system. Quantitative dietary requirements for arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine have been determined for *P. japonicus*. Information on carbohydrate utilization by crustaceans is limited. Generally, simple sugars are poorly utilized by shrimp. Starch is commonly used as a carbohydrate source in shrimp diets and its protein-sparing effect on energy utilization has been demonstrated in *P. monodon*. Chitin is the major structural component of the exoskeleton of crustaceans, and some benefit of supplemented chitin (0.5%) but not glucosamine has been reported in *P. japonicus*.

Most vitamins that have been established as essential nutrients for fish and terrestrial animals are also considered to be essential for various crustacean species. The optimum levels reported for penaeid shrimp include the following (IU or mg kg^{-1}): vitamin D, 4000 IU; vitamin E, 100 mg; vitamin K, 30 mg; thiamine, 15–100 mg; riboflavin, 20 mg; pyridoxine, 80 mg; niacin, 400 mg; biotin, 2 mg; vitamin B_{12}, 0.2 mg; inositol, 2000–4000 mg; choline chloride, 600 mg; vitamin C, 20–215 mg. Dietary deficiencies of these vitamins have been shown to cause reduced growth of penaeid shrimp but specific deficiency signs have not been reported except vitamin C. Black death syndrome, characterized by blackened lesions of the digestive tract and other tissues, is a typical sign of vitamin C deficiency.

Dietary deficiencies of most minerals have been difficult to produce in crustaceans because of the presence of these minerals in fresh water and sea water. Marine shrimp, *P. japonicus* do not require calcium, magnesium, iron or manganese, but do require phosphorus, potassium and trace elements in the diet. Although calcium is not an essential element, a calcium:phosphorus ratio of 1:1 to 1:2 has been recommended. Phosphorus requirement increases with the increase in dietary calcium concentration. Most crustaceans moult to grow and certain minerals lost during this process must be replaced from their diet.

Marine and freshwater shrimp farmed in conventional ponds or tank-based systems are generally fed high quality, nutritionally complete, compounded diets for the duration of the production cycle. These feeds are usually formulated to satisfy all of the known nutrient requirements of the cultured species. However, shrimp can also derive a substantial portion of their nutrient requirements from aquatic organisms produced within the culture system. Sinking pellets or crumbles of various sizes, produced by extrusion or steam-pelleting processes, are widely used for feeding shrimp at various stages of development. Water stability of feed is important because they are slow eaters and must break the feed into smaller particles before ingestion. Feed attractants such as amino acids, fish extracts, shrimp by-products, squid, clam and mussel stimulate the feeding response.

The amount of feed offered to shrimp is determined by the size of shrimps, stocking density, availability of natural foods, dietary energy content and water quality. Daily feed allowances may range from approximately 25% of the body weight for larvae to less than 3% of body weight per day at market size. Under laboratory conditions, feeding frequency is reduced from six times per day for larvae to two or three times per day for juveniles to produce optimum growth and feed utilization. It is important to maintain the water quality at an acceptable level to produce a high standing crop of shrimp, therefore, the amount of feed offered should not exceed the capacity of the system to accumulate the waste products and to maintain sufficient levels of dissolved oxygen. (DEC, SPL)

See also: Shrimp; Prawn

Further reading

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Crypts of Lieberkühn Hollows between the **villi** with groups of undifferentiated cells. These are the only cells of the villi that undergo division. Renewal of the villi is provided by the migration of new cells from the crypts towards the tip of the villi. These cells are among the most rapidly regenerating cells of the body. (SB)

Cubes Pellets of compound feed with a diameter > 15 mm. Very large pellets, normally called rolls or cobs, tend to be used for feeding directly on to the ground; the larger size minimizes wastage and theft by birds. (MG)

See also: Compound feed; Feed blocks; Pelleted feed; Pelleting

Curled toe paralysis A condition of chickens caused by riboflavin deficiency. The chickens walk on the hocks, the toes curling under and inward. It is similar to crooked toe disease, the cause of which is not known. (WRW)

See also: Foot diseases; Vitamin deficiencies

Cutting date Date of first cut of the season will depend on the start of grass growth. The term includes cutting for conservation or green feeding and grazing. In intensive systems the use of fertilizers and irrigation can hasten the start of growth, but extensive systems are reliant on adequate rainfall. Ambient temperature must be adequate for growth. (TS)

See also: Seasonal variation

Cutting frequency The frequency with which forage is cut for conservation or 'green-feeding' throughout the growing season. The frequency will affect both yield (longer intervals give higher yields) and quality (shorter intervals give higher protein and lower fibre concentrations). In intensive systems, with adequate rainfall or irrigation, the cutting cycle may be interspersed with grazing. (TS)
See also: Seasonal variation

Cutting height This depends on the grass species and the cutting frequency. Longer intervals between cuts increase height, indicating greater maturity and, unless this is associated with extra leaf material, there could be a reduction in quality (less protein, more fibre). The chosen cutting height will reflect the need for high bulk versus high-quality material. (TS)
See also: Seasonal variation

Cyanide An anion containing carbon and nitrogen, which very readily complexes with ligands. A common form in nature is hydrogen cyanide, which dissolves in water to form hydrocyanic acid. This smells of bitter almonds and can be detected in the breath of affected subjects. It is extremely toxic, causing pulmonary failure as a result of the capacity of the cyanide ion to bind with cytochrome oxidase and reduce the oxygen-carrying capacity of the cells. Cyanide also stimulates the chemoreceptors of the carotid and aortic bodies, causing hyperpnoea. Death is usually caused by respiratory arrest, however, rather than cardiac irregularities. Following ingestion of cyanogenic compounds, toxic symptoms appear within 1 h and so urgent treatment is essential. Treatment is by intravenous injection of sodium nitrite, which is converted to a tolerable amount of methaemoglobin that has a stronger affinity than cytochrome for the cyanide. To prevent the cyanmethaemoglobin complex releasing cyanide, a second injection of sodium thiosulphate is required, which invokes the enzyme rhodanese to convert the cyanide to the excretable thiocyanate. (CJCP)

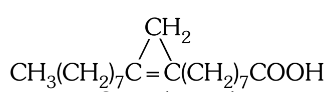
Cyanocobalamin: *see* Cobalamin

Cyanogenic glycosides Cyanogenesis is the process by which plants release hydrogen cyanide (HCN) from endogenous cyanide-containing compounds. It is thought to play a role in plant defence against generalist herbivores. In ruminants, hydrogen cyanide is formed in the rumen and absorbed into the bloodstream. A metabolite of hydrogen cyanide, thiocyanate, can be detected in urine after 1–2 days and can be used in diagnosis.

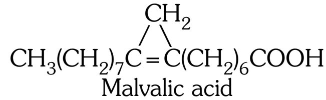
Cyanogenic glycosides are common in tropical fodder trees, which may make them unpalatable and can interfere with nutrient utilization. The cyanogenic glycoside, prunasin, is the toxic component in a number of browse species (serviceberry, *Amelanchier alnifolia*, and chokecherry, *Prunus virginiana*) and also in the eucalyptus tree (*Eucalyptus melanophloia*). Drying, soaking, leaching and fermentation are simple means of detoxifying these potential feed sources. Although grasses generally contain few intrinsic toxins, sorghum does have significant concentrations of cyanogenic glycosides. Cassava (*Manihot esculenta*) roots contain two potent cyanogenic glycosides: linamarin and lotaustralin. Cassava can be fed to livestock only after detoxification by fermentation, boiling or ensiling. Similarly, linseed contains linustatin and neolinustatin, which must be detoxified before feeding. (CJCP)

Cyanogens: *see* Cyanogenic glycosides

Cyclopropenoic fatty acids Naturally occurring cyclopropenoic fatty acids, sterculic and malvalic acid, are found in stercula and cotton seeds.



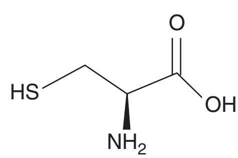
Sterculic acid
8-(2-octacyclopropen-1-yl)octanoic acid



Malvalic acid
7-(2-octacyclopropen-1-yl)heptanoic acid

These compounds are potent inhibitors of Δ9 desaturase, which converts stearic to oleic acid. Their effect is to alter the permeability of membranes. In laying hens, a diet containing sterculic acid gives rise to a condition known as pink–white disease when pink ferroproteins pass from the yolk into the white. Cottonseed oil is the most important edible oil containing cyclopropene fatty acids (concentration range from 0.6 to 1.2%) but for human consumption the oil is processed to reduce the level to 0.1 to 0.5%. (JEM)

Cysteine An amino acid ($HS{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 121.2) found in protein. It is synthesized from methionine (which provides the sulphur) and serine (which provides the carbon skeleton) in the metabolic process known as trans-sulphuration. Of the cysteine not used in protein synthesis or catabolized (to CO_2, SO_4^{2-} and H_2O), some is used for the synthesis of glutathione, some for the synthesis of taurine and some for the synthesis of phosphoadenosine phosphosulphate. Many of the sulphydryl groups of cysteine that exist in protein are oxidized, with formation of a disulphide bridge between two cysteine residues, forming the dimeric amino acid, cystine. Cysteine (or cystine) is capable of supplying up to 50% of dietary need for sulphur amino acids (methionine + cysteine) of growing animals and an even larger portion (up to 80%) of the sulphur amino acid need of adult animals.

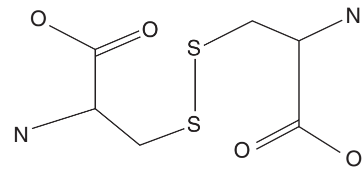


(DHB)

See also: Cystine; Glutathione; Methionine; Taurine

Cysteine dioxygenase One of two enzymes involved in the conversion of L-cysteine to pyruvate. Cysteine dioxygenase, a cytoplasmic enzyme, converts L-cysteine ($HSCH_2{\cdot}CHNH_3^+{\cdot}COO^-$) to L-cysteine sulphinate using molecular oxygen. In this process the sulphur atom of L-cysteine is converted to sulphate (SO_4^{2-}) and the carbon skeleton becomes pyruvate. (NJB)

Cystine An amino acid ($COOH{\cdot}NH_2{\cdot}CH{\cdot}CH_2{\cdot}S{\cdot}S{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$) found in protein. A disulphide bridge within or between peptide chains can be formed when two cysteine groups combine. Following digestion (breaking of peptide bonds), cystine or cystine-containing small peptides are released. Cystine that exists in food proteins, particularly heat-processed proteins, is less digestible (available) than either methionine or cysteine.



(DHB)

See also: Cysteine

Cystinuria (cysturia) An inherited disease of amino acid transport in the renal tubules. Urinary concentrations of cystine, lysine, arginine, ornithine and cysteine–homocysteine-mixed disulphide are elevated. Because of its low solubility, cystine forms calculi in the tubules leading to obstruction, infection and ultimately renal insufficiency. (NJB)

Key reference

Segal, S. and Their, S.O. (1989) Cystinuria. In: Scriver, C.C., Beaudet, S.L., Sly, W.S. and Valle, D. (eds) *The Metabolic Basis of Inherited Disease*. McGraw-Hill, New York.

Cytochrome A class of iron-porphyrin-containing proteins. Cytochromes are intimately associated with the respiratory chain involved in electron transport and the oxidation–reduction reactions of cell respiration. Cytochromes in the mitochondria are a direct link to the use of molecular oxygen as a terminal electron acceptor in aerobic metabolism leading to the production of ATP. (NJB)

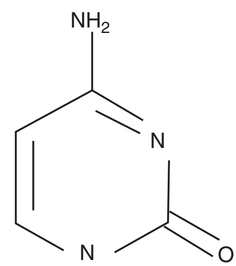
Cytokines A family of low molecular weight (~ 30,000) proteins secreted by various cells with autocrine and paracrine actions.

Cytokines are involved in the coordination of cellular responses in various pathways including immune responses, haematopoietic cell signalling, calcium homeostasis, skeletal modelling and remodelling, wound healing and tissue repair, growth and ordinary replacement of aged cells. Cytokines regulate the intensity and duration of a response by stimulating or inhibiting activation, proliferation or differentiation of cells by regulating the secretion of proteins or other cytokines. Cytokines include interleukins, interferons, colony-stimulating factors and tumour necrosis factors. The specificity of cytokines and cell response is via specific cell surface receptors. For example, white blood cells (macrophages) and other cells (activated T helper cells, T_H) act by secreting cytokines that bind receptors on the surface of specific cells to stimulate proliferation, differentiation or both. Interleukins may induce pro-inflammation responses, killer cell activation and immunoglobulin production while interferons may prevent viral replication. At least 18 interleukins, three interferons and two tumour necrosis factor subclasses have been identified. The two tumour necrosis factors (α and β) have cytotoxic effects on tumour cells. Still other cytokines exist and more will probably be identified. (TDC)

Key reference

Goldsby, R.A., Kindt, T.J. and Osborne, B.A. (2000) *Kuby Immunology*, 4th edn. W.H. Freeman and Co., London.

Cytosine A pyrimidine, $C_4H_5N_3O$, found in both RNA and DNA. In RNA it is cytidine 5′-monophosphate (CMP); when in DNA it is deoxycytidine 5′-monophosphate (dCMP). Cytidine is involved as cytidine diphosphate choline (CDP-choline) in phosphatidylcholine synthesis and as CDP-diacylglycerol in phosphatidylinositol biosynthesis.



(NJB)

D

D value A digestibility coefficient, usually expressed in terms of the dry matter (DMD), organic matter (OMD) or digestible organic matter contained in the dry matter (DOMD). These terms are most often used in forage evaluation for ruminants and their definition needs care as they are not interchangeable. In the UK the 'D' value is usually expressed as DOMD in practical publications while OMD or DMD are used in scientific research.

DMD = dry matter digestibility

OMD = organic matter digestibility

DOMD = digestible organic matter contained in the dry matter

where OM = organic matter = loss on combustion = dry matter (DM) minus ash; and DOM = digestible organic matter = OM in feed minus OM in faeces.

$$DMD = \frac{DMfed - DMfaeces}{DMfed}$$

$$OMD = \frac{OMfed - OMfaeces}{OMfed}$$

$$DOMD = \frac{OMfed - OMfaeces}{DMfed} = OMD*\%OMfood$$

These terms can be expressed as digestibility coefficients (e.g. 0.7) or as percentages (e.g. 70%). Whereas DOMD can be calculated from OMD and the OM percentage in the food, DMD cannot be directly calculated from OMD. Digestibility determined *in vivo* is apparent digestibility, since excreta contain endogenous matter. Most of these digestibility coefficients can also be applied to the two-stage rumen-pepsin *in vitro* technique devised originally by Tilley and Terry (1963) and applied by Alexander and McGowan (1966). Digestibility as D value (DOMD) can be scaled into metabolizable energy (ME) using an assumed value for the gross energy of the digestible organic matter. If this is taken as 19 MJ kg^{-1}, ME (MJ kg^{-1} DM) = 0.15 DOMD%. (IM)

References

Alexander, R.H. and McGowan, M. (1966) The routine determination of *in vitro* digestibility of organic matter in forages – an investigation of the problems associated with continuous large-scale operation. *Journal of the British Grassland Society* 21, 140.

Tilley, J.M.A. and Terry, R.A.A. (1963) A two-stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society* 18, 104.

Dairy cattle Bovine animals bred and kept principally for milk production. (PCG)

Dairy products Milk and products manufactured from milk. Liquid milk is heated for short periods of time to kill pathogens. Pasteurized milk (72°C for 15 s) can be stored for up to 5 days. UHT (ultra-heat-treated) milk (132°C for 2 s) can be stored for up to 12 months; sterilized milk (115–130°C for 10–30 min) can be stored for several months. Heat treatment denatures the whey proteins in milk, giving it a boiled taste that is particularly noticeable in UHT and sterilized milk.

The butterfat contents of liquid milks are 3.9% (whole), 0.1% (skimmed), 1.6% (semi-skimmed) and > 4% (Channel Islands breeds). In homogenized milk the fat globules are broken up and remain distributed throughout the milk so that it does not form a cream layer.

Cream is separated from whole milk mechanically and either sold with a fat content between 15 and 45% or churned into butter. Butter manufacture produces buttermilk as a by-product.

Yoghurt is made by fermenting milk with bacteria that produce lactic acid to coagulate the casein; sugar and fruit or flavouring may then be added.

Cheese is manufactured from coagulated milk proteins (*see* **Casein**) and varying proportions of fat, water and salts. A general method is to coagulate the casein to produce curds and whey, cut and scald the curd, drain off the whey, press, salt and ripen the curd. There are hundreds of varieties of cheese, which obtain their individual characteristics by variations in the production process. (PCG)

Databases Collections of valuable measurements that pertain to a specific production system. The most common uses of databases in animal production are in tables of nutrient composition of the large range of feedstuffs that may be used in animal feeds. These data are used in feed formulation software packages. (SPR)

Date Dates are the fruit of the palm *Phoenix dactylifera*. When mature at 10–15 years old, date trees yield 45–90 kg of dates per tree. The leading date-producing and exporting countries are Saudi Arabia, Egypt, Iran and Iraq. Dates are usually grown for human consumption but may be fed to goats and cattle if they fall from the tree or are of substandard quality. The seeds can be pressed for oil, leaving a residue useful for stock feed. Date trees are drought resistant. The young leaf spines are soft and the branches can be browsed or fed to cattle and goats. (JKM)

Deamination The process by which the nitrogen from amino acids is released as ammonium nitrogen. This can occur by direct production of ammonium nitrogen from the metabolism of cysteine, glutamine, glycine, histidine, methionine, serine, threonine and tryptophan by specific enzymes. Ammonium nitrogen can be produced directly from glutamic acid by L-glutamic dehydrogenase, which links the transamination of nitrogen between amino acids to nitrogen excretion. Ammonium nitrogen can be incorporated into urea for detoxification and excretion. (NJB)
See also: Ammonia; Nitrogen metabolism

Debeaking Erroneous term for beak-trimming, a procedure commonly used in the poultry industry to reduce feather-pecking and cannibalism. Recent studies have shown that the beak is well innervated and therefore the practice is debatable. (MMax)

Decarboxylation The removal of a carboxyl carbon from a substrate with the ultimate production of CO_2. Carbon dioxide production by decarboxylation occurs in the breakdown of carbohydrate-related molecules such as pyruvate, TCA cycle intermediates such as isocitrate and α-ketoglutarate, amino acids such as glutamic acid (in the production of γ-aminobutyrate) and other amino acids (or related compounds) in the production of biogenic amines. (NJB)

Deer The cervid family branched from the ruminant stock some 30 million years ago. There are now 17 living genera, some (especially *Cervus*) still rapidly speciating. Deer are native to all continents except Australasia and Africa south of the Sahara, ranging from equatorial to arctic regions. They occupy a wide variety of habitats, forest, open scrubland, mountain and tundra, and so their natural diets and dietary adaptations vary greatly (Hofmann, 1985).

Date palm nutrient composition.

		Nutrient composition ($g\ kg^{-1}$ DM)					
	Dry matter ($g\ kg^{-1}$)	Crude protein	Ether extract	Crude fibre	Ash	Starch and sugar	NFE
Fruit	660–850	11–25	4–17	39–102	81	760	–
Fresh leaves	–	116–275	15–42	14–23	7–13	–	41–58

NFE, nitrogen-free extract.

The social behaviour of forest species, such as roe, moose, white-tailed deer, mule deer and muntjac (territoriality, small family groups, browsing habits), makes them unsuited to intensive management or domestication. However, those adapted to more open habitats, such as red deer, wapiti, sika, sambar, fallow and reindeer, show herding behaviour and a hierarchical society, mobility and versatile feeding habits, and recently they have been successfully domesticated as farm animals. Deer may also be managed extensively so as to exploit their adaptation to their natural habitat on a low-cost basis. Procedures such as disease control, selective culling and supplementary feeding may then be used to increase their productive potential. In red deer, one adult stag will mate with 20–40 hinds; hinds remain fertile for more than 12 years; and surplus animals may be removed for sale or slaughter at 15 months of age (Blaxter *et al.*, 1988). As a result, a managed herd of deer can be many times more productive than a fully wild herd.

Some typical dietary requirements for domesticated red deer are shown in Table 1. Compared with sheep, red deer have a high metabolic rate. They also generally show a shorter retention time of food in the gut and so digest roughage diets a little less well. As a result their maintenance requirements are rather high (Kay and Staines, 1981).

In the northern hemisphere, red deer calves are born in May or June. They may be weaned from their dam after taking colostrum and reared on a milk substitute. This should be similar to that used for rearing lambs, for deer milk is much richer than cow's milk (Table 2). Alternatively they may be left with their dam at pasture until housed for the winter, or weaned at about 8 weeks of age on to a fattening diet, concentrates plus some roughage, similar to that used for sheep or cattle. Rapid growth and an excellent conversion efficiency (food intake for weight gain) can be achieved (Blaxter *et al.*, 1988; Adam, 1994). Adult red deer will readily take a wide variety of foods, including forage crops and browse, hay and silage, root and fruit crops, pelleted or loose concentrates, protein supplements and mineral–urea blocks. Care should be taken, of course, to introduce new foods gradually.

Deer from temperate or northern regions show a marked seasonality not only in their reproductive cycle but also in growth and fattening, appetite and metabolic rate. They lay down fat and they lactate during summer; during winter, calf growth slackens and adults mobilize their fat. These cycles help to match food requirement to the natural availability of forage. Both antler growth and peak milk production occur during the summer and place similar demands on mineral intake (Table 3). Since food intake is naturally high at this time, such mineral requirements are readily met.

Deer, compared with sheep and cattle, can produce an attractively lean carcass with heavy and highly priced hindquarters. This, together with the popular image of venison, ensures a good price for deer meat, provided that it is hygienically produced and marketed, with due regard for animal welfare. As well-fed adults (but not yearlings) lay down substantial fat reserves by the end of summer, this is an unsuitable time for their slaughter. Other products are antler velvet (of supposed medicinal value), skins and soft dress leather, while the aesthetic appeal of these lean and agile animals serves to promote tourism. (RNBK)

Table 1. Dietary requirements of red deer (from Adam, 1994).

	Dry matter (kg day^{-1})	Crude protein (g kg^{-1} DM)
Calves		
6–8 months (winter)	1.3	100
12–15 months (summer)	2.2	120–170
Hinds		
Pregnant (winter)	2.0	100
Lactating (summer)	3.0	170
Stags		
Maintenance (winter)	3.0	100
Increasing liveweight (summer)	4.0	120

In the northern hemisphere, red deer calves are normally born in May or June.

Table 2. Composition of milk, mid lactation (g kg^{-1}).

	Crude protein (N × 6.38)	Lactose	Fat	Ash	Dry matter	Energy (kJ kg^{-1})
Red deer	75	45	100	11	230	6500
Dairy cow	35	48	35	9	130	2900

Table 3. Minerals (g) deposited in antlers by a 125 kg red deer stag, and secreted in milk by a 80 kg red deer hind during full lactation (Kay and Staines, 1981) and recommended dietary content (Adam, 1994).

	Ca	P	Mg
Antlers	350	160	5
Milk	370	300	20
Recommended dietary content (g kg^{-1} DM)	3–6	2–4	1–2

References and further reading

Adam, C.L. (1994) Feeding. In: Alexander, T.L. and Buxton, D. (eds) *Management and Diseases of Deer.* The Veterinary Deer Society, London, pp. 44–54.

Blaxter, K., Kay, R.N.B., Sharman, G.A.M., Cunningham, J.M.M., Eadie, J. and Hamilton, W.J. (1988) *Farming the Red Deer.* HMSO, Edinburgh.

Hofmann, R.R. (1985) Digestive physiology of the deer – their morphological specialisation and adaptation. In: Fennessy, P.F. and Drew, K.R. (eds) *Biology of Deer Production.* The Royal Society of New Zealand, Wellington, pp. 393–407.

Kay, R.N.B. and Staines, B.W. (1981) *The Nutrition of the Red Deer.* Commonwealth Agricultural Bureaux, Slough, UK.

Wemmer, C.M. (ed.) (1982) *Biology and Management of the Cervidae.* Smithsonian Institution Press, Washington, DC.

Deficiency diseases A deficiency normally refers to an inadequate supply of one or more specific nutrients, rather than a general restriction of intake or a deficiency in any other aspects of an animal's environment. There are seven major classes of nutrients – protein, carbohydrate, minerals, vitamins, lipids, fibre and water – a deficiency of any of which can cause characteristic disease symptoms, such as iron deficiency causing anaemia. Some deficiencies cause asymptomatic disorders that reduce vigour, activity and production in farm animals, e.g. restrictions in energy or sodium intake.

The severity of a nutrient deficiency will depend on an animal's requirement, so that a cow in early lactation may be deficient in energy when offered a diet with an energy density that would be adequate for a non-lactating cow. A deficiency becomes a disease when the welfare of the animal is reduced by the nutrient deficit. Thus, depending on how welfare is defined, an animal either fails to cope with the deficiency or feels unwell as a result. In many circumstances the deficiency is temporary, until homeostatic mechanisms are employed that allow the animal to cope. These may be by increasing the absorption of the deficient nutrient or by reducing output, e.g. of milk. Even if they are only temporary, diseases would normally exist for several days, or regularly for a period of each day, to be classified as such. Theoretically deficiencies can only exist for elements or compounds that are *required* by the animal, but in recent years an essentiality has been demonstrated for many elements that were not previously believed to be required by animals, even though it has not so far been possible to quantify the requirement.

The severity of the deficiency is mainly determined by the animal's capacity to store the element and the fluctuation in intake. Fluctuations in intake may arise from a variable food supply in farm animals foraging on rough grazing or from a deliberate restriction of intake for economic reasons. Towards the end of winter, the availability of feed may be deliberately restricted by farmers in anticipation of the growth of grass in spring. Food availability and intake may also fluctuate with the physiological state of animals; for example, dry sows might be restricted to prevent them from becoming obese. Storage organs, such as the liver for copper and zinc, or the bones for calcium, may accumulate toxic elements in place of essential ones, such as cadmium being stored in the liver and lead in bones, exacerbating or perhaps even triggering a deficiency in the essential element.

If clinical symptoms are evident, the aetiology of a deficiency disease can usually be traced to the nutrient in deficit. However, some farm animals, such as cattle and sheep, having evolved from prey species, do not show overt signs of pain and so diagnosis can be difficult.

The animal's status with regard to many minor or trace nutrients often depends on the intake of other nutrients. Some may have generic effects that influence the availability of several elements, such as the effect of ascorbic acid on the availability of many heavy metals, particularly iron, or the adverse effect on the immune system of selenium or vitamin E deficiencies. Others rely on the similarity in the chemical properties of different elements for their interdependency, e.g. cadmium and sodium, or the formation of stable complexes in the digestive tract, e.g. copper thiomolybdates in ruminants.

Samples that can be taken from farm animals to diagnose a deficiency include blood plasma, saliva, faeces or urine. Occasionally tissue biopsies (e.g. liver) are performed for diagnostic purposes. Occasionally hair, hoof and other tissues are sampled to give a historical record of the progression of the deficiency.

Another aid to diagnosis of a deficiency disease is the animal's behaviour. Many animals that are short of specific nutrients develop an opportunistic appetite to try to obtain the nutrient in deficit. This has been demonstrated for many species whose members are short of sodium, for chickens that are short of calcium and for cattle that are deficient in phosphorus. Sometimes the novel appetite is focused on learnt methods of obtaining the nutrient in deficit; for example, animals with sodium deficiencies lick each other's skin to get salts.

As agriculture has developed in recent years, some nutrients have become routinely deficient in farm animals. For example, the milk yields of dairy cows have increased considerably, leading to a significant likelihood that the cow will be deficient in calcium in the first week of lactation. After a few days, it is able to mobilize the necessary calcium from bones and a clinical disorder is usually avoided. Farmers now often prepare cows for the calcium demands of early lactation by feeding them a calcium-deficient diet for up to 1 month before parturition. This entrains the calcium mobilization pathways in advance of the period of increased requirements. Another example is the deficiency in sodium intake, which arises when large quantities of potassium are used on pasture to stimulate grass growth. Potassium in soil is antagonistic to sodium uptake by plants, and potassium in the rumen is antagonistic to magnesium absorption. This leads to both sodium deficiency, which is easily rectified by salt supplements or sodium fertilizers, and magnesium deficiency, which is not so easily rectified. Magnesium deficiency, or hypomagnesaemia, can sometimes be rectified by adding magnesium salts to the drinking water or feed, or by broadcasting calcined magnesite on the pasture, but none of these mechanisms *ensures* adequate magnesium intake by cattle. As the onset of the disease is sudden, unlike sodium deficiency, the mortality rate is high. Herbivores have an acute appetite for sodium, unlike magnesium and calcium, which suggests that sodium deficiencies have been common throughout their evolution and indeed they are still observed in wild cattle in Southeast Asia.

Calves reared on milk-based diets for veal production may routinely suffer from iron deficiency, manifested as anaemia, because the milk has a low supply of iron. The consequences for the animal – lethargy and fatigue – are not likely to affect the animal's survival adversely and may even increase feed conversion efficiency. However, deficiencies that result from an unsuitable farming system are now increasingly believed by the public to be unacceptable, and in the European Union minimum iron levels in blood are now legally established. Suckling piglets are also prone to iron deficiency and are routinely given an iron injection soon after birth.

Some elements, such as selenium and iodine, can be given to farm animals so that their products are rich in these elements and human consumers will be more likely to obtain an adequate supply. An increasingly important area of research is the extent to which genetic differences in absorption provoke deficiency diseases. The differences have been identified in the absorption of copper, but a better understanding of mineral absorption is needed before genetic differences can be exploited in practice. (CJCP)

Dehull To remove the kernel coat or pericarp of a seed. (JMW)

Dehydration A deficit of water in the body. Dehydration may result from a lack of drinking water, excessive evaporative loss or diarrhoea. (JMW)

Dehydration, body A state in which the body is in negative water balance, i.e. when it loses more water than is ingested as liquid and in food. It may arise from either insufficient intake of water or excessive loss, e.g. from diarrhoea and vomiting, beyond the ability of the kidneys to compensate. The initial response of the body to negative water balance is the withdrawal of water from the interstitial fluid space in an attempt to maintain normal blood volume. Connective tissue, muscle and skin are most affected, leading to the clinical test of prolonged elevation of a skin fold. More advanced dehydration results in a reduction in blood volume, accompanied by haemoconcentration. Milk yield is depressed in lactating animals. In order to produce more metabolic water, there is an increase in the oxidation of fat, then of carbohydrate and finally of protein. Dehydration can contribute to death, especially when combined with another clinical condition, e.g. an electrolyte imbalance.

Racehorses and eventer horses can easily become dehydrated, since they lose large quantities of hypotonic sweat when exercised, especially under hot conditions. Because of the conflicting stimuli regulating the secretion of renin and angiotensin II, such horses may refuse to drink to correct the resultant dehydration. (ADC)

Dehydroascorbate The oxidized form of L-ascorbate (L-ascorbate $\rightleftharpoons$ L-dehydroascorbate + 2H). It is produced when ascorbate participates in oxidation–reduction reactions in cellular metabolism. (NJB)
See also: Ascorbic acid

Dehydrogenase A class of enzymes involved in metabolic oxidation–reduction reactions. They act by removing hydrogen from a substrate or adding hydrogen to a substrate. These enzymes cannot use oxygen as the acceptor but instead use one of three coenzyme combinations: NAD/NADH, NADP/NADPH, FAD/FADH. These coenzymes link metabolic oxidation to the electron transport chain (a series of dehydrogenases involved in oxidation–reduction steps carried out by cytochromes) and link substrate oxidation with molecular oxygen as the terminal electron acceptor, yielding water. (NJB)

Demand feeding Spontaneous feeding 'on demand', or *ad libitum*, when food availability is unlimited. (JSav)

Deoxynivalenol Deoxynivalenol (DON) or vomitoxin is a mycotoxin of the trichothecene class, produced by *Fusarium* fungi. DON causes feed refusal and vomiting in swine, and feed refusal and oesophageal lesions in poultry. Trichothecenes such as DON tend to be produced in moist grain under cool or cold environmental conditions. Wheat and maize are the grains most commonly contaminated by DON. (PC)

Deoxyribonuclease An enzyme, also called DNase, hydrolysing **deoxyribonucleic acid** (DNA) into nucleotides. A DNase (DNase I; deoxyribonucleate 5′-oligonucleotidohydrolase; EC 3.1.21.1) is purified from pancreatic secretions. Another DNase II is purified from the spleen. (SB)

Deoxyribonucleic acid (DNA) A polymer of deoxyribonucleotides, each consisting of a sugar, deoxyribose, and a nitrogenous base, which is derived from one of two purines, adenine or guanine, and one of two pyrimidines, thymidine or cytosine. DNA can be considered the chemical basis of heredity: the genetic code is the sequence of deoxynucleotides found in the genes that make up chromosomes. DNA is made up of two complementary strands in the form of an α-helix. The genetic code is given by the sequence of deoxynucleotides in DNA, each amino acid being represented by a specific set of three. This code is transcribed to messenger RNA, which specifies the complete amino acid sequence of the protein being synthesized. (NJB)

Deoxysugar A monosaccharide containing less oxygen than the parent sugar. Usually, the terminal $-CH_2OH$ group is replaced by a $-CH_3$ group. In bacteria, more than one hydroxyl group may be replaced with hydrogen, producing di- and tri-deoxysugars. The most abundant deoxy sugar in nature is 2-deoxy-D-ribose, the sugar component of deoxyribonucleic acid. Bacterial lipopolysaccharides can contain L-rhamnose (6-deoxy-L-mannose) and L-fucose (6-deoxy-L-galactose). (JAM)

See also: Carbohydrates; Deoxyribonucleic acid (DNA); Monosaccharide

Depigmentation A pigmentation disorder of the skin, mucous membranes, hair, or retina in which melanocytes in these tissues are affected or destroyed. The brown pigment melanin is produced from the amino acid tyrosine by specialized pigment cells called melanocytes. Copper deficiency causes depigmentation of hair, fur, wool and feathers in animals. Depigmentation may also develop due to hyperthyroidism, adrenocortical insufficiency, alopecia, anaemia, certain infectious diseases, excessive sun exposure or albinism in humans and other animals. (SPL)

Desmosine A unique structure of cross-linked lysine, found only in mature elastin. In the biosynthesis of elastin, three lysine residues are oxidized by the enzyme lysyl oxidase; these combine with a fourth lysine to form the cross-linked structure of desmosine. Desmosine stabilizes the structure of elastin, which contributes to connective tissues its properties of extensibility and elastic recoil. (NJB)

Desoxysugar: *see* Deoxysugar

Detoxification A process by which a toxin is changed to a less toxic compound or by which its poisonous effect is reduced. In ruminants, rumen microbes are the first line of active defence against some plant toxins, e.g. ricin in castor bean, mimosine in *Leucaena*, nitrotoxins in *Astragalus*, nitrates in many forage plants, oxalates in *Halogeton*, phyto-oestrogens in clovers, pyrrolizidine alkaloids in *Senecio* and *Heliotropium*, thiaminase in bracken fern and many mycotoxins. Once absorbed, some toxins can be detoxified by enzymes in the gut and intestinal lining, liver, lungs and kidney.

There are antidotes for a few specific plant poisons. Bracken fern poisoning can be treated by butyl alcohol in cattle or by thiamine in horses, fluoroacetate poisoning by glyceryl monoacetate and pentobarbital, hydrocyanic acid poisoning by nitrite or thiosulphate, nitrates and nitrotoxin poisoning by methylene blue or ascorbic acid, oxalate poisoning by calcium hydroxide or calcium gluconate, Jimson weed poisoning by neostigmine and larkspur poisoning by physostigmine. Potassium permanganate and tannic acid will bind to many alkaloids.

Compounds that bind toxins may also be given. Activated charcoal binds to many toxins in the gastrointestinal system; clay minerals and aluminosilicates also bind molecules of certain sizes and configurations. Cyclodextrins are oligomers of glucose with cylindrical hydrophobic cavities surrounded by hydrophilic margins that encapsulate certain small toxins, such as corynetoxins in annual ryegrass (*Lolium rigidum*).

Vaccines against low-molecular-weight toxins are difficult to create. However, there has been some success in developing a vaccine against phomopsin mycotoxins that cause lupinosis, corynetoxins in annual ryegrass and ergot alkaloids in tall fescue. Vaccines against other toxins are being developed. (MHR)

Deuterium A stable isotope of hydrogen. It has one neutron and one proton and is twice as heavy as hydrogen (2.014 vs. 1.008). Its physical and chemical properties are very similar to those of hydrogen. It is used as a non-radioactive tracer in studies of the molecular metabolism of carbohydrates, fatty acids and amino acids. As a tracer in water (^2H_2O) it is used to measure total body water and body water turnover. As doubly labelled water ($^2H_2{}^{18}O$) it is used to estimate CO_2 production and (by assuming a respiratory quotient) the heat production or energy expenditure of free-ranging animals. (NJB)

Development: *see* Growth; Growth factors

Dextrins α-Glucosidic chains of varying length, but with a lower average molecular weight than starch, soluble in water but insoluble in alcohol and ether. They are intermediate products of starch hydrolysis. (NJB)

Diabetes A condition characterized by polyuria and polydypsia. There are two separate disorders. Diabetes insipidus is caused either by insufficient production of antidiuretic hormone or by failure of its receptor in the renal collecting ducts. Diabetes mellitus is associated with hyperglycaemia and the consequent glycosuria as a result of insufficient pancreatic production of insulin or impaired response of its tissue receptors to a normal circulating level of insulin. Refined sugars in the diet should be replaced by fibre-rich foods containing unrefined carbohydrate; the protein content should remain normal but the fat content should be reduced, especially if the animal is overweight. (ADC)

Diaminopimelic acid An amino acid, $H_2N{\cdot}CH{\cdot}(COOH){\cdot}(CH_2)_3{\cdot}CH{\cdot}(COOH){\cdot}NH_2$, (DAPA) found in the peptidoglycan of all Gram-negative and some Gram-positive bacteria, but not Archaea. In Gram-negative bacteria, the peptidoglycan is 10% of the cell wall, while in Gram-positive bacteria it is 90%. It has been used to estimate bacterial biomass outflow from the rumen and the fraction of faecal matter attributed to bacteria. However, the ratio of DAPA to cell biomass is highly variable. (DMS)

Diammonium phosphate Dibasic ammonium phosphate, $(NH_4)_2HPO_4$, is typically manufactured by the acidification of rock phosphate to produce phosphoric acid, which is in turn mixed with ammonia and heated under pressure. Manipulation of temperature and pressure determines whether a mono- or dibasic salt is produced. The dibasic salt is extremely unpalatable and is rarely used in animal feeding stuffs. Consequently, most of the material that does come on to the market is unrefined and the level of contamination usually prevents it from reaching feed grade standard. (CRL)

Diarrhoea The major cause of diarrhoea is a local irritation of the intestinal mucosa by infectious or chemical agents, which often leads to an increased flow of intestinal secretions, distension of the lumen and a consequent increase in motility. Dietary diarrhoea occurs in all species and at all ages but is most common in neonatal animals ingesting more milk than can be digested, perhaps resulting in secondary colibacillosis and salmonellosis. Feeding inferior quality milk replacer to young calves is also a very common cause of dietary diarrhoea. Heat denaturation during the preparation of milk replacers can result in a decrease in the concentration of non-casein proteins, leading to poor clotting in the abomasum and thus reduced digestibility. The use of excessive amounts of carbohydrates and proteins that are not derived from milk also predisposes to diarrhoea in calves, as does the inclusion of too much protein from soybean or fish. The proteases in the digestive tract of pre-ruminant calves and lambs cannot denature the soluble antigenic constituents of soybean protein and so a hypersensitive reaction may develop in the tract of such animals. Similarly, milk replacers made from components of bovine origin may lead to diarrhoea when fed to lambs, piglets or foals.

Dietary diarrhoea can be induced in all species by a sudden change in diet, particularly at the time of weaning. This is particularly important in the early-weaned pig. The cause is probably related to the fact that changes in gut enzyme activity, necessary for the digestion of a new diet, take some time, so that gradual exposure to the new diet is advisable to maintain proper digestion.

Treatment of dietary diarrhoea in the neonate involves cessation of milk-feeding for 24 h and its replacement by oral electrolyte solutions. Milk of the correct composition is then gradually reintroduced. Treatment with an antibiotic may be necessary if secondary infection is suspected, along with oral kaolin or pectin to protect damaged intestinal mucosa. (ADC)

Diastase An obsolete synonym for **amylase**. (SB)

Dicalcium phosphate Dibasic calcium phosphate is usually available in anhydrous ($CaHPO_4$) or dihydrate ($CaHPO_4.2H_2O$) forms. The phosphorus (P) occurs in the highly available *ortho* (PO_4^{3-}) form. The crystalline product is usually prepared by the treatment of rock phosphate with hydrochloric acid. Acid treatment of bones or heat defluorination of rock phosphate are alternative methods of production. Pure anhydrous dicalcium phosphate contains 22.8% P by weight but, depending on the origin and method of production, the actual level is usually between 18% and 20.5%. The corresponding value for the dihydrate is 17% to 18%. (CRL)
See also: Rock phosphate

Dicarboxylic acids Organic acids containing two ·COOH groups. Examples in metabolism are oxalate ($^-OOC{\cdot}COO^-$), succinate ($^-OOC{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$), fumarate ($^-OOC{\cdot}CH{=}CH{\cdot}COO^-$) and oxaloacetate ($^-OOC{\cdot}CH_2{\cdot}C{=}O{\cdot}COO^-$). Aspartate ($^-OOC{\cdot}CH_2{\cdot}CHNH_3{\cdot}COO^-$) and glutamate ($^-OOC{\cdot}H_2{\cdot}CH_2{\cdot}CHNH_3{\cdot}COO^-$) are dicarboxylic amino acids. (NJB)

Dicoumarol (coumarin) White and yellow sweet clover (*Melilotus albus* and *M. officinalis*) are biennial legumes that grow throughout much of the USA. The plant's pleasant odour is due to coumarin, a non-toxic substance that is converted to the anticoagulant dicoumarol when moulds grow on clover hay or silage. Dicoumarol is a vitamin K antagonist and animals poisoned by it lack the critical proteins needed for blood coagulation. Affected animals bruise easily and bleed excessively. Some may bleed to death from a relatively small injury or surgery such as castration, dehorning, or vaccination. Prevention lies in avoiding mouldy feeds or limiting the dose by intermittently feeding only small amounts of affected clover hay or silage. (LFJ)

Diet All food consumed over a specified period. The term includes any material that enters the digestive tract, regardless of whether or not it is nutritionally available. It can be applied to a single feed or a combination of feeds, e.g. roughage and concentrate fed to ruminant animals. (SPR)

Diet-induced thermogenesis: *see* Heat increment of feeding

Dietary fibre Dietary fibre is the name given to the polysaccharides of plants that cannot be hydrolysed by the digestive enzymes of higher animals. It includes cellulose, hemicelluloses, pectic substances, fructans and β-glucans. Lignin, a group of complex polyphenolic compounds, is usually also included. The dietary fibre complex is the major source of energy via fermentation in ruminants and a minor source in non-ruminant species. Fermentation yields short-chain fatty acids, acetate, propionate, butyrate and lactic acid, carbon dioxide, methane and hydrogen. An estimated 400–600 different bacterial strains produce enzymes that degrade these carbohydrates. Typically, 60–80% of the energy and two-thirds of the amino acids needed daily by adult ruminants are produced by the microbial fermentation. If starch is present in the diet of the ruminant, it is typically fermented in the rumen, whereas in non-ruminants it is digested in the stomach and small intestine. Variable amounts of starch, particularly in legumes and severely treated grains, are not susceptible to endogenous enzymes in non-ruminants: this fraction of starch is termed resistant starch. It passes into the large intestine where it is rapidly and completely fermented.

The rate and extent of fermentation of the dietary fibre polysaccharides are determined by physical and biochemical characteristics of the plant material. If there is extensive lignification, microbial action is hindered and fermentation of the material is incomplete before it leaves the rumen. The extent of silicification and cutinization also affects microbial fibre degradation. Tannins, essential oils and polyphenols, if present, inhibit cellulases and proteases and slow rumen digestion. Solubility also determines fermentation rate. Soluble dietary fibre in forages includes unlignified pectic substances and hemicelluloses, β-glucans and fructans. Soluble carbohydrates are rapidly and completely fermented both in the rumen and in the large intestine of non-ruminants. Structural carbohydrates in plants include cellulose, hemicelluloses and pectins. They may be associated with lignin. These components are generally more extensively fermented in the rumen than in the large intestine of non-ruminants. For example, wood and newsprint are not degraded in non-ruminants, whereas in the rumen 0–40% of wood and about a quarter of newsprint is fermented. Straw, cottonseed hulls and tropical grasses are either not fermented or poorly fermented in the large intestine of non-ruminants, but one-third to two-thirds of them is fermented in the rumen.

Dietary fibre is analysed essentially by removing all of the non-fibre components from the plant material. However, many methods of fibre analysis either do not remove non-fibre components adequately or fail to recover completely material that is a part of the dietary fibre complex. The neutral detergent fibre (NDF) procedure (Van Soest and Wine, 1967) is a gravimetric method that is widely applied to animal feeds. It was designed to recover plant cell wall material and does not recover storage or soluble fibre components, though a modification of the NDF method allows recovery of a soluble fibre fraction (Mongeau and Brassard, 1993). The NDF method measures all cellulose, variable amounts of the hemicelluloses and essentially no pectins or β-glucans. Enzymatic treatment with amylase is necessary to remove starch from the NDF residue (Robertson and Van Soest, 1981). Nitrogen also is incompletely removed by conventional NDF analysis. In the Association of Official Analytical Chemists (AOAC) method, a dry sample is defatted (if it contains more than 5% by weight of fat), treated with proteases and amylases, dried and weighed. Then one aliquot of the remaining fibre residue is ashed; Kjeldahl nitrogen is measured in the duplicate aliquot and converted to crude protein (× 6.25). The weights of ash and crude protein are subtracted from the residue weight to give total fibre. The AOAC method is not without potential error – firstly because starch is not always removed completely and secondly because, during the ethanol precipitation step, simple sugars co-precipitate with the fibre residue when they are present in high concentrations, such as in fruits or feeds containing sugar products. Both sources of error produce an inflated dietary fibre value. The most accurate method of measuring dietary fibre is to obtain a residue free of simple sugars and starch, acid-hydrolyse it with sulphuric acid to generate the constituent monosaccharides and individually quantitate these, usually by either HPLC or GLC. Colorimetric quantitation of these mixtures of monosaccharides is not accurate because the mixture contains essentially unknown amounts of different monosaccharides which absorb at different wavelengths. All fibre analysis methods are labour intensive and require considerable analytical expertise to obtain accurate or even reproducible results on a variety of samples. (JAM)

See also: Carbohydrates; Gums; Hemicelluloses; Oligosaccharides; Pectic substances; Pentosans; Storage polysaccharides; Structural polysaccharides

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Van Soest, P.J. and Wine, R.H. (1967) Use of detergents in the analysis of fibrous feeds. IV. Determination of plant wall constituents. *Journal of the Association of Official Analytical Chemists* 46, 829–825.

Diffusion A process of molecular mixing of gases or liquids when pure substances are either poured together or are separated by a semipermeable membrane and allowed to mix. In a cellular setting gases and substrates diffuse down electrochemical gradients across membranes by either simple diffusion (no carrier) or facilitated diffusion, where a carrier protein is involved. (NJB)

Digesta The contents of the digestive tract, synonymous with chyme. Digesta consist of undigested feed mixed with secretions, desquamated mucosal cells and microorganisms. (SB)

Digestibility A measure of the degree of net absorption in the digestive tract of dietary nutrients. Macromolecules such as starch and proteins need to be degraded to absorbable units, i.e. monosaccharides and amino acids. This is done by the digestive enzymes of the animal as well as those of **gastrointestinal microflora**. In carnivores and omnivores, the animal's own enzymes predominate, whereas in non-ruminant herbivores microbial activity usually predominates. Microbial activity in the rumen converts food nutrients into microbial matter and volatile fatty acids, both of which are then utilized by the host animal.

Digestibility is influenced by a number of factors relating to treatments of the foodstuffs and complete diets, e.g. milling and processing. Processing can improve digestibility; for example, heat can destroy antinutritional factors such as protease inhibitors in legume seeds and thereby reduce endogenous protein losses; chemicals such as sodium hydroxide can make lignified cellulose more available for microbial enzymes in ruminants; addition of feed enzymes, such as glucanase and arabinoxylase, can reduce viscosity in the small intestine of poultry and piglets. All these treatments improve digestibility. Food processing may have a negative influence, in particular on the digestibility of proteins. Heat causes the formation of inter- and intramolecular covalent bonds that are resistant to enzymatic digestion. In the presence of reducing sugars (e.g. fructose) and amino acids, the **Maillard reaction** leads to the formation of complex adducts between the sugar and amino acids, especially lysine. The Maillard reaction can also occur during storage of dried foods and make lysine unavailable for absorption.

Starch is generally made more available by heat processing but this can also convert available starch into a form that is unavailable for enzymatic degradation. **Resistant starch** is produced by rearrangements in the molecular structure of amylose, which constitutes about 20% of starch and is generally less available than amylopectin.

The digestibility of a nutrient is not a constant value, like a chemical analysis of the nutrient in a particular sample of feed. Feeding conditions (e.g. method and level of feeding) and the particular animal (its species, sex, age and physiological stage) influence digestibility.

The digestibility of a nutrient after passing through the entire digestive tract can be determined by total collection of faeces over a suitable period. Digestibility measured directly from the difference between the intake (I) and output in digesta or faeces (O) of the nutrient is called the apparent or net digestibility (AD):

$$AD = (I - O) / I$$

However, the excreted matter also includes the endogenous loss of the particular nutrient, which has been digested and absorbed but has then re-entered the gut in the form of endogenous secretions. After correction for this loss (E), the true digestibility (TD) of the dietary nutrient can be calculated:

$$TD = (I - O + E) / I$$

The endogenous losses of a nutrient were traditionally estimated by measurements of the losses in animals given diets devoid of that nutrient. However, for some nutrients at least, endogenous secretions may be modified by the diet and these estimates may not represent what occurs under normal circumstances, when the animal eats a complete diet. For this reason, other corrections are used. Undigested food and unreabsorbed endogenous secretions may, furthermore, be metabolized by the microflora, being either degraded or converted to microbial matter. In non-ruminants, microbial metabolism occurs predominantly in the large intestine. The digestibility of protein and amino acids is particularly influenced by microbial metabolism. Most of the protein in faeces is microbial, and because the microflora can synthesize amino acids there may be little relation between the amino acid composition of the undigested food and that of the faeces. This in turn means that digestibility of amino acids measured over the entire digestive tract may be very misleading. Lipids are less metabolized by the intestinal microflora but fatty acids can be elongated and unsaturated fatty acids may be partly hydrogenated by the microbial metabolism in the large intestine. Carbohydrates not available for digestion in the small intestine, due to either physical inaccessibility or chemical structures not hydrolysed by the mammalian enzymes (in dietary fibre), are the main energy sources for the microflora. The end-products of microbial fermentation, i.e. the short-chain fatty acids, are absorbed by the host animal and contribute to the energy supply.

A complete characterization of nutrient availability in the animal therefore includes measurements of digestibility in the different compartments of the gastrointestinal tract, i.e. in non-ruminants, of digesta at both the ileal and faecal level, respectively. In ruminants, measurements of degradation in the rumen are of particular importance, due to a relatively predictable and constant composition of the outflow from the rumen. In animals with a less significant microbial activity, e.g. carnivores such as mink, ileal sampling is of less importance for a proper characterization of digestibility.

Sampling of digesta for measurements of digestibility in different compartments requires a **cannula**. If only a fraction of digesta is collected, an indigestible **marker** must be added to the diet so that the proportion of the whole flow that is collected can be calculated. For a correct measurement of the digestibility of a nutrient, the flow rate of the marker needs to be the same as that of the nutrient. Furthermore, an ideal marker must not be absorbed and affected by the digestive tract or the microbial population in the tract and it should be closely associated with or physically similar to the undigested nutrient in question. No existing marker totally satisfies all these requirements. The combined use of internal and external markers can improve the measurements, e.g. insoluble ash can be used as an internal marker together with chromic oxide, one of the most commonly used external markers.

To determine the digestibility of nutrients that are modified in the large intestine, especially amino acids, digesta are sampled at the terminal ileum to determine ‘ileal digestibility’. The simplest method of obtaining samples of digesta from the terminal ileum is to sacrifice the animals, taking the samples under terminal anaesthesia. For repeated sampling, various kinds of cannula may be used. A simple T-cannula allows only partial sampling and needs the inclusion in the diet of an indigestible marker. The cannula is relatively small and may give unrepresentative samples with coarse or fibre-rich feeds. A more advanced technique, the post-valvular ileocaecal cannula, involves a large cannula placed in the caecum opposite the ileocaecal valve. It can be steered with a nylon cord in such a way that, during the collection, digesta are directed into the cannula, so that, during the sampling period, all the digesta leaving the ileum are collected. An alternative surgical approach, which avoids the use of a cannula, is to bypass the large intestine by ileorectal anastomosis.

In fish, digestibility is measured by several methods for faeces collection, including dissection, stripping (i.e. pressing digesta out of the rectum with the fingers) or anal suction of the individual fish, or alternatively, immediate pipetting, continuous filtration, or decanting of tank water.

By the use of marker technique, the determination of digestibility is based on the increase of the marker in relation to the nutrient in the digesta or faeces. AD is calculated from analyses of the concentrations (g kg^{-1}) of nutrient (N) and marker (M) in the experimental diet and in samples of digesta (or faeces), n and m, respectively.

$$AD = (N - n.(M/m)) / N$$

Other approaches to determining digestibility are based on: (i) the rate of appearance of the nutrient in the body by measuring the difference in the arteriovenous concentration across the portal-drained viscera together with the portal blood flow; this approach may underestimate absorption due to uptake of the nutrient by the tissue of the gut; (ii) isotopic techniques, e.g. labelling the experimental animal with ^{15}N so as to distinguish (labelled) endogenous protein from (unlabelled) dietary protein; this gives a direct measure of the real digestibility of dietary protein, uninfluenced by endogenous protein loss; however, there may be some recycling of (unlabelled) nutrient from the diet into endogenous secretions during the feeding period; and (iii) chemical modification of the dietary protein, e.g. treatment with *o*-methyl-isourea in order to guanidinate lysine to homoarginine and then to determine lysine digestibility; this method assumes that the chemical reaction is distributed equally between digestible and indigestible lysine, that the treatment does not influence the general digestibility of the protein, and that homoarginine is digested and absorbed to the same extent as lysine.

Other methods include predictions from: (i) *in situ* digestibility based on incubations in bags (*in sacco*) in the digestive tract, e.g. after incubation in the rumen or throughout the intestine (mobile nylon bag) with collection at the end of the ileum through a cannula, or in the faeces; (ii) *in vitro* digestibility based on incubation with enzymes similar to those occurring in the digestive tract; (iii) chemical composition; and (iv) physical methods based on **near infrared**, NIT, **nuclear magnetic resonance** or other methods, alone or in combination with chemical analyses.

Availability is often used as a synonym for digestibility but also has a different meaning (*see* **Availability**). (SB)

See also: Markers; Protein digestibility

Further reading

D'Mello, J.P.F. (2000) *Farm Animal Metabolism and Nutrition*. CAB International, Wallingford, UK, 438 pp.

Digestible energy That part of the gross energy of a food substance or complete ration which is not expelled as the gross energy of faeces. It is widely used to express both the energy value of a diet and the energy requirements of animals. (JAMcL)

See also: Energy balance

Digestible organic matter: *see* D value

Digestion The process of breaking down dietary components to make them available for absorption from the gastrointestinal lumen by epithelial cells. Food particles are reduced in size by mechanical and chemical means. The mechanical breakdown is performed by chewing in the mouth and by contractions of the muscular walls of the gastrointestinal tract. Chemical breakdown is mainly effected by enzymes secreted in digestive juices. Food constituents of large molecular weight, such as proteins, starch and lipids, have to be broken down to low-molecular-weight compounds before they can be absorbed. A large number of specific enzymes are involved in their breakdown, some from the animal and some from colonizing microorganisms in the digestive tract.

Most digestive enzymes are found in all species. However, their activity varies with age and responds to variations in the diet. The digestion of the food may be initiated in the mouth, where it may be disintegrated by chewing. Although birds have no teeth, they may use their beaks to reduce the size of food components. During the process of mastication, saliva is added. In the saliva of many animals an α-amylase initiates the enzymatic degradation of starch. In very young pigs, salivary amylase is low; it increases slightly between 2 and 3 weeks of age and then falls to very low levels. In young (suckling) animals, a lipase initiates the degradation of milk lipids. The saliva provides a source of N (from urea and mucoproteins), P and K, which in ruminants are essential for the microorganisms in the rumen.

Some species have a forestomach: birds have a **crop** which serves as a storage organ in which microbial fermentation may occur together with a continued action of salivary amylase on starch degradation; in ruminants the **rumen**, together with the reticulum and omasum, are considered as forestomachs to the abomasum, which corresponds to the true (gastric) stomach of non-ruminants.

Protein digestion begins in the stomach, where pepsins cleave some of the peptide linkages. Like many of the other enzymes involved in protein digestion, pepsins are secreted in the form of inactive precursors (proenzymes) and activated in the gastrointestinal tract. The pepsin precursors are called pepsinogens and are activated by gastric hydrochloric acid. Pepsins are most active at pH 1.5 to 3 and hydrolyse the bonds between aromatic amino acids, such as phenylalanine or tyrosine, and a second amino acid. A gelatinase that liquefies gelatin is also found in the stomach. Rennin (chymosin), a milk-clotting enzyme, is present at birth and disappears after weaning. Pepsin activity is very low (or absent) during the first 2 weeks after birth but then increases rapidly, together with HCl production.

In the small intestine, shortly after passing the pylorus, the digesta are mixed with an alkaline juice which neutralizes the acid digesta from the stomach and also contains a variety of digestive enzymes from the pancreas: proteases, amylase, lipases and nucleases for digesting proteins, starch, lipids and nucleic acids. In some species the pancreatic duct is joined by the hepatic duct that transports bile from the liver. Bile salts are important for lipid absorption.

Polypeptides formed by digestion in the stomach are further degraded in the small intestine by the proteolytic enzymes of the pancreas and intestinal mucosa. The pH is about 6.5. Trypsin, the chymotrypsins and elastase act at interior peptide bonds in the peptide molecules and are called endopeptidases. The carboxypeptidases of the pancreas and the aminopeptidases of the brush border are exopeptidases that hydrolyse the amino acids at the carboxy- and amino- ends of the polypeptides. Some amino acids are liberated in the intestinal lumen, but others are liberated at the epithelial surface by the aminopeptidases and dipeptidases in the brush border of the mucosal cells. Some di- and tripeptides are actively transported into the intestinal cells and hydrolysed by intracellular peptidases, with the amino acids entering the bloodstream. Thus, the complete digestion of protein to amino acids occurs at three locations: the intestinal lumen, the brush border, and the cytoplasm of the mucosal cells.

Starch consists of amylose and amylopectin. Large quantities of pancreatic amylase are secreted from the pancreas into the duodenum in most non-ruminants, except the horse. In bovine species there is generally little pancreatic amylase. Thus, the pre-ruminant calf cannot utilize starch, and adult cattle fed diets rich in grain may develop digestive disturbances when large amounts of starch enter the small intestine. Carnivores have little or no amylase activity. α-Amylase does not hydrolyse the chain branches of amylopectin or the terminal bonds. Therefore, the products of amylase action in the intestinal lumen are disaccharides such as maltose and isomaltose, trisaccharides and limit dextrins with at least five and an average of eight glucose units. These products must be further hydrolysed to their monosaccharide constituents before they can be transported into the epithelial cells. The enzymes for performing these last hydrolyses are attached to the membranes of the microvilli of the brush border and include maltase, isomaltase, glucoamylase and limit dextrinase. Other saccharases are lactase, sucrase and trehalase. Lactase activity is high in mammals at birth and remains high for the first 2–3 weeks of life, after which it declines rapidly. Birds do not have lactase activity and ruminants do not have sucrase activity. In pigs, sucrase and maltase activities are low at birth and then rise with age. Enzyme changes in early-weaned pigs occur more rapidly than in sow-reared pigs, but age has a greater effect than diet on the development of intestinal brush-border enzymes.

Lipids are hydrophobic and need to be emulsified (breakdown of fat globules into smaller globules) before they can be digested by the hydrolytic enzymes lipase and phospholipases. They are initially emulsified in the stomach as a result of stomach motility and are further emulsified in the small intestine by bile salts and lecithin secreted from the liver. The major component of lipids, triglycerides, are only partly digested before absorption. Fatty acids in position 1 and 3 are hydrolysed and, after forming micelles (microemulsions), become available for absorption, together with the remaining 2-monoglyceride, glycerol, cholesterol and other lipids.

Nucleic acids, DNA and RNA, are digested by deoxyribonuclease and ribonuclease secreted from the pancreas and are further degraded to pentoses and purine and pyrimidine bases by nuclease and related enzymes attached to the brush border. Absorption of digested products is completed in the ileum.

In the large intestine, microbial enzymes contribute to the digestion in all animal species and are in many cases of significant importance. The major microbial end-products of fermentation are short-chain fatty acids (SCFAs) and ammonia, which are absorbed. SCFAs are an important energy source for the epithelial tissue but may also contribute considerably to the general energy supply of herbivorous animals, e.g. up to 75% in the horse. In ruminants, microbial digestion plays a particular role because the major part of digestion takes place in the rumen. (SB)

See also: Digestibility; Gastrointestinal tract; Intestinal absorption

Digestive disorders The function of the digestive system is to break down food particles, physically and chemically, into a form that is suitable for absorption into the blood system and subsequent utilization for metabolic processes. There are many digestive disorders in modern animal farming systems, principally because the nature of the food supply is different to that available to their ancestral progenitors. The digestive system of farm animals evolved to digest foods that were often very different to those that can be easily provided in modern farming systems. In addition, the genetic modification of farm animals to increase productivity requires that the nutrient density of the diet be increased above that which the wild ancestors of farm animals would have consumed. This is important for the energy and protein supply for ruminants, which evolved to utilize coarse grasses.

In the case of lactating cows, a diet of coarse grasses and browse material has been necessarily replaced by lush grass, with a high water-soluble carbohydrate content, and cereal grains containing starch that is rapidly digested in their rumen. Excessive processing of cereals exposes the starch to rapid fermentation. After a meal, the rapid production of fatty acids as a result of bacterial growth on the readily available substrate can lead to a reduction in rumen pH below the normal 6–7 (clinical acidosis), which reduces the potential growth of cellulolytic bacteria in particular and is manifested as loss of appetite and production. Also in dairy cows, the inadequate supply of acetate and butyrate, which are the precursors of milk fat synthesized *de novo* in the mammary gland, leads to a low milk fat syndrome, which can be rectified by reducing the quantity of rapidly digestible substrate fed at any one time. The feeding must be changed either to fibre-based energy sources, such as fodder beet, or to a starch-based energy source in small quantities at regular intervals of the day. Some benefit can also be obtained by feeding the cereals in a mixture with forages.

The fermentation of food particles produces gases, principally carbon dioxide and methane, which are liberated via the mouth by eructation. The rapid digestion of starch can lead to the production of excessive gas which, with diminished contractions of the reticulorumen, result in the animal becoming bloated. This ruminal tympany can be observed on the left-hand side of the animal, when viewed from behind. Some legumes, such as lucerne or clovers, produce a stable foam in the rumen, through which the gases cannot be liberated. Others, such as bird's-foot trefoil, contain tannins that effectively bind the proteins to reduce the rate of digestion and make them 'bloat-safe'. The feeding of fibrous forages will be beneficial in cases of bloat, as it reduces the rate of digestion. Ruminants will go to considerable lengths to consume adequate fibre to stimulate rumination. Ruminal atony predisposes ruminants to tympany, but the consumption of pseudofibrous material can cause digestive disorders, such as calves that lick each other's coats and develop hairballs, or chickens that get an impacted crop. Cattle also develop abscesses when they consume plants with awns that irritate the gastrointestinal tract.

Salivation is an essential process to add moisture to the food, which together with mastication prepares the food for passage into the gastrointestinal tract. It also adds digestive enzymes, principally amylases and buffer salts. The salts are particularly important to increase rumen pH in cattle and sheep, which allows digestion of fibre to proceed. Excessively wet feeds, such as lush grass, which may have a dry matter concentration of only 10–12%, may promote acidotic conditions in the rumen. Saliva also contains mucins, which are believed to counteract ruminal tympany – a problem that is worst following consumption of herbage of low dry matter content.

Vomiting is a digestive disorder that functions to reduce the digestion of potentially harmful material. It can also be triggered by motion sickness in animals in lorries or suffering from intense fear or an infection. A stereotyped vomiting disorder can develop in primates in stressful conditions. Diarrhoea, too, functions to reduce the time for which potentially toxic elements are present in the gastrointestinal tract, but can also be triggered by gastrointestinal infection, typically by parasites or bacteria. Parasites may damage the absorptive surface of the gastrointestine, especially the intestinal villi, thus reducing mineral uptake. Diarrhoea is commonly caused by an excessive intake of rapidly digestible nutrients. One of the most common instances occurs when ruminants graze lush pasture in spring. In this case the absorption of some critical minerals, such as magnesium, can be reduced by the short turnover of feed in the rumen.

Stress, which is common in many intensively managed farm animals, will exacerbate several digestive disorders, including diarrhoea and vomiting. The frequency of defecation, as well as the dry matter content of the faeces, will indicate stress. The extent to which dairy cows are stressed by contact with their herdsperson can be estimated by whether they defecate when they are milked by that person. Gastric ulcers develop in pigs in intensive housing, due to excessive acid production.

Low intakes of food can reduce digestibility, at least in the short term, due to insufficient nutrients to support an adequate concentration of microorganisms in the rumen. In the long term, digestibility usually increases, due to increased chewing of the food and reduced losses of nitrogen and other nutrients in faeces. Excessive intakes of food, apart from the problems of bloat referred to above, can cause difficulties if the food particles enter the wrong compartments. In milk-fed calves the milk normally bypasses the rumen to be digested in the abomasum; but if the reticular groove does not function adequately, such as is common in calves drinking large quantities of milk from buckets with the head facing downwards, rather than suckling with the head held horizontally, milk may enter the rumen and cause diarrhoea, or 'calf scours'. Specific nutrients consumed in excessive quantities, such as lipids, can upset the bacterial digestion in the rumen. Similarly, the consumption of some minerals (e.g. potassium) in excess can reduce the absorption of others (e.g. magnesium) through competitive inhibition.

Digestive disorders are a serious problem in farm animals and can lead to low growth rates and low milk production. This is particularly the case in high-producing ruminants, where there is a significant difference in the diet fed from that available to their ancestral progenitors. Further research is required to devise feeding regimes for farm animals that cater for their level of productivity. (CJCP)

Digestive enzyme inhibitors Substances that inhibit the activity of one or more digestive enzymes. Nutritionally, the most important of these are the **protease inhibitors**, which are widespread in the seeds of many plants, especially legumes. They are proteins which form stable inactive complexes with digestive enzymes, especially trypsin and chymotrypsin, and are called **trypsin inhibitors**. The activity of these inhibitors, both in their relative and their total amounts, varies greatly amongst species of legume, and between varieties of the same species. They are inactivated by appropriate heat treatment and such treatment often forms part of the processing of the seeds for inclusion in feeds, especially for non-ruminants. Diets containing large amounts of trypsin inhibitors cause hypersecretion and enlargement of the pancreas, reduce the digestion of dietary proteins and increase the loss from the gut of endogenous nitrogen.

Amylase inhibitors also occur in certain legume seeds but do not appear to be of great nutritional importance.

The actions of digestive enzymes on plant proteins can also be impaired by the presence in the diet of other **antinutritional factors**, such as non-starch polysaccharides and phenolic compounds, and by the physical barrier of indigestible plant cell walls which impede access of digestive enzymes to the substrates within the cells. MFF

Digestive system The complex of organs that participate in the digestion of food. The system comprises the entire **gastrointestinal tract** and its accessory organs. These include the salivary glands, the **pancreas** and the liver, which secrete enzymes, bile acids and other substances into the gut lumen, and the portal circulation, which carries away the products of digestion to the rest of the body. (MFF)

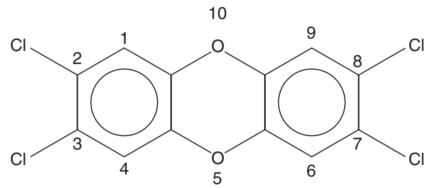
Dihomo-γ-linolenic acid All *cis* 8,11, 14 eicosatrienoic acid, molecular structure $CH_3{\cdot}(CH_2)_4{\cdot}(CH{=}CHCH_2)_3{\cdot}(CH_2)_5{\cdot}COOH$, molecular weight 306.5, shorthand designation 20:3 n-6. A fatty acid of the n-6 family synthesized from linoleic acid by successive Δ6 desaturation and chain elongation; it is also called homo-γ-linolenic acid. (DLP)

Dihydrofolate $C_{19}H_{23}N_7O_6$, the first intermediate in the conversion of folic acid (a B vitamin) to its tetrahydrofolate form by the enzyme folate reductase. After modification by addition of γ-glutamyl residues, tetrahydrofolate is the coenzyme form of the vitamin. Tetrahydrofolate and the folate system are critical to the synthesis of the purines used in DNA synthesis. (NJB)
See also: Folic acid

Dilution rate The rate at which fluid or solids in the freely mixing, constant-volume content of a compartment of the gut (e.g. reticulorumen) is replaced. Units are % h^{-1}, fraction h^{-1}, etc. (RNBK)

Dimethylsulphoxide (DMSO) $(CH_3)_2{\cdot}SO$, a hygroscopic liquid that is miscible with water. It readily penetrates tissues and is used as a solvent for delivery of drugs to the bloodstream by topical application. (NJB)

Dioxin A family of more than 70 chemical compounds, known as polychlorinated dibenzo-*para*-dioxins, that have an identical carbon–oxygen 'skeleton' and contain one to eight chlorine atoms. The most widely studied is 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD), a known carcinogen, teratogen and mutagen. Dioxins were found as contaminants in the herbicide trichlorophenoxyacetic acid (2,4,5-T) and also as a component of the defoliant agent orange and in wood preservatives (pentachlorophenol). Dioxins can be formed by combustion at low temperature in the presence of carbon and chlorine. They persist in the environment and accumulate in the fatty tissue of living organisms.



TCDD

(JEM)

Dipeptidase A peptidase that specifically hydrolyses dipeptides. Dipeptidases are located together with tripeptidases and aminopeptidases in the **brush border** of the epithelial cells of the small intestine, mainly the jejunum. (SB)
See also: Digestion

Dipeptide R·C=O·NH·C·R, a molecule formed of two amino acids linked by a peptide bond. In the digestion of protein, some dipeptides are formed and absorbed into the enterocyte prior to being hydrolysed to single amino acids. In special cases dipeptides are formed from cellular amino acids. These include carnosine (β-alanylhistidine), anserine (β-alanyl-1-methylhistidine) and balenine (β-alanyl-3-methylhistidine). (NJB)

Direct calorimetry Direct calorimeters not only measure the total heat given off by animals, but also partition it into its two components, evaporative and non-evaporative. Non-evaporative or sensible heat is heat given off from an animal by radiation to surrounding surfaces, by convection to the surrounding air and by conduction to any objects with which the animal is in contact. Evaporative heat loss occurs because the conversion of liquid water into vapour requires heat energy. The latent heat of vaporization is the heat required to vaporize unit mass of water; it varies from 2490 to 2390 J g^{-1} (595–572 cal g^{-1}) within the temperature range

0–40°C. When water is vaporized in the respiratory passages during normal respiration and panting, or at the skin surface during perspiration, the latent heat of vaporization is given up by the animal. This heat loss by the animal is transferred to the air in the form of increased humidity; the enthalpy of the air (which is a measure of its energy content and depends on temperature, humidity and pressure) is increased.

Direct calorimeters are classified into four types (isothermal, heat-sink, convection and differential) according to how sensible heat is measured. In isothermal calorimeters the sensible heat is measured as it passes through the walls, floor and ceiling of the animal chamber; these surfaces have heat-sensitive linings which generate voltages proportional to the heat passing through. In heat-sink calorimeters the chamber surfaces are thermally insulated and the sensible heat from the animal is taken up by a heat exchanger; the heat is measured as the product of the temperature rise of the coolant and its rate of flow. Convection calorimeters also have insulated surfaces and ideally all sensible heat from the animal is taken up by the ventilating air, whose temperature increase multiplied by flow rate provides the measure of the heat. This method tends to be slow in response because after a change in the level of heat output there is a delay while the chamber itself, especially its insulated walls, adjusts to the new level. To overcome the delay, differential calorimeters employ two similar chambers, one containing the animal and the other an electrical heat source; the power provided to the heater is controlled to produce the same increase in air temperature as that in the animal chamber and it thus represents the sensible heat output of the animal. In heat-sink, convection and differential calorimeters, evaporative heat is measured as the increase in humidity of the ventilating air, usually sensed by dewpoint hygrometers or wet-and-dry-bulb thermometers.

The earliest calorimeters for farm animals were of the heat-sink type and much pioneering work was done in them 100 years ago. None of today's sophisticated electronic control systems were available and most calorimeters required a team of three or four scientists for their operation. The precision was truly remarkable and demonstrated (over periods of days) agreement between direct and indirect calorimetry to within 1%. At the time this was hailed as proof that the first law of thermodynamics applied to living systems as well as to mechanical ones. Nowadays that would be accepted as axiomatic and the agreement between direct and indirect calorimetry would be regarded as proof of the accuracy of the measuring systems.

In recent years the technique of heat-sink calorimetry has been revived and refined but mainly applied to studies on humans. For animals, recent use of heat-sink, convection and differential calorimeters has been confined to studies on laboratory animals and poultry. The most favoured method for farm animals has become the isothermal one, the modern form of which is the gradient-layer calorimeter.

In the gradient-layer calorimeter the sensible heat from the animal generates a small temperature gradient across a thin uniform layer, usually of plastic material, as it passes into a water-cooled jacket surrounding the chamber. The mean temperature gradient (i.e. temperature difference) across the layer is measured by multiple and/or widespread sensors on either side (thermocouples, thermistors or resistance thermometers) and generates a voltage output that is proportional to the integrated heat flow through all surfaces, i.e. the sensible heat output from the animal. Evaporated water is reconverted into liquid by passing exhaust air between cooled plates that return its humidity to the original level it had before entering the chamber; the heat of re-condensing it, which is equal to the evaporative heat loss of the animal, is again measured by gradient layers covering the plate surfaces. Because the gradient layers are thin and the temperature differential across them no more than a fraction of a degree, the time response to changes in heat output is only a few minutes. The principal limitation to the speed of response of a gradient-layer calorimeter is not the calorimeter itself, but the relatively slow response to heat changes of any cage or bars fixed inside it to restrain the animal.

Ventilation of a direct calorimeter has to be sufficient to ensure control of air temperature inside the chamber and to avoid condensation of evaporated water inside it. Pre-conditioning all the ventilating air and then exhausting it to the environment would be wasteful of power and so most of the air is usually recirculated round a closed circuit, with only a small proportion being voided to the atmosphere and replaced with fresh air. The oxygen and carbon dioxide concentration differences between fresh and exhaust air can be made of the order of 1%, and conveniently measurable so that indirect and direct calorimetry may be performed at the same time. (JAMcL)

See also: Calorimetry; Heat balance; Indirect calorimetry

Further reading

McLean, J.A. and Tobin, G. (1987) *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, 338 pp.

Disaccharidases Enzymes that hydrolyse molecules made up of two sugars. In animals they are found in the brush border of the enterocytes of the small intestine. The enzyme that hydrolyses the two-sugar unit maltose from starch digestion is maltase; that hydrolysing lactose is **lactase**; and that hydrolysing sucrose is **sucrase**. (NJB)

Disaccharides Sugars made up of two monosaccharide molecules. They can be reducing sugars, which have a potential carbonyl carbon, or non-reducing sugars, which do not. Disaccharides important in animal nutrition include the reducing sugars maltose (made up of two glucose units) and lactose (made up of glucose and galactose) and the non-reducing sugar sucrose (made up of glucose and fructose). Another non-reducing disaccharide of note is trehalose; other reducing disaccharides include cellobiose, gentiobiose, melibiose and turanose. (NJB)

Disorders, nutritional: *see* Nutritional disorder

Dispensable amino acids: *see* Non-essential amino acids

Distillers' residues Materials that arise from (or remain after) the distilling process. Distilling, which is basically the conversion of cereal starch into ethyl alcohol, takes two forms. Malt distilling uses only malted barley as a substrate and grain distilling traditionally used maize and malt but recently, in Scotland at least, increasing proportions of wheat have been used. Residues suitable for use as animal feeding stuffs arise at all stages of the distilling process, from the initial screening of malt or cereal grains to the liquids remaining after the alcohol has been distilled off.

As in brewing, ground malt, other cereals or both are mixed with hot water to form a 'mash' in which the enzymatic conversion of starch to disaccharide sugar takes place or is completed. The liquid phase (wort) containing the soluble components, primarily sugars and some protein, may be separated prior to fermentation (usual in malt distilleries) or yeast may be added to the whole mash. When fermentation is complete the alcohol is distilled off. The mix of liquid and solids remaining after fermentation of and distillation from the whole mash is known as thin stillage. Solids and liquid are separated when distillation is complete.

The solid residues, which are primarily the fibrous portion of the cereal grain, whether extracted before or after fermentation and distillation, are known in Scotland as draff whilst the liquids are known as 'pot ale' (malt distilling) and 'spent wash' (grain distilling). These liquids contain disrupted yeast cells as well as residues of substances solubilized from malt and cereal grains and are usually concentrated by evaporation to produce pot ale and spent wash syrups. Traditionally much of the syrup was dried to produce a fine, mildly hygroscopic meal known as dried distillers' solubles. More usually now, the syrups are mixed back with the solid residues. This mix may be made available as 'super draff' or dried and pelleted to produce distillers' dark grains (distillers' grains with solubles). Occasionally, though rarely now, the solid residues may be dried without the addition of a syrup, when they are referred to as distillers' light grains. Syrups may also be used directly or blended with other materials such as molasses to produce liquid feeding stuffs.

Composition of distillers' residues.

	Dry matter (g kg^{-1})	Crude protein (g kg^{-1} DM)	Ether extract (g kg^{-1} DM)	Crude fibre (g kg^{-1} DM)	Ash (g kg^{-1} DM)	MER (MJ kg^{-1} DM)
Pot ale syrup	450	360	30	< 5	100	14.5
Spent wash syrup – maize	360	300	70	< 10	80	16.0
Spent wash syrup – wheat	300	350	20	25	60	15.0
Malt distillers' dark grains	890	260	60	140	55	12.0
Maize distillers' dark grains	890	300	100	90	50	14.0
Wheat distillers' dark grains	890	300	60	75	50	12.5

MER, metabolizable energy for ruminants.

When referring to distillers' residues it should always be made clear from which cereal they were derived, e.g. malt screenings, maize distillers' light grains, pot ale syrup or wheat distillers' dark grains.

Distillers' residues are used in the diets of pigs, poultry and ruminants but their fibrousness and the nature of the protein make them most suited to feeding ruminants. Typical crude analyses of three syrups and three types of dark grains are as shown in the table. (CRL)

Further reading

Crawshaw, R. (2002) *Co-product Feeds – Animal Feeds from the Food and Drinks Industry.* Nottingham University Press, Nottingham, UK, 307 pp.

Gizzi, G. and Givens, D.I. (2001) Distillers' dark grains in ruminant nutrition. *Nutrition Abstracts and Reviews Series B: Livestock Feeds and Feeding* 71(10), 1R–19R.

Diurnal variation A term applied to numerous circadian rhythms and used to describe predictable daily variation in the intensity of a physiological function. This variation is thought to occur in all living organisms. The 24-hour light/dark cycle is involved in setting the daily rhythms of neural activity, body temperature cycle, sleep, feeding and fasting, physical activity cycle, blood concentrations of hormones and metabolites, etc. (NJB)

See also: Circadian rhythm

Docosaenoic acids Unsaturated fatty acids with 22 carbons. In the n-3 (or ω3) family the first double bond occurs on carbon 19 (i.e. 22–3) whereas in the n-6 (ω6) family the first double bond is on carbon 16. (NJB)

Docosahexaenoic acid (DHA) An unsaturated 22-carbon fatty acid with six double bonds (22:6, $\Delta^{4,7,10,13,16,19}$), a member of the n-3 family. In metabolism it can be synthesized from α-linolenic acid by sequential desaturation and two-carbon elongation reactions. DHA can be obtained directly from fish oils and is in high concentrations in the brain, retina and testis. In the retina it is a component of the membrane phospholipid fraction and is thought to lead to the enhanced fluidity needed for the visual process. It is particularly concentrated in the *sn*-2 position (i.e. 2-carbon of glycerol) of phosphatidylethanolamine. (NJB)

Docosapentaenoic acid A 22-carbon unsaturated fatty acid with five double bonds (22:5, $\Delta^{7,10,13,16,19}$), a member of the n-3 family. (NJB)

Domestic fowl The genus *Gallus*, belonging to the order Galliformes, suborder Phasiani, family Phasianidae, subfamily Phasianinae. The four species in the genus, which have the common name junglefowl, have their origin in South-east Asia: the red junglefowl, *Gallus gallus*, the grey junglefowl, *Gallus sonneratii*, the Ceylon junglefowl, *Gallus lafayetii*, and the green junglefowl, *Gallus varius*.

The most widespread is the red junglefowl, within which there are five subspecies: *G. g. murghi, G. g. spadiceus, G. g. jabouillei, G. g. gallus and G. g. bankiva.* As a species the red junglefowl is not threatened. It is most numerous in Thailand, where *G. g. spadicus* and *G. g. gallus* have part of their habitat range. Recent DNA analyses of these subspecies have indicated that *G. gallus* was the originating species of the domestic fowl. Domestication, from about 6000 BC, exploited the bird for sport and food. Breed development across Asia and Europe was limited until the 19th century, when the larger Chinese breeds arrived in Europe and the USA. The majority of breeds are for show purposes. Those developed for commercial purposes have a mature body size ranging from 1.5 to 6.5 kg. Breeds at the lower end of the range are used for **egg production** and those at the upper end are used for **meat**.

Both laying hens and meat chickens are derived from the same species. The modern hybrid layer can be divided into two main groups: the light breeds and the heavy breeds. The former are mainly derived from White Leghorns, laying white eggs, while the heavy, less feed-efficient brown layers come mainly from Rhode Island Red stock. Worldwide there are currently some ten major breeds, with most breed companies offering a choice of at least three strains: brown and white egg layers and a more traditional strain for extensive/alternative systems.

Modern breeds are capable of producing 20 kg of egg mass output to 76 weeks, with a feed conversion ratio (FCR) of 2–2.2:1. This is typically obtained by producing 320+ eggs, average weight 63 g, on a daily consumption of around 112 g of feed. Breeds may differ in average egg weight and have different shell quality characteristics. Some are more feed efficient than others but no one strain is perfect, since different markets require different products. Alternative systems require greater egg size, shell egg markets emphasize shell quality, while for the liquid-egg market feed efficiency is most important.

The world market for meat birds, be it chicken or turkey, is now dominated by five major companies, along with some smaller organizations producing speciality products. Several companies offer a choice of products, depending on market requirements, while others have only a simple compromise bird. Heavy meat breeds now dominate the world stage. Historically there were light breeds where the breeder bird produced large numbers of chicks, which grew less efficiently, with lower meat yields. With the huge worldwide demand for poultry meat and the move away from whole carcasses to portions or stripped meat, the high-yielding feed-efficient breeds have succeeded.

A modern broiler breeder produces 140 chicks to 65 weeks of age with a feed intake per chick of about 350 g. The broilers can be slaughtered over a wide weight range, typically from 32 days to 50 days of age. This is to provide everything from whole small chicken carcasses to heavy males for meat stripping. Males and females are normally grown separately to allow maximum efficiency of production. The breeds differ in their growth pattern and yield characteristics but are very similar in weight for age, FCR and mortality.

Birds are normally kept in controlled environment sheds on the floor with *ad libitum* access to feed and water. Broiler performance is continuously improving, due to genetic selection, with birds typically reaching target weight 1 day earlier each year. This gives a corresponding improvement in feed efficiency of several points per annum.

Metabolism does not differ greatly between breeds, although the pattern of early growth is breed specific. The nutrient requirements are set out in manuals provided by the breed companies. In practice, integrated companies with more than one breed tend to produce only one set of diets. (WKS, KF)

Dopamine Dopamine (3-hydroxytyramine or 3,4 dihydroxyphenethylamine) is one of the catecholamines and is a neurotransmitter. It is produced by a hydroxylation and decarboxylation of the aromatic amino acid L-tyrosine in the substantia nigra in the brain. In Parkinson's disease, production of dopamine is insufficient to maintain dopaminergic neuron function. (NJB)

See also: Neurotransmitter

Double isotope techniques Also called double labelling, used to trace the fate of nutrients or metabolites in the body. For example, an amino acid labelled with both ^{15}N and ^{13}C can provide information on the metabolic fate of both the nitrogen and the carbon in the amino acid molecule. **Doubly labelled water** is used to estimate CO_2 production. (MFF)

Doubly labelled water Water containing isotopes of both hydrogen and oxygen, usually deuterium (^2H) and ^{18}O. Its usual use is for the estimation of **carbon dioxide** production. The principle of this method is that when doubly labelled water ($^2H^{18}O_2$) is introduced into the body, both elements are lost as water but oxygen is lost additionally as CO_2. By measuring the rate of decline in the concentrations of both isotopes in the body water pool, this additional loss of oxygen can be estimated and, from it, the rate of CO_2 production. The method can integrate CO_2 production over a period of days or weeks and is thus particularly suitable for measurements in free-living animals. (MFF)

Draught animals: *see* Working animals

Dressing percentage Carcass weight as a proportion of the liveweight at slaughter. Carcass weight may include the head, feet, tail, etc., but sometimes does not. (MFF)

Dried grass The procedure for drying grass differs from hay and barn-dried haymaking because it involves the rapid evaporation of plant juices by hot air with minimum losses of nutrients. Although this process is the most effective in retaining the nutritional value of the fresh grass, it is also extremely costly. Both capital outlay and running costs are high. The nutritive quality of dried grass is high and the process is commanding greater attention due to the need to rely less on imported concentrates. Dried grass is normally marketed with protein contents of between 14 to 20% dry matter (DM), metabolizable energy > 10.8 MJ kg^{-1} DM, and a DM content > 90%. The final dried grass material may be sold finely chopped or in the form of pellets. Dried grass is a very palatable feed and the forage substitution rate (kg reduction in forage DM intake per kg DM of supplement fed) is similar to that of average grazed grass and better than good quality silage of maize or grass. (RJ)

Dried lucerne Dried lucerne (alfalfa, *Medicago sativa*) is usually chopped and then dried at a very high temperature (800°C) before further processing by pressing or pelleting. The high-temperature drying process not only removes the water content of the plant but at the same time reduces the degradability of the proteins, protecting approximately 50% of the protein from degradation in the rumen, making it available for digestion in the small intestine. Dried lucerne contains only 10% of crude protein as non-protein nitrogen (NPN), against 55% of crude protein as NPN for lucerne when it is ensiled.

Typical analysis of dried lucerne.

Dry matter (DM)	88%
Protein	18–20% of DM
Metabolizable energy	10.0 MJ kg^{-1} DM
Neutral detergent fibre	42–45% of DM
Acid detergent fibre	32–35% of DM
Oil	3% of DM
Ash	11% of DM
β-Carotene	80 mg kg^{-1}
Vitamin E	120 mg kg^{-1}
Calcium	3% of DM
Phosphorus	0.3% of DM

(RJ)

See also: Lucerne

Dried milk Milk (whole or skimmed) dried to a powder by spray drying or roller drying. (PCG)

Dried skimmed milk Skimmed milk dried to a powder, usually by spray drying. (PCG)

Dried whey Whey dried to a powder by spray drying. (PCG)

Drinker A device for providing fresh drinking water to domestic livestock. This can range in size from a bath tub or trough with a ball-cock mechanism for flow control, as used for cattle or sheep out at grass, to a tiny nipple, as used by caged laying hens. A drinker can be as simple as a manually filled basin for extensive ducks, or as complex as a time-regulated bell drinker that allows broiler breeders to consume only a set volume of water each day. Sheep and cattle drinkers tend to be large vessels with simple mechanisms to stop wastage. For pigs, on the other hand, drinkers often incorporate a pressure switch activated by the snout to control the flow of water. For intensive poultry also it is important to avoid wastage. Spillage from nipple drinker systems is often reduced by the use of a cup hung underneath. In most production systems smaller and more refined drinkers are used with infant livestock, such as mini jars for poultry, small nipples for pigs and plastic teats for calves and lambs. (KF)

Drinking behaviour There are several methods of drinking used by domesticated animals. While cattle, horses and sheep form their lips into a tube and suck, pigs gulp water and poultry depend on gravity for transferring water to the alimentary tract. When drinking from bell or cup drinkers (usually situated below head height), domestic fowls make a series of angled dips of the open beak into the water and raise the head between each dip to let the water pass from the mouth into the oesophagus. When drinking from nipple drinkers (usually above head height), they extract water with varying efficiency and let it trickle down while keeping the head raised. Typically, fowls spend more time drinking from nipples (about 6% of time) than from bell or cup drinkers (about 3%), because water flow rate is limited with nipple drinkers.

Feed intake is the main determinant of water requirement when ambient temperature is within the thermoneutral zone, and most drinking occurs in close association with spontaneous meals. Typically, animals consume about 1.6–2.2 times as much water as food per day, by weight. However, some drink more than would be expected from their daily food intake, possibly as a consequence of environmental stress, and such excessive drinking (polydipsia) can be very marked in animals subjected to chronic food restriction. When ambient temperature is above the thermoneutral zone, animals need to drink more water to replace evaporative water loss due to sweating and panting. Physiological control of water intake is based mainly on changes in cellular hydration, through osmoreceptors, but also on changes in plasma volume, through the rennin–angiotensin system. Water consumption and the ratio of water to food intake are increased by high dietary mineral and protein concentrations. (JSav, JMF)

Drinking water: *see* Water

Drought Drought occurs where the supply of water falls below the critical demand in an area over a prolonged period. The demand is usually a function of human activities and droughts can therefore be considered man made. In contrast, an area with low rainfall is described as arid, but the ecology of the flora and fauna are adapted to the periodic absence of water.

Droughts lead to feed shortages and loss of production principally in grazing stock, and usually have their origin in the rainfall and plant production of the preceding season. The declaration of drought will be made after a short dry period in the case of high output stock, such as dairy cows, where as little as 1 month without rain may substantially reduce production, and after a long period in the case of stock of low productivity, such as Merino sheep, where a drought may extend for several years before a serious loss of productivity is experienced. Thus intensification of pasture and animal production will increase the risk of drought and increase the variation in profitability of the enterprise. Drought will also influence the diseases affecting grazing stock, with plant poisoning being common as animals search for fodder, as well as osteomalacia and botulism. The congregation of livestock around small waterholes can facilitate the spread of infectious diseases such as tuberculosis and brucellosis.

The impact of droughts can be buffered by feeding supplements to livestock, by sale of stock or their agistment or, in highly intensive systems, by the use of artificial irrigation for livestock crops. Usually grain or hay is used as a supplement. It is important that a drought management strategy is planned in years between droughts. The strategy should include estimates of drought frequency, the cost of supplementation, the financial gain from maintaining livestock growth and the impact on stock welfare. Drought frequency can now be estimated in many regions, since rainfall records have been kept for at least 100 years. For example, it can be determined that a major drought will occur in central east Australia every 7 years, whereas in the south-east of that country it will only occur once every 11 years. (CJCP)

Dry matter One of the terms used to describe the proximate composition of feedstuffs. Most feedstuffs have water as part of their weight. In most cases dry matter is determined by the weight loss of samples dried in an oven at temperatures above 100°C for 12–24 h. Weight loss is equated to water and dry matter is calculated accordingly. (NJB)

Dry season A time when no rain is expected. In the tropics either one or two dry seasons are normal. The long dry season is usually relatively cool and can last many months. Plant growth ceases; termite damage and senescence reduce standing biomass. Livestock depend on crop residues. In extreme years, stock losses are common. (TS)

See also: Wet season

Drying feed crops The purpose of drying crops for animal feed is to allow safe storage with minimal losses and contamination.

Grain

Some advantages of drying grain are that it: (i) increases quality of harvested grain by reducing crop exposure to weather; (ii) reduces harvesting losses, including head shattering and cracked kernels; (iii) reduces dependency on weather conditions for harvest; (iv) allows use of straight combining for small grains; (v) reduces size and/or number of combines and other harvest-related equipment and labour required due to extending harvest time; and (vi) allows more time for postharvest field work. Some disadvantages are: (i) the original investment for drying equipment and annual cost of ownership; (ii) the operating costs for fuel, electricity and labour; and (iii) possible need for further investment in equipment for the extra grain handling that is required.

The length of time for which grain can be stored without significant deterioration is determined by the temperature and the moisture content at which it is stored. Table 1 shows the maximum recommended moisture contents for storage with duration for some typical feed grains. Short-term storage generally refers to storage under winter conditions while long-term storage includes the effect of summer conditions.

Table 1. Recommended moisture contents (%) of selected grains for storage.

	Short term (less than 6 months)	Long term (more than 6 months)
Barley	14	12
Maize	15.5	13
Oats	14	12
Rye	13	12
Wheat	14	13

Grain can be stored at a higher moisture content without significant fungus development when stored at colder temperatures. Table 2 shows the relationship between moisture and temperature and its effect on allowable storage time for cereal grains.

Table 2. Guidance on storage time (days) for cereal grains.

Moisture content (%)	Temperature (°C)					
	−1	4	10	16	21	27
14	*	*	*	*	200	140
18	*	200	90	50	30	15
22	190	60	30	15	8	3
26	90	35	12	8	5	2
30	60	25	5	5	3	1

* Storage time may exceed 300 days.

Airflow rate, air temperature and atmospheric relative humidity will influence drying speed. In general, higher airflow rates, higher air temperatures and lower relative humidities increase drying speed. Raising the temperature of the drying air increases the moisture-carrying capacity of the air and decreases the relative humidity. As a general rule of thumb, increasing the air temperature by 7°C doubles the moisture-holding capacity of air and cuts the relative humidity in half.

The drying rate depends on the difference in moisture content between the drying air and the grain kernel. The rate of moisture movement from high-moisture grain to air with low relative humidity is rapid, but the moisture movement from wet grain to moist air may be very small. At high relative humidities, dry grain may pick up moisture from the air.

There are a number of different grain driers available commercially, including natural air, low temperature and high temperature, or batch and continuous flow. Driers can also be classified according to the direction of airflow through the grain: cross-flow, counter-flow and concurrent-flow. These driers are normally operated by specialist contractors or installed on large arable farms.

Forage

Some drying is essential for the preservation of forage crops such as grasses, legumes or whole-crop cereal silage for livestock winter feed. As forage crops mature and the succulent leafy material is replaced by stem and seed heads, the moisture content will decline naturally. With grass and legume crops, a further field curing or wilting of mown crops will be required in order to reduce the moisture content and reduce the potential effluent loss during storage as baled silage or bunker silage. High moisture (> 80%) of forage crops may lead to an undesirable clostridial fermentation, which may increase losses and reduce the feed nutritional value and palatability. Reducing the moisture content of forage crops to < 70% will ease the method of transportation of harvested crop from field to storage, with higher levels of dry matter being transported per trailer load. In the UK the main method of reducing forage crop moisture content is field wilting.

Field wilting

Field wilting of forage crops is the most common method of reducing moisture content of crops using natural resources of wind and solar energy. Wilting of crops for silage or haymaking requires herbage to be cut with a mower and left in the field for varying periods of time prior to lifting and harvesting. In poor weather conditions, dry matter content of crops will increase only slightly and in extended wilting periods soluble sugars and protein content will be reduced. In contrast, during good weather conditions wilting will be rapid, with minimum losses in soluble sugars and protein content. Under these conditions the dry matter content of the crop may exceed 350 g kg^{-1}.

Natural dry matter losses in wilted crops are normally small, provided that the wilting period is up to 2 days. If the pre-wilting period is extended and accompanied by poor weather, then losses of DM up to 10% of the total crop have been reported.

Mechanical treatment of field-mown crops using turning and tedding the swath can substantially increase the drying rate. Spreading of mown grass within 1 h can increase the rate of water evaporation by up to five times, mainly as a result of water evaporation through open stomatal guard cells. Following this time period the stomata will close and plant water loss will need to pass through the thick cell walls.

Barn-drying

Barn-drying was popular in the UK during the 1960s, both in methods of ventilation and in a shift from batch drying to storage drying. However, even at its peak barn-drying accounted for no more than a small proportion of the total hay crop made in the UK and, as field haymaking declined from 1970 onwards, it was replaced by ensilage. Thus few large-scale units were installed and most of the limited number of barn-drying installations still operating are likely to be storage driers, holding between 50 and 100 t of hay.

High-temperature drying

High-temperature drying is undoubtedly the most efficient method of conserving a green forage crop. Total loss of dry matter, from standing crop to dried product, can be as low as 3%; furthermore, because the crop can be cut for drying at a much more immature growth stage than is practicable for either hay or silage, the nutritive value of the dried product can be much higher. High-temperature drying is also largely independent of weather conditions. Because of this potential, a considerable programme of research on high-temperature drying was conducted during the 1960s. Largely as a result of this research, production of dried grass in the UK rose from 65,000 t in 1965 to over 200,000 t in 1972, and further major expansion was predicted. However, grass-drying is based on the burning of fossil fuel, generally oil, to evaporate the water in the fresh crop, with up to 300 l of oil being needed to produce 1 t of dried grass from a crop cut at 80% moisture content. Sharp increases in the price of oil during the 1970s made grass-drying much more expensive and greatly reduced the economic benefits of dried grass as a livestock feed. As a result there was a steady fall in the amount of dried grass produced in the UK, down to the present annual level of about 70,000 t. Most of this is from drying specialized crops such as lucerne, with an annual output of more than 5000 t, and the operators who have continued in production have remained competitive by wilting the cut crops in the field before bringing them to the drying plant, thus greatly reducing fuel consumption and increasing drier output. The situation in the UK contrasts sharply with that in a number of other EU countries, and since 1980 total EU production has more than doubled, to 4,500,000 t of dried green crop a year, mainly as a consequence of EU support for dried green crops. (RJ)

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Duck Ducks are kept for meat, eggs, feathers and down, and liver fat. Most of the world duck population (917 million) is found in China (636 million), where they were domesticated more than 2500 years ago. The domestic duck originates from the green-headed mallard *Anas platyrhynchos* in the tribe Anatini (dabbling ducks) in the subfamily Anatinae of the family Anatidae. There are about 40 species of the genus *Anas*.

The Muscovy or Barbary duck (*Cairina moschata*) is not derived from the wild mallard and belongs to the Cairina tribe (perching ducks and geese); it is a native of Central and South America and is more closely related to geese than to the domestic duck. The incubation period for its eggs is 35 days instead of 28 days for other ducks. Unlike other domesticated drakes, which have curled feathers on the upper tail, Muscovy drakes have none. Plumage comes in a range of colours but white is most common in commercial production. They prefer to graze and have a slightly curved bill to harvest grass seeds. They are often used to incubate eggs and make excellent mothers. Body weights of the sexes are quite different, drakes weighing about 5–6.5 kg and females 2.5–3.5 kg. Crossing the Muscovy drake with the Pekin female gives a mule offspring that is fast-growing with less fat and higher lean in the carcass, but sterile. At 63 days the male weighs about 4.0 kg with a feed conversion ratio (FCR) of 2.6 and a breast meat yield of 16%. Growth rate of the female is 10% lower.

Numerous breeds of duck are used to produce eggs and meat. Outside Asia, the Khaki Campbell is the most common because of its low body weight and high egg production, often in excess of 300 eggs per year. Pekin ducks, traditionally used for meat production, are today, through selection, also prolific layers. In Asia, selection has often focused on the ability to forage in rice fields. Light-bodied, high-producing ducks, such as the Indian Runner and Alabio, stand upright, allowing them to move between the rice plants in the traditional systems (Farrell, 1995). In Taiwan, the Brown Tsaiya is the only egg-laying breed; it produces up to 325 eggs per year and weighs 1.5 kg. For meat production, the White Pekin is the most popular.

Ducks, unlike most other avian species, do not have a distinct crop. Instead, there is a widening of the oesophagus where food sits temporarily. They feed briefly, then drink copious amounts, resulting in watery excreta (which leads to wet litter problems). Ducks are hardier than chickens; they are less prone to avian diseases, have a high reproductive rate, run in flocks and are easier to manage. Common viral diseases are hepatitis, enteritis (duck plague), avian influenza and fowl cholera, a bacterial infection.

Over the last few years, duck production has increased by almost 10% per year, faster than any other farmed animal. Of the world's 2.9 million metric t annual production of duck meat, China's contribution was 2 million t, or 69%. Other major producers in South-east Asia are Thailand, Vietnam and Malaysia. Roast Pekin duck is a traditional Chinese dish. Other traditional products include smoked duck, pressed duck and salted duck. In western countries, emphasis has been on breast meat yield, reduced fat, and further processing for sale as cut portions. France has the highest production in Europe (23,500 t), where there has been emphasis on the Muscovy ducks, whose meat colour and characteristics are not unlike bovine red meat. Drakes are usually prepared in cut-up portions because of their size, whereas the females are marketed whole. Liver fat (*see* **Geese**) from ducks is a major industry in several countries: in France, mule ducks are commonly used for this. Starting at about 10 weeks of age they are force-fed several times a day for 2 weeks or more, producing livers that weigh 400–700 g.

Duck eggs are not popular in most western countries. They contain 30% more fat than hen eggs, are normally larger, and vary in colour from white to brown to blue-green. In Asia, they are eaten in many forms. In the Philippines, the 'balut', an embryonated egg, incubated to day 19, is a delicacy. Salted eggs and century eggs are traditional methods of preserving duck eggs, giving them a characteristic taste. In Taiwan, 95% of duck eggs are processed in these ways but in Indonesia most are eaten fresh.

Today's Pekin genotypes of mixed sex can grow to 3.5 kg in 6 weeks with an FCR of about 2.3:1, a carcass yield of 72%, a fat content of 20%, and breast meat yield of the eviscerated carcass of 14–16%. Typical mature body weight is < 5 kg for males and > 4 kg for females. Until recently, carcass fat of up to 30% was not uncommon in Pekin ducks. Duck meat is substantially more expensive than chicken meat because of higher costs of processing, generally poorer FCR and higher labour needs.

Intensive systems may be fully enclosed, with straw bedding. Ducks are sometimes raised on a slatted floor or wire mesh over a pit, or with a mix of bedding and mesh floor for the feeders and waterers because ducks tend to defaecate when eating. Adequate ventilation is essential to remove the ammonia in excreta. If they are overcrowded or the diet is inadequate, feather pecking of wing tips, back and vent is not uncommon. Ducks may have access to an outdoor run, and

Intensive systems for ducks may be fully enclosed, with straw bedding.

many producers, especially in Asia, provide them with a pond. Ponds are not essential for raising ducks, but they may improve feather production and facilitate mating. In China, ducks are raised in large numbers and invariably with access to water. Laying ducks are provided with nest boxes with bedding at ground level and usually against the back wall of the house.

In traditional systems in Asia, ducks are herded in rice fields where they scavenge for fallen rice grains. In the flooded fields, they also feed on snails, fish, insects and small crustacea and are returned to outside or indoor pens at night. They lay their eggs in the early morning before they are released into the fields. The system has a low cost, with low inputs and minimum feed supplementation. The ducks lay seasonally, producing 60–90 eggs per year.

Artificial **incubation** of eggs has caused difficulties in the past, resulting in low hatchability. Treatment of eggs, pre-incubation, and conditions in the incubator differ from those for hen eggs. Pekin ducks are not good sitters, and in Asia Muscovy ducks are often used to incubate their eggs. There are also ingenious traditional incubating systems. Some rely entirely on heat from the developing embryos: the eggs are kept on trays in baskets and are turned twice daily by hand, resulting in a hatchability of > 85%. Artificial brooding of ducklings lasts for only 10–14 days.

For meat production, there may be two or sometimes three diets (0–14 days, 15–35 days and 36–49 days). The first 2 weeks are critical. With the rapid progress in breeding for growth rate and lean deposition, requirements for nutrients, particularly for amino acids, have had to be re-examined. Most of the information on nutrient requirements is difficult to access. As with other poultry, lysine, threonine and methionine are the most critical amino acids. A fixed relationship has been established between lysine and other amino acids ('ideal protein'). Shown in Table 1 are published specifications for meat-type Pekin ducks of a commercial strain. For maximum intake, diets should be pelleted, as ducks do not like powdery feed.

Table 1. Nutrient requirements (g kg^{-1}) of meat-type Pekin ducks for starter (1–21 days) and finisher periods (21–49 days) on a total and digestible basis.

	Starter		Finisher	
Energy (MJ kg^{-1})	12.1		12.6	
Crude protein	220		175	
	Total	Digestible	Total	Digestible
Arginine	12	10	10	7.8
Leucine	14		11	
Lysine	11.6	9.5	9	7.2
Isoleucine	7	6.8	5	4.9
Methionine	4.4	3.4	3.2	2.9
Methionine + cystine	8.6	6.7	7.7	5.4
Tryptophan	2.1		2	1.4
Threonine	7.2	6.2	6.6	5

Specifications for Muscovy and mule ducks are about 10% less. Mineral and vitamin requirements of ducks are similar to those of broiler chickens except for niacin, for which the requirement is higher (55 mg vs. 35 mg kg^{-1}). Zinc requirement is slightly higher and calcium lower for ducks. The ingredients used are the same as for other avian species. Ducklings are highly susceptible to mycotoxins, which may be a particular problem in groundnut meal and maize in the humid tropics.

Pekin egg-laying ducks are now producing almost as prolifically as commercial hens. For maximum production, they are grown to specific target weights for age so that they come into lay at an ideal body weight. There are three diets: starter, grower and developer; then two diets, either layer or breeder, which differ only slightly in that most minerals and vitamins are higher in the breeder diet for deposition in the egg and the developing embryo. Shown in Table 2 are the recommendations for some nutrients used by a large commercial Pekin duck producer for females weighing 3 kg, and those of the smaller Khaki Campbell (1.7 kg) laying a 60 g vs. 80 g egg.

Lysine in the layer and breeder diets is more generous than in diets of commercial brown-egg layers, and those specified for Khaki Campbells. For *foie gras* production, wet ground maize, sometimes with fat, is usually force-fed. There is some discussion as to whether a more balanced diet would be more appropriate to give better carcass characteristics in ducks that are still growing. (DF)

Table 2. Nutrient requirements (g kg^{-1}) for layer ducks during growth and production.

	Starter	Grower	Developer	Layer/breeder	Khaki Campbell
Energy (ME MJ kg^{-1})	11.9	12.1	11.6	11.5	12
Crude protein	220	175	155	195	180
Lysine	11	8.5	7	10.0 (8.0)*	7.9
Methionine	5	4	3	4.0 (3.6)	3.4
Methionine + cystine	8	7	5.5	6.8 (6.4)	6.2
Threonine	6.9	5.7	4.9	7.0 (5.8)	5.7
Tryptophan	2.4	2	1.6	2.2 (1.6)	1.7
Calcium	9	9	9	29	32.5
Phosphorus (available)	5.5	4.2	4	4.5	4.5
Sodium	1.7	1.6	1.6	1.6	1.8

*Digestible basis.
ME, metabolizable energy.

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Dumas method A method for meauring the amount of nitrogen in organic compounds. A weighed amount of sample is mixed with copper(II) oxide and heated in a tube. All nitrogenous compounds present in the sample are converted into nitrogen gas, which is separated from other gases and collected. The volume of nitrogen gas is measured and from this the total mass of nitrogen in the sample is calculated. For nutritional studies it is an alternative to the Kjeldahl method. (SPL)

Duodenum The proximal section of the small intestine, between the pylorus and the jejunum, where digesta leaving the stomach are mixed with secretions from the pancreatic and bile ducts. (SB)

Dyschondroplasia Dyschondroplasia (chondrodystrophy, osteochondrosis) occurs as a congenital lesion in manganese deficiency in calves, associated with impaired synthesis of chondroitin sulphate, and seen as enlarged joints and deformed limbs. Copper deficiency with molybdenosis causes overgrowth of epiphyseal cartilage, associated with impaired activity of lysyl oxidase, and seen as lameness with obvious swellings, in calves, foals and deer. (WRW)

See also: Leg weakness; Manganese

E

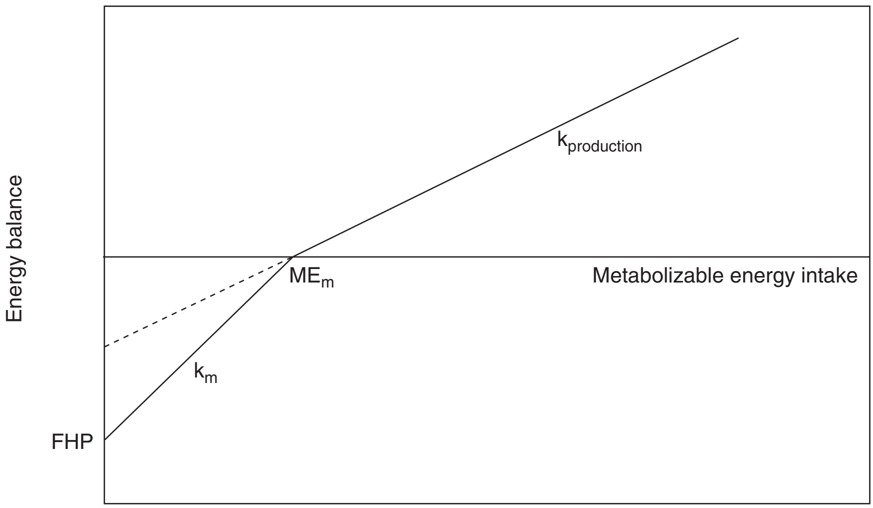
Early weaning Removal of young mammals from their mother at a time before that which is normal under natural conditions. If left undisturbed, piglets will not wean themselves until 12–16 weeks of age. In farm practice, the age at weaning can vary widely and the term 'early weaning' has different meaning in different countries. Within the European Community, animal welfare legislation specifies that weaning may not take place at less than 3 weeks of age. Commercial weaning ages typically vary between 3 and 5 weeks. However, weaning at much younger ages is possible and is practised in some countries as a means of improving both sow output and herd health management. The practice of segregated early weaning involves weaning piglets at 10–18 days of age, whilst still protected by maternally derived antibodies, and removing them to a clean site, away from infectious challenges of the breeding herd. The nutritional requirements of the piglets depend heavily on the age at weaning. Younger pigs have little experience of eating solid food and have an immature digestive enzyme system. They are very susceptible to enteric disorders and therefore require highly digestible diets containing milk products and cooked cereals. (SAE)

See also: Piglets

Eel Some species of the freshwater eel family (Anguillidae) are of importance to aquaculture, with the Japanese eel (*Anguilla japonica*) and the European eel (*A. anguilla*) being the principal cultured species. The family has a worldwide distribution, with the greatest number of species in South-east Asia and the south-western Pacific, including Australia and New Zealand. All species are catadromous, living in fresh water but returning to sea to spawn. The larvae have not been reared successfully and so all culture relies on the availability of wild juveniles (elvers) returning from the sea.

Since the optimum temperature for eel growth is in excess of 20°C, their culture in temperate climates requires the use of recirculation systems for most efficient use of heated water. Pond culture is practised in south-eastern Asia. Cannibalism and variable growth are also problems in eel culture. About 150,000 t of cultured eels are marketed annually, with over 90,000 t being consumed in Japan. Italy, Japan and China are the major producers of eels. (RHP)

Efficiency of energy utilization Energetic efficiency is defined as the ratio between energy output (in useful end-products) and the corresponding energy input. It can be obtained from the relationship between **energy balance** and **metabolizable energy** (ME) intake (see figure). The slope of this line is interpreted as the efficiency of energy utilization (k). Historically, the relationship has been represented as having two linear segments. Below **maintenance**, the slope of the line between fasting heat production (FHP) and the metabolizable energy intake for maintenance (ME_m) indicates the efficiency with which dietary nutrients are used for maintenance purposes, relative to mobilizing body reserves for that purpose. This relative efficiency has been called the efficiency for maintenance (k_m) and depends on both the diet and the body reserves used when the animal is actually fed below maintenance. The slope of the line above maintenance is the energetic efficiency for production (e.g. growth, lactation). With increasing ME intake, growing animals deposit an increasing fraction of energy as lipid (relative to protein). As the energetic efficiencies of protein and lipid deposition differ, the linear relation is therefore overly simple.



Relation between the energy balance and metabolizable energy intake.

Because k_m is a relative efficiency, its value typically exceeds that of the efficiency of production and may even exceed unity. The maintenance energy requirement is essentially a requirement for adenosine triphosphate (ATP). It is difficult to express the efficiency of ATP synthesis as a fraction of energy input 'retained' as ATP; nevertheless, the (relative) efficiency with which nutrients can be used for ATP synthesis can be compared (see table). It appears that glucose and lipids can be used relatively efficiently for ATP synthesis, whereas volatile fatty acids are used 10–18% less efficiently. The efficiency of using amino acids for ATP synthesis is considerably lower. Part of this inefficiency is due to the incomplete oxidation of amino acids. The nitrogen of amino acids is excreted as urea, which involves both a physical loss of energy (as urea) as well as the energy expenditure to synthesize it (2 ATP/N).

The theoretical efficiency of protein synthesis is approximately 85% (*see* **Energy costs**) but the actual efficiency is often lower, due to protein turnover. The efficiency of depositing protein in animal tissue appears to be considerably lower (approximately 60%) than that of depositing protein in animal products such as milk or eggs (75%). Part of this difference may be due to difference in protein turnover between these types of production.

The theoretical energy expenditure for ATP synthesis from various substrates.

Source	kJ mol^{-1} ATP	Source	kJ mol^{-1} ATP
Glucose	74.0	Phenylalanine	124.0
Tri-stearin	75.7	Tyrosine	107.0
Acetate	87.4	Histidine	149.8
Propionate	85.4	Arginine	133.6
Butyrate	81.2	Serine	116.0
Lysine	102.2	Glycine	149.2
Methionine	129.3	Alanine	104.5
Cysteine	178.4	Glutamate	91.8
Threonine	100.0	Proline	92.5
Tryptophan	134.0	Aspartate	103.9
Isoleucine	88.4	Valine	92.7
Leucine	90.6		

In the 20th century, considerable research has been carried out on the energetic efficiency of fat deposition. In ruminants, a major part of the energy supply is derived from the end-products of fermentation. The metabolic utilization of these end-products (and the associated cost of fermentation) is less efficient than that observed in non-ruminant animals. As with the efficiency for ATP synthesis, the efficiency for fat deposition in non-ruminants increases in the order protein, carbohydrate, lipid. (JvanM)

Efficiency of feed conversion (FCE) The efficiency of conversion of feed into productive output (e.g. meat or eggs) is the

major cost in most animal enterprises and so it is often used to indicate the efficiency of the system. Efficiency is commonly expressed as the weight of productive output divided by the weight of feed eaten (the term 'gain:feed' is also used in growing animals). Differences in feed conversion efficiency therefore indicate differences in the availability and utilization of the feed supplied, the proportion of the available nutrients that are required for body maintenance and the nutrient composition of the productive output (the ratios of protein:lipid:ash). Feed conversion ratio (feed:gain) is inversely related to FCE (gain:feed) and is also used to describe the efficiency of feed utilization. (SPR)
See also: Feed conversion ratio (FCR)

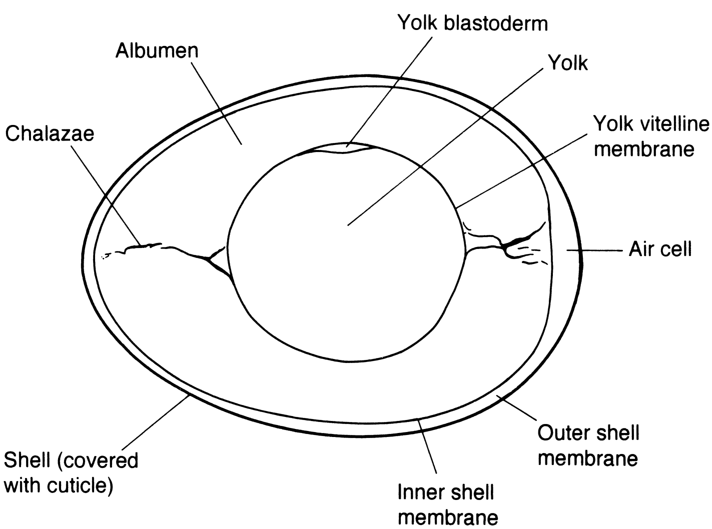
Egg composition The structure of an egg can be defined according to the parts of the reproductive tract. Thus the ovaries form the yolk, the magnum the albumen, the isthmus the shell membranes, and the uterus or shell-gland the shell and cuticle.

The domestic hen's egg has a yolk with a solids content of approximately 50%, of which lipid accounts for 31–36%, protein 15–17%, carbohydrate 0.2–1.0% and ash 1.1%. The composition of the yolk lipid is approximately 66% triglyceride, 29% phospholipid and 5% cholesterol. The energy content of the hen's egg is approximately 623 kJ 100 g^{-1} compared with, for example, 776 kJ 100 g^{-1} for the duck's egg. While the duck's egg contains more total lipid than the hen's egg (13.8 g 100 g^{-1} cf. 10.0 g 100 g^{-1}, respectively), the amounts of total saturated fatty acids differ only slightly. The amounts of total monosaturated fatty acids are significantly greater in duck's eggs (6.5 g 100 g^{-1} cf. 3.8 g 100 g^{-1}), with cholesterol levels in the duck's egg being more than double those in the hen's egg (884 mg 100 g^{-1} cf. 425 mg 100 g^{-1}).

The albumen in the hen's egg consists primarily of water (on average 88%), the remainder being protein (approximately 10%); lipid, carbohydrate and ash each account for less than 1%.

The fibrous shell membranes are proteinaceous and are characterized by high contents of histidine, cystine and proline while being relatively low in glycine.

The bulk (approximately 98%) of the shell is inorganic in nature, being predominantly calcium carbonate in the form of calcite. The organic matrix accounts for the remainder of the shell. The matrix permeates the shell and is linked to the shell membranes via the organic cores that are embedded in the cone layer. The shell may be capped by either an organic (e.g. chicken, grouse) or inorganic (e.g. gannet, shag) layer. The glycoprotein

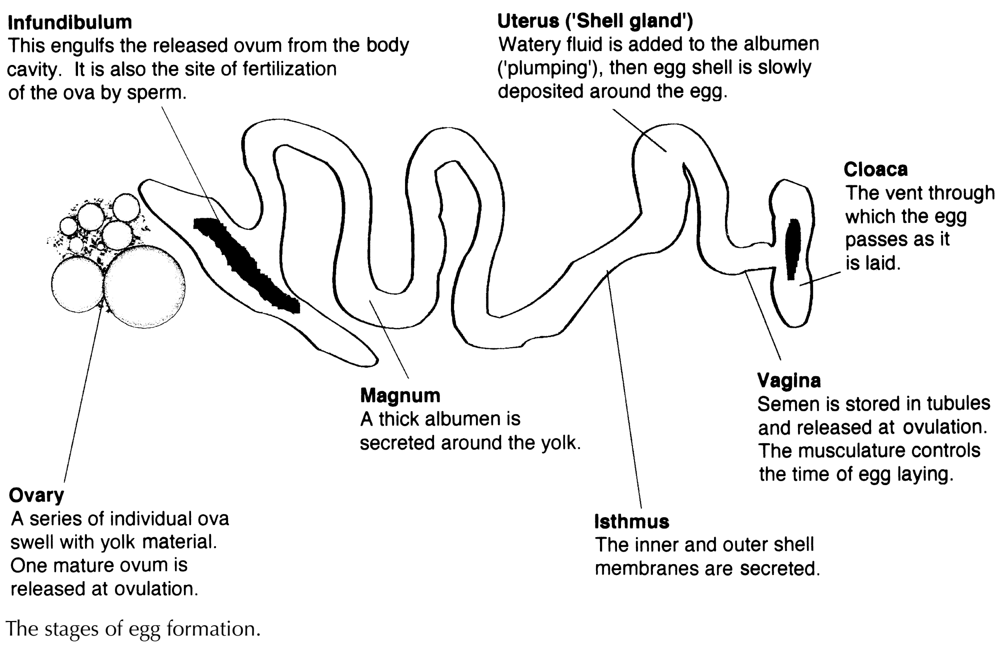


The structure of the egg.

cover on the shell of the hen's egg is constructed from spheres (< 1 μm) forming an uneven layer some 0–13 μm thick. The spheres are mainly protein (90%), the amino acids having a high glycine content. (NS)

Egg formation At hatch, the left ovary of the domestic hen contains several thousand ova, but fewer than 2000–3000 will be ovulated during the bird's natural productive life. The number of ova recruited into the ovarian hierarchy at any one time is rarely more than ten and more commonly only six to eight. When ova are in the hierarchy, yellow yolky material (vitellin) produced by the liver under the influence of oestrogen is transferred to the developing follicles so that each ovum increases its weight by about 2 g day^{-1} over a period of 9–10 days. Ovarian follicles have a blood supply to most of their surface, with the exception of a narrow avascular strip called the stigma. During the final day of follicular development, plasma progesterone in the follicular veins rises, stimulating the hypothalamus to release GnRH, which, in turn, stimulates the release of luteinizing hormone by the anterior pituitary, triggering ovulation. At ovulation, the follicle splits along the stigma to release the ovum. The empty follicle, which is anatomically similar to the mammalian corpus luteum, starts to degenerate within a day of ovulation and has disappeared within about a week of ovulation. During this time, it produces a hormone that plays an important role in controlling the expulsion of the fully formed egg from the vagina at oviposition.

Within 15 min of its release from the ovary, the ovum is engulfed by the funnel-shaped proximal end of the oviduct (infundibulum). After a further 15 min, the ovum passes into part of the oviduct called the magnum where, over a 3 h period and in response to mechanical contact with the oviducal walls, albumen proteins are deposited on to it. Moving on to the isthmus, the developing egg spends the next 1.5 h having fibres extruded on to it which form the inner and outer shell membranes. During the initial 5 h in the uterus or tubular shell gland, the egg is plumped by the accumulation of water and electrolytes. Additionally, the fibres of the shell membranes are organized into the mamillary cores that will fix the mineral shell to the shell membranes. The egg finally enters the shell gland pouch where, over a period of 10–14 h, calcium carbonate crystals are



The stages of egg formation.

deposited to form the shell proper. Calcium ions (Ca^{2+}) for shell formation may be from the diet, via the upper small intestine blood system, from a labile form of calcium phosphate in medullary bone stores in the long bones or, in desperate situations, from cortical bone. In brown-shelled eggs, the pigment porphyrin is secreted in the final 6–10 h of egg formation. Total egg formation time varies with lighting regime, age and size of egg, but is generally about 24–25 h. (PDL)

Egg production Egg production systems differ across the world, but there is a tendency for the larger companies to use cage-based systems for housing hens for egg production, while the smaller companies and home producers use extensive systems. Although domestic hen eggs dominate the world table-egg market, other types of poultry are also kept for their eggs. The Indian Runner duck, for example, is kept for its eggs across the world, but particularly in Asia. Ducks are kept almost exclusively in floor-based or free-range systems.

Cage-based systems first became popular for hens because they were perceived to offer a means of keeping birds in such a way that they had ready access to feed and water while being protected from adverse weather conditions, predators and pathogenic organisms. The rapid development of the cage system and, in particular, the mechanization that allowed cages to be stacked six or more tiers high, allowed large numbers of birds to be kept in a building with a relatively small floor area. While egg production from well-run cage units is very high and the overall mortality low, public concerns about the welfare of birds kept in these so-called intensive systems has led in Europe (with similar concerns now being expressed in the USA) to the proposed replacement of the traditional cage system by ‘enriched cages’. These cages allow the birds greater freedom of movement; they provide for dust bathing and perching and have abrasive surfaces for keeping the claw at an acceptable length. Alternative systems of production have been increasing in popularity, particularly for the producer who sells eggs into a niche market. These more extensive systems, which include ‘barn’ and ‘free-range’, are characterized by larger colony sizes and the ability of the bird to move freely within the housing and, for free range, to access land outside the housing.

The type of system used to house the laying bird determines in part the bird’s nutritional requirements. The energy requirements of birds in extensive systems are higher than those of birds kept in cages because they are more active and, in the case of birds allowed access to range (especially in northern climates), exposure to lower environmental temperature. As energy requirements influence the amount of feed consumed, it is to be anticipated that feed intake is depressed at temperatures above the house set temperature and increased at lower temperatures. Energy requirements will also be affected by egg output – an egg contains up to 418 kJ of energy.

The protein requirements of the laying hen vary according to the number of eggs being laid. The percentage protein in the diet increases to a maximum of approximately 19% at peak production and then falls back to a pre-laying level that may be only 15%. The amino acids that have a significant impact on the laying bird are arginine, lysine, methionine, cystine and tryptophan. When an imbalance in the amino acid profile occurs it is frequently a deficiency in methionine that is identified. If the environmental temperature remains elevated for a significant period of time, the birds’ feed intake is lower (as discussed above) and the percentage protein in the diet may need to be increased.

Shell quality is a nebulous concept, determined in part by the egg’s end-use (i.e. table, processing or hatching), but one of the key nutritional parameters that is cited as being related to shell quality is the calcium requirement. This is to be expected, given that the shell consists predominantly (98%) of calcium carbonate in the form of calcite (cf. aragonite or vaterite). The calcium and phosphorus requirements of the bird change depending on the number of eggs being laid, the age of the birds (calcium uptake becomes less efficient as the bird ages) and the amount of feed being consumed (e.g. high temperatures or feed high in energy both depress feed intake). These factors result in the percentage calcium requirement varying from $< 2\%$ to $> 5\%$, depending on the environment, feed constituents, age of the bird, stage in the production cycle, etc.

Another factor that needs to be taken into account is the form in which the calcium is presented to the bird. Shell formation takes some 18 h and tends to take place during the hours of darkness, with the egg being laid soon after the lights are switched on. Calcium should be provided, therefore, in a form that can be resorbed by the bird during the hours of darkness, when the bird is unlikely to be eating. If calcium is provided as a finely ground powder it is likely to pass rapidly through the gizzard and be unavailable to the bird at the time when it needs it most. For this reason the majority of the calcium should be provided as coarsely ground limestone or oyster shell. Laying birds will, if the demand for calcium is high (as in high-output lines of laying hens), supplement dietary calcium with calcium that has first been incorporated into the labile cortical bone. Cortical bone will be maintained at the expense of the less labile medullary bone if the demand for shell calcium is constant. Eventually this will cause so-called 'cage layer fatigue' and the associated increase in bone breaks reported in high-output flocks.

Phosphorus is not incorporated into the shell in any significant amount but, because of its role in bone biology, its inclusion in diets can affect shell quality. Recommended daily intakes of available phosphorus in layer rations are in the order of 400–450 mg. It is important to note that this figure refers to *available* phosphorus, as some 40% of phosphorus in a laying-hen diet is present as phytate, a bound organic form that is difficult for the bird to access.

It is common practice to feed pigments to laying hens in order to provide the consumer with eggs that have a yolk of a consistent colour, irrespective of the hen that laid the egg or the point in the production cycle.

(NS)

See also: Egg composition; Egg formation; Eggshells; Eggs

Eggshells Eggshells consist primarily of calcium carbonate in the form of calcite. Shell mineralization commences in the isthmus region of the oviduct, immediately prior to the egg entering the uterus or shell-gland where the bulk of mineralization takes place over about 18 h. During this period the opportunity exists for shell formation to be disrupted by a number of events or conditions.

Disease (e.g. infectious bronchitis) or nutritional factors (e.g. high levels of lathyrogens) can cause wrinkled shells. The wrinkled shell results from either the failure of the shell membranes, which form the foundation for the shell, to tension correctly during plumping (e.g. as caused by infectious bronchitis) or the structure of the membranes being perturbed (e.g. as caused by lathyrogens). The normally smooth texture of the shell results from the distinct outer layer of the shell (surface crystal layer) being overlaid by an organic layer – the so-called cuticle.

If the bird is stressed it is possible that the egg can be expelled from the oviduct before the mineralization process has been completed. The resultant partially formed shell will, depending on its thickness, feel rough when compared with normal shells, mineralization having proceeded as far as the formation of the cone or palisade layers. Also, where mineralization has not proceeded beyond the fusion of the cone tips, the shell will be flexible: the form and strength are provided by the shell membranes and influenced by the underlying albumen.

The presence of two eggs in the oviduct at the same time can also cause thin-shelled eggs. If both eggs arrive at the same time in the oviduct they will have equally thin shells, but if one arrives much earlier than the other it will have all, or almost all, of its full complement of calcium carbonate while the other egg will have little or no shell. In the former circumstance the eggs will have a 'slab-sided' appearance caused by the two eggs pressing against each other in the shell gland.

So-called equatorial or shoulder bulges (where the shell has a thickened appearance around the equator) are the result of the shell being broken around the equator during the early stages of mineralization. Typically this is caused by the bird being stressed; the consequent constriction of the oviduct results in the shell being broken. The crystalline calcium carbonate shell is formed by a process known as epitaxis. Thus the existing crystal face dictates the crystal form. If the mineralizing face is disrupted, as occurs when the shell is broken, subsequent mineralization will take place on an uneven surface, both physically and in terms of activation energy, causing the uncontrolled and irregular deposition of calcite.

Mineralization in the shell gland is terminated in part by a rise in the concentration of phosphate; however, if stressed, the bird may secrete excess phosphate into the shell-gland, causing calcium phosphate to be deposited as a 'white dusting' or 'splashing' over the surface of the shell. (NS)

Eggs As a source of nutrients the egg presents the consumer with a number of benefits over many other foods. Eggs are rich in balanced proteins (with a biological value of 93.7%) and are a good source of unsaturated fatty acids, vitamins A, B, D, E and K, iron, phosphorus and trace minerals. Concerns about the effect on blood cholesterol of eating eggs are now considered to have been overemphasized: dietary cholesterol intake has little effect on plasma cholesterol levels in healthy individuals.

Cooking may destroy some nutrients or can enhance nutrient availability. Thus riboflavin levels have been shown to be reduced by up to 20% by some forms of cooking. While unlikely to have a significant impact in healthy adults eating a balanced diet, the egg proteins ovomucoid and ovoinhibitor have been shown to be have anti-tryptic activity. Similarly the protein avidin binds to biotin making in unavailable. Heat treatment can destroy these anti-nutritive factors and thus release vitamins, improving their availability.

Eggs are used in foods not only for their nutritive value but also for their functional properties. The albumen proteins allow eggs to be used as coagulators (e.g. in custards, scrambled egg) and foaming agents (e.g. in cakes, meringues) while the yolk is used extensively as an emulsifying agent in, say, batter, mayonnaise and salad dressings. The yolks may also be used as colorants; for example, the xanthophylls provide the pale golden colour associated with cakes and pasta. (NS)

Eicosanoids A group of physiological substances derived from 20-carbon unsaturated fatty acids. The source of the fatty acids for the biosynthesis of these compounds is from the two position of membrane phosphatidylcholine. Eicosanoids are classified as **prostaglandins**, **thromboxanes**, **leukotrienes** and **lipoxins**. They are local hormones and act through cell membrane receptors and signal transduction to elicit cellular change. Two pathways are involved in their synthesis: the cyclooxygenase pathway results in the production of prostaglandins and thromboxanes; and the lipoxygenase pathway produces leukotrienes and lipoxins. Dihomo-γ-linolenic acid (eicosatrienoic acid, $\Delta^{8,11,14}$) gives rise to a series of prostaglandins, thromboxanes and leukotrienes. Arachidonic acid (eicosatetraenoic acid, $\Delta^{5,8,11,14}$) gives rise to a separate series of prostaglandins, thromboxanes and leukotrienes and lipoxins. Finally α-linolenic acid, after being converted to a 20-carbon unsaturated fatty acid (eicosapentaenoic $\Delta^{5,8,11,14,17}$), gives rise to a separate series of prostaglandins, thromboxanes and leukotrienes. These compounds are potent and can have physiological effects at concentrations as low as 1 ng ml^{-1}. (NJB)

Eicosapentaenoic acid A 20-carbon fatty acid with five double bonds (C20:5 $\Delta^{5,8,11,14,17}$), a member of the n-3 family. It can be formed from α-linolenic acid (C18:3 $\Delta^{9,12,15}$) by 2-carbon elongation and desaturation and is involved in production of prostanoids via the cyclooxygenase pathway and leukotrienes by the lipoxygenase pathway. (NJB)

See also: Eicosanoids

Elaidic acid An 18-carbon unsaturated fatty acid, $CH_3{\cdot}(CH_2)_7{\cdot}CH{=}CH{\cdot}(CH_2)_7{\cdot}COOH$, the *trans* form of oleic acid, the form encountered in nature. (NJB)

Elastase An **endopeptidase** (pancreatopeptidase E; EC 3.4.21.36) that hydrolyses those peptide bonds that involve neutral amino acids: it is particularly active on elastin. It is secreted from the pancreas as the precursor proelastase, which is activated in the duodenum by trypsin. (SB)

Electrolytes Soluble ions in body fluids. Electrolytes participate in maintaining electrochemical gradients and osmotic pressure. Sodium, potassium, magnesium and calcium are the major cations and chloride, phosphate, bicarbonate, organic acids and protein the major anions. Sodium is the major extracellular cation; potassium and magnesium are the major intracellular cations. Phosphate, proteins and bicarbonate make up the majority of the intracellular anions. It is the unequal distribution of ions across cellular membranes that generates electrochemical potentials and the osmotic pressure required for cells to function. (NJB)

Embden–Meyerhof pathway: *see* Glycolysis

Embryonic development: *see* Fetal growth

Emulsifier A substance used to stabilize an emulsion, in animal feeding most commonly to make a liquid mixture of fat and water. The table gives emulsifiers that are listed in the Feedingstuffs (UK) Regulations 2000.

Emulsifier	E number
Lecithins	E322
Propylene glycol alginate	E405
D-Glucitol	E420
Mannitol	E421
Glycerol	E422
Sodium, potassium and calcium salts of edible fatty acids	E470
Monoacyl and diacylglycerols	E471
Esterified monoacyl and diacylglycerols	E472
Sucrose esters of fatty acids	E473
Mixture of sucrose esters and monoacyl and diacylglyerols	E474
Polyglycerol esters of non-polymerized edible fats	E475
Propylene glycol esters of fatty acids	E477
Stearoyl-2-lactylic acid	E480
Sodium stearoyl-2-lactylic acid	E481
Calcium stearoyl-2-lactylic acid	E482
Stearyl tartrateq	E483
Glycerol poly(ethylene glycol)ricinoleate	E484
Dextrans	E486
Sorbitan monostearate	E491
Sorbitan tristearate	E492
Sorbitan monolaurate	E493
Sorbitan mono-oleate	E494
Sorbitan monopalmitate	E495

(MG)

Endocrine glands Ductless glands that secrete hormones into the bloodstream. Unique hormones are released by each of the endocrine glands. The pineal gland is in the brain near the third ventricle, and the pituitary is in the brain near the base of the skull. The thymus is at the base of the neck near the heart and the thyroid lies on each side of the trachea. There are two parathyroids, on the left and right sides of the trachea, next to the thyroid. The two adrenal glands are located above the kidneys and the pancreas is located near the liver. The two ovaries are located in the lower abdomen, while the two testes are normally outside the body in the scrotum. (NJB)

Endogenous protein Endogenous protein comprises all non-dietary nitrogen (N) compounds entering the lumen of the digestive tract. These N compounds include enzymes, the glycoproteins of saliva, gastric juice, bile and pancreatic secretions and mucus (mucopolysaccharides) secreted from the mucus cells throughout the intestinal tract. The largest component is contributed by desquamated intestinal cells, which can amount to 30–60% of the total protein that enters the intestinal lumen. Trypsin is the most abundant of the pancreatic enzymes, and proteases the most abundant class of enzymes. **Urea** is an important non-protein component of endogenous nitrogen.

Most endogenous proteins are digested by pancreatic proteases and are processed identically to dietary proteins. A few proteins (e.g. intrinsic factor that is necessary for absorption of B_{12} in the ileum) largely escape luminal digestion.

Generally, most of the endogenous protein from the stomach and small intestine is reabsorbed (at least 0.65–0.75) in the ileum. Most unreabsorbed endogenous protein is converted to microbial protein, some in the ileum but more in the large intestine. N from fermented endogenous protein utilized for energy by the bacteria is either incorporated into microbial protein or absorbed as ammonia in the hindgut, increasing apparent overall N digestibility.

Endogenous protein loss changes with feed intake and, in feed evaluation, it is practical to express endogenous protein loss in relation to the dietary intake, i.e. in g kg^{-1} dry matter (DM) intake. The amount and amino acid composition of endogenous protein is influenced by a number of dietary factors, in particular fibre and **antinutritional factors** (ANFs). In the pig, endogenous protein losses from the ileum vary from less than 10 to more than 30 g kg^{-1} DM intake. Endogenous losses in the faeces are smaller and less variable.

Endogenous protein can be considered to be composed of two fractions: a minimal (basal) loss and a feed-specific (extra) loss, mainly resulting from the effects of dietary protein, fibre and ANFs. The total loss (ileal or faecal) can be measured after a preliminary labelling of the experimental animals with ^{15}N and measuring the dilution of dietary ^{14}N in the digesta or faeces by comparing the ^{15}N:^{14}N ratio in the digesta or faeces with that of the blood. The basal loss can be measured by feeding N-free diets (or diets with 100% digestible protein at ileal level) that do not contain fibre or ANFs.

Endogenous protein loss has a significant influence on experimentally determined values for the digestibility of protein and amino acids. Their digestibility is now commonly measured at the terminal ileum because amino acids are practically not absorbed in the large intestine but are metabolized by the microflora which change the amount and composition of the resulting protein that appears in faeces. Correction for the basal endogenous losses of amino acids is now commonly used for the calculation of true or standardized ileal digestibility of amino acids. Endogenous protein in the ileal digesta of growing pigs has a characteristic amino acid composition, with a relatively low contribution of most essential amino acids (except threonine, cystine and tryptophan) compared with ideal protein. (SB)

See also: Protein digestibility; Protein digestion

Further reading

Boisen, S. and Moughan, P.J. (1996) Dietary influences on endogenous ileal protein and amino acid loss in the pig – a review. *Acta Agriculturae Scandinavica, Sect. A, Animal Science* 46, 154–164.

Endopeptidase A proteolytic enzyme that has the capacity to hydrolyse internal peptide bonds in a protein, in contrast to an exopeptidase, which hydrolyses terminal peptide bonds. Important endopeptidases in the digestive tract include pepsin and rennin in gastric secretions, enterokinase from duodenal epithelial cells and trypsin, chymotrypsin and elastase from the pancreas. (SB)

Endorphins Peptides produced by the brain and having a morphine-like effect. They are part of the pro-opiomelanocortin peptide family and are derived from the 31-amino-acid carboxyl terminal of the 91-amino-acid β-lipotropin. β-Endorphin contains the full 31-amino-acid sequence; α- and γ-endorphins have 15 and 14 amino acids, respectively. Endorphins bind to the same receptors as do opiates and play a role in pain perception. (NJB)

Endosperm In angiosperm seeds, the tissue that surrounds the embryo. The endosperm and embryo together comprise the inside of cereal grains, with the endosperm forming the major component. Starch and protein stored within the endosperm support the initial growth of the germinating embryo. The endosperm accounts for the nutritional and economic importance of cereal grains and oilseeds. (ED)

See also: Cereals; Grain

Endotoxaemia The presence of endotoxins in the blood. This generally occurs with the proliferation of Gram-negative bacteria, such as that seen with *Escherichia coli* mastitis. Endotoxins are highly inflammatory and pyrogenic and result in massive increases in vascular permeability. A common result of endotoxaemia is loss of circulating blood volume and loss of cardiovascular function (shock). (BLS)

Endotoxins Heat-stable bacterial toxins produced primarily by Gram-negative bacteria. They are included in the bacterial lipopolysaccharide cell wall. Endotoxins are highly pyrogenic and cause extensive increases in vascular permeability. They are similar regardless of the species of bacteria and have similar activity and pathogenicity.

(BLS)

Energy The capacity to do work. Energy exists in many forms, including chemical energy, mechanical energy and heat. On earth, the primary source of energy is the sun. Solar radiation warms up the atmosphere and surface of the planet and some of it is absorbed by chlorophyll in growing plants to synthesize organic material from carbon dioxide and water. This process, photosynthesis, stores energy in chemical form as plant tissue. The chemical energy of plants may in turn be used in the short term as fuel for fires or as food for humans and animals, or it may be stored over millennia, building up reserves of fossil fuel. Metabolism of food makes energy available for the maintenance of essential body functions, such as respiration and circulation of the blood, and for growth. Metabolism is an oxidative process in which carbon from the food is combined with atmospheric oxygen, with the release of energy as heat, but the total amount of heat or energy produced from the oxidation of any food material is very nearly the same whether it is burned quickly or digested in the body. It may not be identical, because the final state (temperature and pressure) of the products of the reaction may differ between the two processes.

In the body, some of the energy of food is converted into other forms of chemical energy (body growth, milk, eggs, etc.) and by draught animals into mechanical energy, but a high proportion of the total energy intake is returned to the environment as heat or as the residual chemical energy of excreta. Even mechanical energy is rarely retained in a useful retrievable form, but lost as heat in overcoming, say, the friction of a plough or cartwheels; an exception is when animal power is used to raise loads, such as water out of a well.

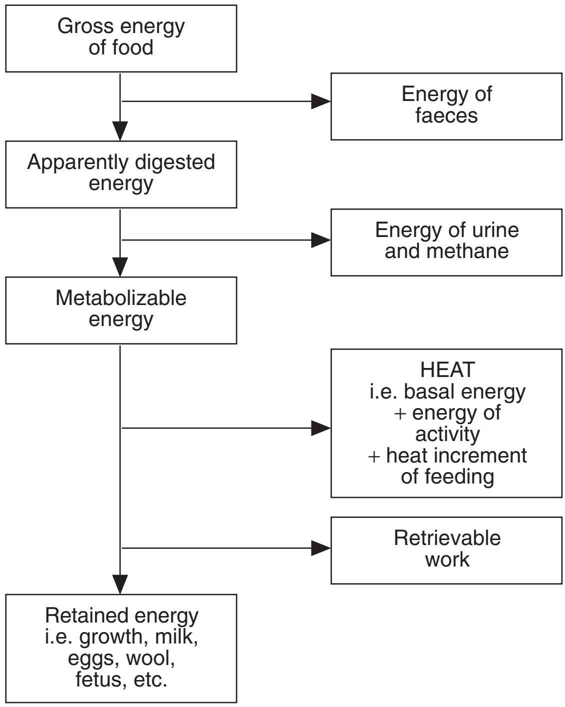
Because of its many diverse forms, energy may be measured in a variety of units. Mechanical energy is defined in terms of the energy expended when a mass of material is moved a given distance against a specified force; electrical energy is that expended when a given level of power is consumed for a specified time; thermal definitions of energy relate to the heat required to increase the temperature of a mass of water by one degree. All energy units are precisely related to one another and some useful conversion factors include the following.

1 joule (J) = 1 watt second (W s) = 0.239 calories (cal)
1 kilojoule (kJ) = 0.278 watt hours (W h) = 0.239 kilocalories (kcal)
1 megajoule (MJ) = 0.278 kilowatt hours (kW h)
1 calorie = 4.184 joules (J)
1 kilocalorie (kcal) = 4.184 kilojoules (kJ) = 1.162 watt hours (W h)

(JAMcL)

See also: Energy balance; Energy costs; Energy metabolism; Energy units; Energy utilization; International units

Energy balance The principle of conservation of energy necessitates that food energy intake is balanced by energy retained or lost. The partition of the gross (chemical) energy of food into its major subdivisions is illustrated in the figure. Some food is undigested, resulting in loss of energy as faeces. The difference between the energy content of the food and the energy content of the faeces is termed the apparently digested energy; the adjective 'apparently' being included because some faecal material is not of immediate dietary origin but consists of cells or secretions of the alimentary tract. Cellulose and other complex food constituents that are not susceptible to digestion by the animal's own digestive enzymes are converted into digestible end-products by bacterial fermentation especially in the rumen, but also in the gut of all species. This results in the production and expulsion of combustible gases methane and, to a lesser extent, hydrogen. The **digestible energy** consists of nutrients that are absorbed from the gut. Waste products from their further metabolism are lost as energy excreted in urine; the remaining energy is the **metabolizable energy** of the food. It has to provide for the energy requirements of the body. Firstly, there is the basal energy requirement for maintenance of respiration, blood circulation and other vital func-



tions. The minimal rate of energy utilization by a resting animal in a comfortable environment is known as the basal metabolic rate; to this must be added the extra energy cost that occurs after taking a meal (the **heat increment of feeding**) and any additional energy required for activity, thermoregulation or other muscular work. Any metabolizable energy left over from meeting these demands may be retained in the body as new tissue growth or used for the production of milk, wool or eggs.

If the metabolizable energy of the food is insufficient to meet the demand, energy retention can be negative and the body consumes its own energy reserves. Normally the level of food intake is regulated to meet the demands of maintenance plus growth in the young, or production in the pregnant or feeding mother; otherwise excess food intake leads to the deposition of body fat. Conversely, a deficiency leads eventually to emaciation.

The gross energy of food, the energy retained in the body and the energy of faeces, urine and combustible gases are all forms of chemical energy. The energy concerned with body function and activity is non-chemical and is generally converted into heat. In most forms of exercise, mechanical work (like the work involved in vital body functions) is transformed into heat in the course of its execution. The rate at which metabolic heat is produced in the body is known as the metabolic rate or as the rate of heat production.

In accordance with the principle of conservation of energy, the heat balance equation may be written as follows:

Gross energy of food = energy of faeces
+ energy of urine
+ energy of methane
+ retained energy
+ retrievable mechanical work
+ heat production.

It is possible, with varying degrees of difficulty, to measure all of these energy components in a living animal. Food, faeces and urine may be collected and sampled; their energy contents can then be measured using a bomb calorimeter. Heat production can be measured by one of the techniques of **calorimetry**.

Using **indirect calorimetry** by enclosing the animal in a respiration chamber or by employing a mask technique, heat production is calculated very accurately from the rates of oxygen consumption and carbon dioxide production. The energy loss as combustible gases can also be measured in a respiration chamber. Energy retention can be measured using the **carbon and nitrogen balance** method, or by the difference between metabolizable energy and heat production.

In addition to the overall energy balance, there must also be a balance between the rates of heat production and heat loss, otherwise body temperature alters. Healthy warm-blooded animals usually have an efficient thermoregulatory system for maintaining deep body temperature within close limits but alterations in the temperature of regions close to the skin surface and in the limbs can be considerable, resulting in some storage of heat. The rate of heat loss by an animal can be measured in a direct calorimeter. When a direct animal calorimeter also has a facility for indirect measurements, it is possible to measure the differences between rates of heat production and loss and to relate these to changes in body temperatures. (JAMcL)

See also: Heat balance

Energy content: *see* Energy value

Energy costs It is difficult to give a precise estimate for the energy cost of maintenance functions. According to Baldwin (1995), nervous tissues contribute 15–20% to the maintenance energy requirement and **protein turnover** 10–15%; Na^+ resorption by the kidneys, heart function and respiration contribute 6–11% each. Part of the energy cost is due to the utilization of **adenosine triphosphate (ATP)** for physiological functions; another part is related to an inevitable loss of energy (as heat) in the biochemical transformation of dietary nutrients to ATP and animal products. For example, when glucose is used, 81% of the energy input can be conserved as lipid. However, as ATP is formed during this synthesis, the overall efficiency is slightly higher (84%). Theoretically, the efficiency of using dietary lipid for lipid deposition exceeds 97%. The only cost involved is the ATP utilized for the resynthesis of triacylglycerides from fatty acids and glycerol.

The efficiencies mentioned above are based on the minimal costs of converting one nutrient to another. Other costs (i.e. related to digestion, absorption and transport) are not specifically accounted for but are included in experimental values of efficiency. For example, after a meal, part of the digested energy is stored (temporarily) as glycogen in the muscle or liver. Depending on how the energy of glycogen is recovered, this temporary storage of glucose is associated with an additional energy cost of 3–5%. Likewise, animals may store energy as body lipid, which may be used later for ATP synthesis. Baldwin (1995) calculated that storing glucose temporarily as fat is associated with an additional energy cost of 23%. Apparently, this is the price paid for storing energy in a very compact form.

Protein turnover (i.e. the repeated synthesis and hydrolysis of peptide bonds) also represents a considerable energy cost. If it is assumed that 100 g of protein is the equivalent of 1 mol of amino acids and that five ATP (from glucose) are required for protein synthesis, the maximum efficiency is $2380/(2380 + 5 \times 74) = 87\%$. Using sources other than glucose for ATP further reduces the efficiency of protein deposition. One additional cycle of degradation and synthesis requires (at least) another five ATP, thereby reducing the efficiency to 76%. The value of k_p derived from experiments (approximately 60% for protein deposition in growth) suggests that considerably more ATP is required. The extent of protein turnover is affected by several factors. Visceral organs (especially the gastrointestinal tract, liver and kidneys) contribute to protein turnover and to the overall energy expenditure. There are also indications that dietary protein increases protein turnover. (JvanM)

See also: Efficiency of energy utilization

Key reference

Baldwin, R.L. (1995) *Modelling Ruminant Digestion and Metabolism*. Chapman & Hall, London, 578 pp.

Energy deprivation: *see* Starvation; Undernutrition

Energy expenditure Synonymous with **heat production**. That part of the metabolized energy which is not productively retained as growth, milk, eggs, etc., but is lost as heat. (JAMcL)

Energy intake Energy intake is a function of species, breed, body mass, age, physiological state, the form and composition of the diet and environmental factors. Energy intake can be expressed in terms of gross, digestible, metabolizable or net energy. Because of the relatively wide differences in digestibility coefficients of feeds, particularly for ruminants, it is generally preferable to express energy intakes as **digestible energy** (DE) or **metabolizable energy** (ME) intake, both of which are reasonably easy to measure.

One way of describing energy intake is in terms of multiples of the **maintenance** energy requirement, i.e. the amount of energy needed to maintain zero energy balance. Growing pigs and high-producing lactating cows and sows can consume up to about 3 times maintenance (3 M), whereas egg-laying breeds of domestic poultry voluntarily consume about 1.5 M and mature non-lactating animals tend to consume between 1 and 1.5 M. Whilst energy intake increases as body weight increases, the response is not linear. With pigs, for example, a study on individually fed growing boars from 20 to 300 kg showed that DE intake (MJ day^{-1}) was 4.0 $W^{0.5}$ but some studies have erroneously concluded that intakes peak around 100 kg liveweight and subsequently decline. Similar results to those for the boars have been reported for sheep fed very highly digestible diets. Animals tend to eat to a predetermined energy 'ceiling' unless there is a physical limitation to intake, such as low digestibility of the feed. Such a situation is more likely with ruminants on high-forage diets. With non-ruminants, increasing the energy content of the feed tends to reduce dry matter intake but energy intake tends to increase. For example, a 10% increase in energy content of a broiler diet gives approximately a 5% increase in energy intake.

Energy intake is also affected by the physical form of the feed; for example, chop length of forage affects the voluntary intake of ruminants. Poultry, particularly broilers, consume up to 10% more energy as pelleted feed compared with mash. Energy intake is also affected by **environmental temperature**: at low temperatures (outside the thermoneutral zone) energy intake tends to increase to cover the additional heat loss incurred. The opposite effect occurs at high temperatures, as the animal has difficulty in disposing of the heat increment arising from metabolism of feed. Domestic fowl have a poorly defined thermoneutral zone and energy intake tends to increase linearly with falling temperature below 30°C. Within the range 15–30°C the reduction in intake per °C increase in temperature averages approximately 1.6%.

Other environmental factors that affect energy intake include feed accessibility, trough design and group size. Pigs in groups tend to consume 10–15% less energy than those housed singly and large group size and limited trough space further reduce energy intake. Large differences in intake between individual animals under uniform conditions have been reported in several studies. For example, the average DE intake of pigs over the liveweight range 35–90 kg was 28 MJ day^{-1} but individual intakes varied from 20 to 38 MJ day^{-1}.

Under normal production conditions cattle are usually encouraged to maximize energy intake and this applies, in most cases, to pig and poultry meat production. However, sows are normally restricted during gestation to about 26 MJ DE day^{-1} to avoid excessive weight gain and maintain fecundity. After peak egg production it is usually desirable to restrict laying hens to approximately 1.2 MJ ME day^{-1} to maximize feed efficiency. Broiler breeders have to be restricted during growth and the laying cycle to prevent leg and fertility problems. (KJMcC)

See also: Environment–nutrition interactions; Voluntary food intake

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Agricultural Research Council (1980) *The Nutrient Requirements of Ruminant Livestock*. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Agricultural Research Council (1981) *The Nutrient Requirements of Pigs*. Commonwealth Agricultural Bureaux, Farnham Royal, UK.
AFRC (1993) *Energy and Protein Requirements of Ruminants*. CAB International, Wallingford, UK.

Energy metabolism All the energy exchanges that occur in a living animal or cell. They originate from the chemical energy of food, which is the prime source of energy for all body processes and activities, including growth.

Only part of the chemical energy of food can be utilized in the body; some food constituents can be assimilated immediately through the intestinal walls into the bloodstream; some have first to undergo chemical transformation in the gastrointestinal tract into a more digestible form; some are totally indigestible. Indigestible and waste by-products are voided as faeces and urine. In all species, but especially in herbivorous animals, which pre-digest food by fermentation in the rumen, a further waste product is methane. The remaining energy is **metabolizable energy**, which is involved in many chemical transformations in the organs of the body. This part of the process is termed intermediate metabolism. It includes some reactions that build up energy-rich compounds (anabolism) and others that break down energy-rich compounds to release energy (catabolism). Anabolic and catabolic processes are continuous and simultaneous, with an equilibrium between them. A prime example is the energy-rich compound **adenosine triphosphate** (ATP), which can release energy on being reduced to adenosine diphosphate (ADP). Such compounds may be used to provide energy quickly at high rates for, say, muscular movement, the energy store being replenished later by reconversion of ADP to ATP, this being coupled to the oxidation of food-derived nutrients that provide the energy required. This is an example of short-term energy storage; such temporary storage is quantitatively small in comparison with the overall level of energy metabolism. In a wider sense, growth is an anabolic process and consumption of body fat during undernourishment is a catabolic one; these are long-term and quantitatively large methods of energy storage and de-storage.

The metabolizable energy is available to promote synthesis of body tissue (meat or fetus), milk, wool or eggs; it can also be used by draught animals to do mechanical work. A large proportion is transformed into heat that is lost to the environment. The level at which metabolism proceeds is determined by both energy requirement and the availability of food. A minimal energy level (**basal metabolism**) is needed to maintain essential body functions such as respiration and blood circulation. Eating itself involves further energy expenditure in finding, chewing and absorbing the food (known as the **heat increment of feeding**). Additional energy is required for activity and mechanical work. Only after these requirements have been met is excess metabolized energy available for retention in the body as growth or production (milk, eggs, wool or fetus). Production rates are generally increased up to a certain limit by additional food intake. Production and skeletal growth in the young, however, do not cease if food intake is insufficient, but proceed by catabolism of body reserves, mainly fat.

All metabolized energy not retained for production, growth or retrievable work is converted into heat. In warm environments, most of the heat produced is wasted and animals have to find means to get rid of the excess heat to the environment. Conversely, in cold environments, heat is useful to the animal; indeed in very cold environments animals may be forced to metabolize additional food energy simply in order to keep warm.

(JAMcL)

Energy requirements In a thermoneutral environment, the energy requirement of an animal is the sum of the energy retained in animal products and the associated **adenosine triphosphate (ATP)** costs (i.e. the cost of ingestion, digestion and metabolism). The energy content of secreted animal products (e.g. milk or eggs) can be determined relatively easily in a **bomb calorimeter**, whereas the energy retained by the animal (e.g. growth or gestation) requires a **comparative slaughte**r technique or (indirect) **calorimetry**. It is virtually impossible to determine directly the ATP required for physiological processes. The main problem is that energy is released as heat during the transformation of nutrients to ATP as well as during the actual ATP utilization. Consequently, energy requirements are expressed in terms of energy, such as **metabolizable** or **net energy**.

Maintenance

The **maintenance** energy requirement is defined as the energy requirement of a non-producing animal (i.e. no production of milk, eggs or wool, no fetal growth and no net deposition of body protein or lipid). In addition, it is assumed that the animal is healthy and is kept in a thermoneutral and stress-free environment. Physiological components of maintenance include blood circulation, nutrient transport and absorption, respiration, excretion and tissue turnover that is unrelated to production. Although there is general agreement on the conceptual and qualitative description of maintenance, it is more difficult to quantify maintenance unambiguously in farm animals. During fasting, animals catabolize body reserves in order to supply ATP for essential body functions and so fasting heat production is often used as an indicator of the maintenance requirement; however, it is an indirect measurement because the efficiency with which body reserves are used for ATP synthesis is not considered. Maintenance energy requirements are often expressed as a metabolizable energy (ME) equivalent, which has the drawback that the value is not independent of the diet. A zero **energy balance** (i.e. either induced experimentally or by statistical extrapolation) ensures that all metabolizable energy is used for maintenance functions. The maintenance energy requirement represents an important fraction of the energy intake, ranging from 25–30% of ME intake for very productive animals (such as high-producing dairy cows or rapidly growing pigs and poultry) to 100% of ME intake in mature non-producing animals. For mature species, maintenance requirements are typically expressed per kilogram of metabolic body weight (kg $BW^{0.75}$) and range from 290–330 for cattle to 400–440 kJ ME kg^{-1} $BW^{0.75}$ day^{-1} for sows. Normal physical activity is also considered part of the maintenance energy requirement and may represent an important fraction of it. In a comparison between species, the cost of activity (kJ kg^{-1} $BW^{0.75}$) has been found to range from 2.4 (rats) to 30 (pigs) per 100 min of standing. The heat generated in metabolic processes is usually sufficient to maintain a constant body temperature but animals in **cold environments** may need to divert energy from productive processes to thermogenesis in order to maintain a constant body temperature. In that case, the energy requirement of the animal includes all the heat that is produced (i.e. the ME intake).

Weight gain (protein and fat deposition)

Most of the energy gain in farm animals is retained as protein and lipid. Although glycogen is important for the short-term storage of energy, it plays a minor role in the long-term energetics of gain. The energy requirement for body weight gain depends on the protein and lipid composition of the gain. The gross energy values of body protein and lipid are approximately 23.7 and 39.8 kJ g^{-1}, respectively. Although these values can be used to calculate the energy content of body weight gain, they do not reflect the energy cost of gain. The latter also includes the cost of nutrient absorption, transport and metabolism. The cost of protein (PD) and lipid deposition (LD) has been estimated experimentally by a factorial approach:

$$ME = ME_m + 1/\,k_p\,PD + 1/k_f\,LD$$

where ME_m is the maintenance energy requirement, k_p is the marginal efficiency of protein deposition and k_f the marginal efficiency of lipid deposition. Although it is acknowledged that there is considerable variation in reported values for marginal efficiencies, k_p is typically much lower than k_f (60 and 80%, respectively, in growing pigs). Consequently, more energy is required to deposit 1 kJ of energy as protein than as lipid. The greater energy requirement for protein deposition is due to the ATP needed for peptide bond formation (augmented by **protein turnover**). It is important to realize that k_p and k_f reflect the conversion of metabolizable energy to retained energy and are therefore diet dependent.

Gestation and egg production
From an energetic point of view, gestation in farm animals is a complex process. Apart from the development of the fetuses, maternal tissues such as the uterus, placenta and udder grow and become metabolically more active during gestation. Moreover, the female may not have reached maturity or may be in the process of restoring body reserves following a previous lactation and so fetal growth may be accompanied by growth of maternal tissues. The energy retention by the fetuses is typically assumed to be proportional to the birth weight and number of young born. Fetal growth (mainly protein) and growth of the placenta and maternal tissues are relatively minor during the initial phase of gestation and are often described by exponential functions. During gestation, a considerable fraction of the energy expenditure is due to oxidative metabolism (i.e. ATP synthesis and utilization) by the uterus and placenta and this expenditure may even exceed that of the fetus(es). The complexity of gestation and methodological differences result in widely different estimates of energy requirements of gestation between species. It is less difficult to determine the energy requirement of reproduction in poultry. Based on the energy value of egg constituents, at least 7 kJ g^{-1} egg mass is needed. The metabolizable energy requirement for egg production is typically assumed as being 8.7 kJ g^{-1}. This requirement covers the synthesis of egg energy as well as the energy required for synthesis (e.g. formation of the egg shell).

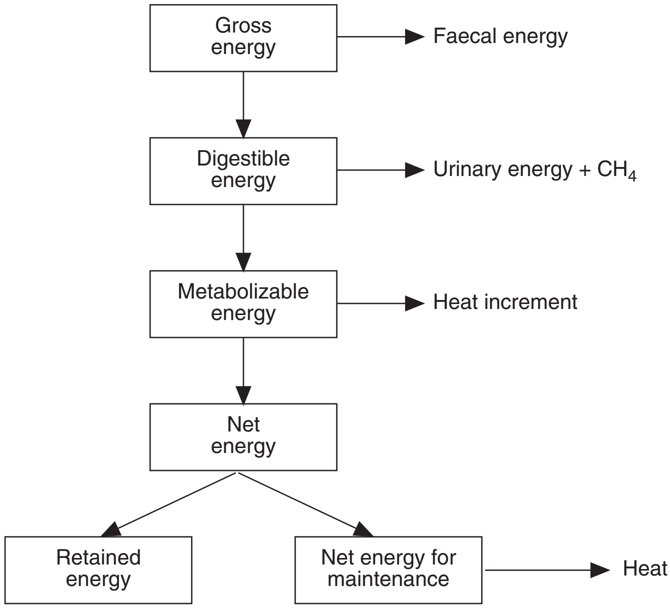
Lactation
The energy retained in milk is a function of the protein, fat and lactose contents of the milk. The heat of combustion of these products is approximately 38.9, 23.9 and 16.5 kJ g^{-1}, respectively. In ruminants, lactose can be synthesized from gluconeogenic precursors such as propionate, whereas non-ruminants may use dietary glucose. The actual energy requirement for milk synthesis appears to be considerably greater than that calculated theoretically from transforming nutrients to milk components, especially in ruminants. The experimental efficiency of using dietary energy for milk production is 60–65% in ruminants and 70% in sows. This difference is partly due to differences in the nutrients used for milk fat synthesis (e.g. volatile fatty acids obtained from fermentation vs. carbohydrates). In early lactation, the energy requirement for milk production (and maintenance) may exceed the intake capacity of the animal, resulting in mobilization of body reserves. The efficiency with which this occurs is relatively high (80–90%). (JvanM)
See also: Energy systems

Energy retention: *see* Energy balance

Energy source A feed included in diets primarily for the energy it supplies (in contrast to protein sources). The major sources of energy in animal feeds are carbohydrates (such as starch in cereal grains and cellulose in forages) and lipids (such as the oils in oilseeds). (JMW)

Energy systems Energy systems have been developed as a means of relating the supply of dietary energy to the animal's requirement (see figure). The objective of an energy system is to attribute a value to a feed that can be compared with a requirement expressed using the same units. Most current energy systems are based on (or variants of) digestible energy (DE), metabolizable energy (ME) or net energy (NE). It is important to realize that, in refining energy systems, energy values become not so much a property of the feed alone but more a function of both the diet and the animal's productive processes.

Digestible energy (DE)
The DE content of a diet corresponds to the gross energy (GE) content minus the energy lost in the faeces. The faecal energy corresponds to the energy of undigested dietary nutrients as well as a (small) endogenous fraction. DE values cannot easily be determined in poultry, because the urine is excreted with the faeces. DE values may be extremely variable and may range from 0 to 100% of the gross energy value. The (apparent) DE value may often be calculated from digestible nutri-



Relation between energy systems.

ents. For example, the DE value of feeds (for growing pigs) has been determined by regression as:

$$DE = 0.0229 \times DCP + 0.0389 \times DEE + 0.0115 \times DCF + 0.0175 \times ST + 0.0169 \times Sugars + 0.0183 \times DRes$$

where DCP is the digestible crude protein content, DEE the digestible ether extract, DCF the digestible crude fibre content, ST the starch content, Sugars the sugar content and DRes the digestible residue content (i.e. organic matter minus the other digestible nutrients), all expressed in g kg^{-1} dry matter (DM). It should be noted that the coefficients correspond to the (approximate) GE values for each nutrient. Several equations of this type have been proposed and are all built on the premise that digestible energy is supplied by the components of organic matter. It must be ensured that DE values are representative of the situation to which they are applied, as the digestibility of a nutrient may be affected by feeding level or physiological stage of the animal. Although DE values of feedstuffs can be easily determined, the biological basis for establishing DE requirements is rather weak.

Metabolizable energy (ME)

The ME value of a feed corresponds to the DE value minus the energy lost in the urine and as gas. All ME is retained in animal products or lost as heat. The energy losses in the urine, mainly as urea in mammals or as uric acid in birds, are principally due to the incomplete oxidation of amino acids. Urinary energy represents 2–5% of GE for non-ruminant animals and 4–6% for ruminants. Urea has an energy value of 22.6 kJ g^{-1} N (34.4 kJ g^{-1} N for uric acid). Thus, each additional gram of protein that is not deposited as protein will theoretically result in an additional urinary energy loss of $0.16 \times 22.6 = 3.6$ kJ g^{-1} protein. Thus, the ME value of dietary proteins that are deposited as protein will equal the DE value (23.8 kJ g^{-1}), whereas that of oxidized amino acids will be $23.8 - 3.6 = 20.2$ kJ g^{-1}. Consequently, the ME value of protein is not a property of the protein content per se, but depends on the utilization of the protein. This has led to the suggestion that ME should be corrected to zero balance or constant N retention. As with DE, ME also contains an endogenous component that is not (directly) of dietary origin. Also the gaseous energy (methane and hydrogen originating from microbial fermentation) cannot be used by the animal. Although this is a minor fraction for non-ruminants (0–2% of GE), it may represent 6–10% of the GE in ruminants. The measurement of methane and hydrogen production requires specialized equipment. Consequently, ME values are often calculated as a function of DE, digestible nutrients and/or organic matter digestibility.

Net energy (NE)

Net energy can be defined as the 'useful' energy for the animal and is equivalent to the ME value minus the **heat increment of feeding**. The latter is the heat loss associated with ingestion, digestion and metabolism of nutrients and can be obtained by regression of the **energy balance** (or heat production) on the ME intake. The slope of this line is the efficiency of production ($k_g = \Delta EB/\Delta ME$) and the NE value can then be calculated as $k_g \times$ ME (the heat increment is $(1 - k_g) \times$ ME). The relation between the energy balance and ME intake is not necessarily linear and NE values are therefore not constant. The NE value of a diet can also be seen as the sum of the NE values for maintenance and production. The NE for production corresponds to the energy that is stored in animal products (e.g. growth, milk, eggs) whereas the fasting heat production is typically taken as an estimate for the NE for maintenance. Although the energy retained in milk and eggs can easily be measured, measurement of the energy balance requires the **comparative slaughter** technique or **calorimetry**. Both techniques are costly and time consuming, which limits extensive measurement on feeds. For most species, NE values have been measured experimentally and this information has been exploited to predict the NE value from the chemical composition or ME value of the feed. These (statistical) relations explain a large fraction of the biochemical efficiency of nutrient transformation. In growing pigs, the NE/ME ratio (for maintenance and growth) for protein, ether extract, starch and dietary fibre correspond to approximately 0.58, 0.90, 0.82 and 0.58, respectively. The value for starch is similar, whereas that for lipid is slightly lower than the theoretical efficiency for lipid deposition. The value for protein is considerably lower than the theoretical value, suggesting that other processes (e.g. **protein turnover**) contribute to the efficiency. The observation that the efficiency of using protein for protein deposition is very similar (0.60, which is essentially an ATP cost) supports this idea. The result is that, relative to an ME classification, feedstuff rich in protein and fibre have a low NE value (in pigs), whereas those rich in fat have a higher value. The advantage of using an NE system (relative to ME or DE) is that it corresponds more closely to the actual energy utilization by the animal. On the other hand, it results in different NE values for each type of production and therefore becomes less of a diet characteristic per se. (JvanM)

Energy units The Standard International (SI) unit of energy is the **joule** (J), which is the work done when a force of 1 newton acts over a distance of 1 m. The **calorie**, another unit of energy, is the heat required to raise the temperature of 1 g of water through 1°C. The relationship 4.184 J cal^{-1} is known as the mechanical equivalent of heat.

Use of SI units is recommended whenever possible but calories (cal), kilocalories (kcal) and pounds (lb) are widely used in agriculture. The SI unit of time is the second (s) and the SI unit of power is the watt (1 W = 1 J s^{-1}). In agricultural practice, one is dealing with rates of heat output and food energy intake in the range 1 W to 10 kW, but food intake and requirements are usually reckoned per 24 h. This inevitably leads to the use of hybrid units such as kilojoules per hour, megajoules per day, kilowatt-hours, kilojoules per pound, etc., as well as joules and calories. Some useful conversion factors are as follows.

Units of energy, including work and heat (mass $\times$ distance^2 $\times$ time^{-2}):

- 1 joule (J) = 1 watt second (W s) = 0.239 calories (cal)
- 1 kilojoule (kJ) = 0.278 watt hours (W h) = 0.239 kilocalories (kcal)
- 1 megajoule (MJ) = 0.278 kilowatt hours (kW h)
- 1 calorie = 4.184 joules (J)
- 1 kilocalorie (kcal) = 4.184 kilojoules (kJ) = 1.162 watt hours (W h)

Units of power or work-rate (mass $\times$ distance^2 $\times$ time^{-3}):

1 watt (W) = 1 joule/second (J s^{-1}) = 3.6 kJ/hour (kJ h^{-1}) = 86.4 kJ day^{-1} = 0.239 cal s^{-1}
1 kilowatt (kW) = 1 kJ s^{-1} = 3.6 MJ h^{-1} = 86.4 MJ day^{-1} = 0.239 kcal s^{-1}
1 joule/second (J s^{-1}) = 1 W = 0.239 cal s^{-1}
1 kilojoule/hour (kJ h^{-1}) = 0.278 W
1 megajoule/day (MJ day^{-1}) = 11.6 W
1 calorie/second (cal s^{-1}) = 4.184 J s^{-1}
1 kilocalorie/hour (kcal h^{-1}) = 1.162 W

Units of energy/mass (distance^2 × time^{-2}, used for energy value of foods, heats of combustion, energy expended in doing mechanical work):

1 joule/gram (J g^{-1}) = 0.239 cal g^{-1}
1 kilojoule/kilogram (kJ kg^{-1}) = 0.239 kcal kg^{-1} = 0.454 kJ lb^{-1} = 0.1084 kcal lb^{-1}
1 megajoule/kilogram (MJ kg^{-1}) = 108.4 kcal lb^{-1}
1 kilojoule/pound (kJ lb^{-1}) = 0.239 kcal lb^{-1} = 2.205 kJ kg^{-1} = 0.527 kcal kg^{-1}
1 calorie/gram (cal g^{-1}) = 4.184 J g^{-1}
1 kilocalorie/kilogram (kcal kg^{-1}) = 4.184 kJ kg^{-1} = 0.454 kg lb^{-1} = 1.90 kJ lb^{-1}
1 kilocalorie/pound (kcal lb^{-1}) = 4.184 kJ lb^{-1} = 2.205 kcal kg^{-1} = 9.224 kJ kg^{-1}

(JAMcL)

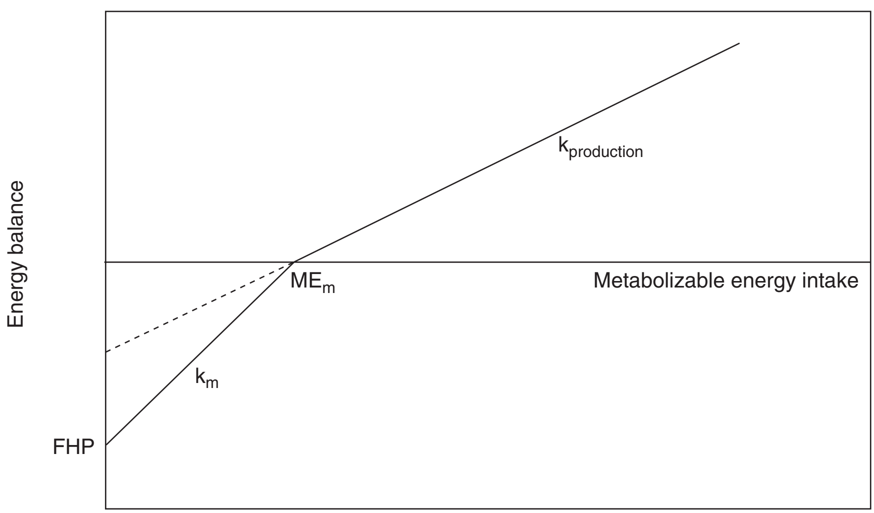
See also: Calorific factors; International units

Energy utilization The **metabolizable energy** (ME) cost of forming an animal product (e.g. milk, eggs, body tissue) is the extra ME intake required for the formation of the product over and above the ME required for the animal's **maintenance** (ME_m). The gross energy of the product is its heat of combustion. For cow's milk this is approximately 3 kJ g^{-1}, for sow's and ewe's milk 5 kJ g^{-1} and for hen's eggs 6 kJ g^{-1}. For growth in most species the gross energy of weight gains is of the order of 6–10 kJ g^{-1} after birth when the gain is mainly protein, rising to 25–30 kJ g^{-1} at maturity when the gain is mostly fat.

The efficiency of energy utilization is the ratio between energy output (in product) and the corresponding energy input. It can be obtained from the relationship between **energy balance** and metabolizable energy intake (see figure). The slope of this line is interpreted as the efficiency of energy utilization (k). The relationship is usually represented as having two linear segments and can be expressed by the equation

$$ME = \text{Gross energy of product}/k + FHP/k_M$$

At ME intakes above maintenance, k is the efficiency of utilization of ME for formation of product (k_L for lactation, k_F for fattening, etc.). Below maintenance, the slope of the line between fasting heat production (FHP)



Relation between the energy balance and metabolizable energy intake.

and the metabolizable energy intake for maintenance (ME_m) indicates the efficiency with which dietary nutrients are used for maintenance, relative to mobilizing body reserves for that purpose. This efficiency for maintenance (k_m) depends on both the diet and the body reserves used when the animal is actually fed below maintenance. With increasing ME intake above maintenance, growing animals deposit an increasing fraction of energy as lipid (relative to protein). As the energetic efficiencies of protein and lipid deposition differ, the linear relation is therefore overly simple.

The efficiency of utilization of ME is generally higher for higher quality (i.e. higher metabolizability) foods. For maintenance, k_m is usually of the order of 0.65–0.85, for lactation k_L = 0.55–0.65, for growth k_G = 0.35–0.55 and for milk-fed growing animals up to 0.7. For egg production k_E = 0.7. The ME cost of an entire pregnancy is approximately 7.5 J per J gross energy of a newborn calf, i.e. an efficiency of 0.13. If food intake is insufficient for essential needs such as fetal or skeletal growth or milk production these functions still proceed, albeit at reduced rates, obtaining their energy from catabolism of body reserves (mainly fat). The (relative) efficiency for this is usually of the order of 0.9.

Because k_m is a relative efficiency, its value typically exceeds that of the efficiency of production and even may exceed unity. The maintenance energy requirement is essentially a requirement for **adenosine triphosphate (ATP)**. It is difficult to express the efficiency of ATP synthesis as a fraction of energy input 'retained' as ATP. Nevertheless, the (relative) efficiency with which nutrients can be used for ATP synthesis can be compared (see table). It appears that glucose and lipids can be used relatively efficiently for ATP synthesis, whereas volatile fatty acids are used 10–18% less efficiently. The efficiency of using amino acids for ATP synthesis is considerably lower. Part of this inefficiency is due to the incomplete oxidation of amino acids. In mammals, the nitrogen of amino acids is excreted as urea, which involves both a physical loss of energy (as urea) as well as the energy expenditure to synthesize it (2 ATP/N).

The theoretical energetic efficiency of **protein synthesis** is approximately 85% but the actual efficiency is often lower due to protein turnover. The efficiency of depositing protein in animal tissue appears to be considerably lower (~60%) than that of depositing protein in animal products such as milk or eggs (~75%). Part of this difference may be due to a difference in **protein turnover** between these types of production.

In ruminants, a major part of the energy supply is derived from the end-products of **fermentation**. The metabolic utilization of these end-products (and the associated cost of fermentation) results in lower efficiency than that observed in non-ruminant animals. As with the efficiency for ATP synthesis, the efficiency for fat deposition in non-ruminants increases in the order protein, carbohydrate, lipid. (JAMcL, JvanM)

The theoretical energy expenditure for ATP synthesis from various substrates.

Source	kJ mol^{-1} ATP	Source	kJ mol^{-1} ATP
Glucose	74.0	Phenylalanine	124.0
Tri-stearin	75.7	Tyrosine	107.0
Acetate	87.4	Histidine	149.8
Propionate	85.4	Arginine	133.6
Butyrate	81.2	Serine	116.0
Lysine	102.2	Glycine	149.2
Methionine	129.3	Alanine	104.5
Cysteine	178.4	Glutamate	91.8
Threonine	100.0	Proline	92.5
Tryptophan	134.0	Aspartate	103.9
Isoleucine	88.4		
Leucine	90.6		
Valine	92.7		

Further reading

Agricultural Research Council (1980) *The Nutrient Requirements of Ruminant Livestock.* Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Agricultural Research Council (1981) *The Nutrient Requirements of Pigs*. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Janssen, W.M.M., Terpstra, K., Beeking, F.F.E. and Bisalsky, A.J.N. (1979) *Feeding Values for Poultry.* Spelderholt Institute for Poultry Research, The Netherlands.

Energy value The concentration of energy in a feed, usually expressed as megajoules (MJ) per kg dry matter (DM). (JMW)
See also: Digestible energy; Gross energy; Metabolizable energy; Net energy

Englyst method An *in vitro* procedure for the determination of resistant starch. The sample is treated with a combination of mammalian and bacterial amylolytic enzymes under controlled conditions for various periods of time to give estimates of rapidly digestible starch (RDS), slowly digestible starch (SDS) and total starch (TS). Resistant starch is calculated as TS − (RDS + SDS). (MFF)

Enrichment (isotopic) The concentration of a particular isotope in a sample of the element. Because each isotope has a certain natural abundance, enrichments are usually referred to as that value and expressed as 'atoms percent excess' (ape). For example, the natural abundance of ^{15}N, i.e. the proportion of all nitrogen on earth that is of mass 15, is about 0.36%. So a sample with an enrichment of 2.48% has ape 2.12. (MFF)

Ensiling: *see* Silage

Enterocyte A cell of the single layer of columnar cells on the surface of the villi of the small intestine. Enterocytes are in direct contact with the intestinal contents. They have a directional orientation toward the intestinal lumen. On their luminal surface are the microvilli (brush border) which dramatically expand the contact surface and contain some of the digestive enzymes (e.g. lactase and sucrase) and transporters. (NJB)

Enterokinase A proteolytic enzyme (enteropeptidase: EC 3.4.21.9), secreted by epithelial cells of the duodenum, that specifically activates trypsin by the cleavage of a lysine–isoleucine peptide bond leading to the removal of an aspartyl-rich octapeptide from the NH_2-terminal of the inactive zymogen, trypsinogen. (SB)
See also: Protein digestion

Environment–nutrition interaction Climate is not the only component of the environment that affects nutrition (lighting and social environment are also important) but it is the one that receives most attention. The underlying cause of climate–nutrition interactions is that mammals and birds are homeothermic (or endothermic), which means that they maintain a near-constant body temperature. This can occur only if heat production equals heat loss. Over a range of ambient temperature, known as the thermoneutral zone, or zone of minimal thermoregulatory effort, constant body temperature is maintained by physical means, with no change in metabolic rate. This zone is narrow in poultry, intermediate in pigs and relatively broad in ruminants. Below the thermoneutral zone, **energy intake** usually increases as ambient temperature decreases. Above the thermoneutral zone, energy intake decreases. The rate of decrease above thermoneutrality usually shows two phases. Initially, intake decreases at a rate that reflects the decrease in metabolic rate and the consequent decrease in maintenance energy requirement. As temperature increases still further, there is often an increased rate of decline in energy intake, which may be a mechanism for reducing the heat increment of feeding. There is usually a further acceleration in the decline of food intake with the onset of hyperthermia. Farmed fish are poikilothermic (or ectothermic) and their body temperature is close to that of the surrounding water. Their metabolic rate and nutrient requirements therefore increase with ambient temperature, following the Q_{10} relationship (i.e. a temperature increase of 10°C caused a two- to threefold increase in rate from the initial level).

Intake of dietary energy is the nutritional variant most directly affected by ambient temperature. To maintain the required intakes of essential nutrients it may therefore be necessary to alter the ratio of nutrients to energy as temperature varies. This may be most practicable in the case of housed pigs and poultry, where there is good control of the composition of the diet. The most widely applied dietary alteration is to increase the ratio of essential amino acids to energy as temperature increases. This has some beneficial effect in allowing growth rates to be sustained at high ambient temperature. However, it is not always successful in preventing a reduction in growth rate or production. There are clearly direct (physiological) effects of high temperature that cannot be prevented by dietary adjustment. It has sometimes been suggested that providing more energy in the form of fat rather than carbohydrate should be beneficial at high temperatures because of its lower heat increment, but this has not invariably been borne out in practice.

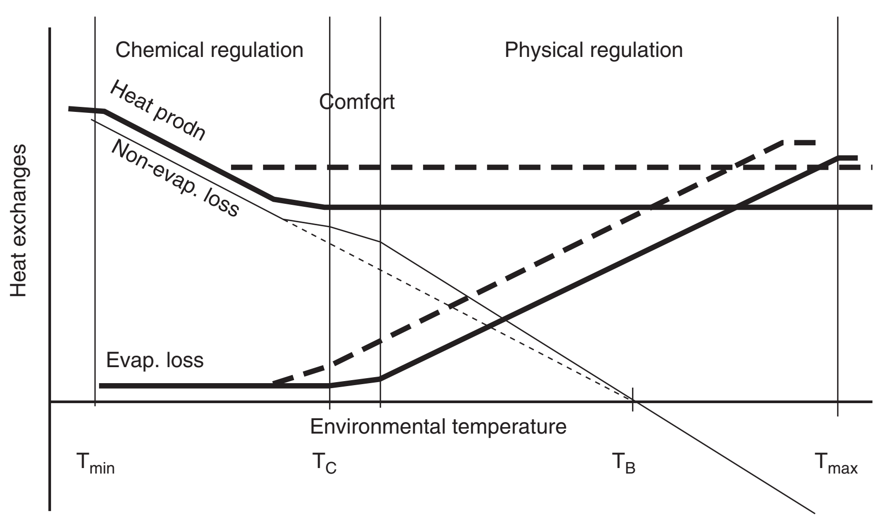
Increased dietary vitamin supplementation (especially with vitamins E and C) has been shown to alleviate some of the effects of heat stress. This is most likely to be due to their antioxidative effects, particularly in protecting the cell membranes of metabolically active tissues such as the liver.

Breeds indigenous to hot climates are generally better able to maintain their characteristic level of production at temperatures that severely limit the performance of imported 'modern' genotypes. However, their greater tolerance can be seen as a consequence of the lower metabolic intensity accompanying their lower rate of production. (MMacL)

See also: Environmental temperature; Heat increment of feeding; Hyperthermia; Temperature, body; Thermoregulation

Environmental temperature The effects of environmental temperature on heat exchanges of animals are illustrated in the figure, which is a model generally applicable to all homeothermic (warm-blooded) animals. Homeotherms maintain their deep-body **temperature** (T_B, usually measured as rectal temperature) close to a fixed normal level of around 38°C. T_B varies between species and tends to be higher (up to 40°C) in small animals than in large ones.

Except in cold and extremely hot conditions, the rate of heat production is not affected by the environment but is determined largely by the levels of food intake and activity; it is shown in the model as a horizontal straight line between the two environmental temperatures T_C and T_{max}. T_C is known as the critical temperature.



Effect of environmental temperature on heat exchange.

The heat exchange between an inanimate object and its surroundings is proportional to the temperature difference between them (Newton's law of cooling). It is obviously an over-simplification to apply this law to an animal – which is clearly not inanimate and has the ability to alter its rate of heat loss by various means, both reflex and behavioural, as well as to lose heat by evaporation – but for simple consideration of non-evaporative heat exchanges (i.e. convection, conduction and infrared radiation to the immediate surroundings) an animal may be thought of as two separate inanimate objects: one with minimal insulation for warm environments and the other with maximal insulation for cold ones. These are represented in the model as two straight lines of different slopes (insulation), both passing through or extrapolating to the point of zero heat exchange at the environmental temperature that corresponds to T_B. The transition between these two lines is shown in the model as occurring over a short range of environmental temperature above T_C.

Since T_B remains near to a fixed level, it follows that heat balance is only maintained if **evaporative heat loss** is regulated at a level equal to the difference between heat production (which is constant) and non-evaporative heat loss. Evaporative heat loss thus decreases from a high level at T_{max} to near zero at T_C, and it is represented in the model by a straight line whose slope is equal but opposite to that of non-evaporative loss.

At environmental temperatures below T_C, evaporative loss is at a fixed minimal level consistent with minimal respiratory activity; it appears on the model as a horizontal line slightly above zero heat loss. In this cold region, heat balance is achieved by increasing heat production; it is shown as a straight line following the increased non-evaporative heat loss as the temperature falls. A limit occurs when the animal attains its so-called summit metabolism and is unable to increase heat production any further (at T_{min}).

Between T_{min} and T_{max}, which represent limiting environmental conditions for survival, lie the zones of chemical and physical body-temperature regulation. In the chemical zone, starting at the critical temperature (T_C, sometimes also known as the lower critical temperature), heat production is increased by increased voluntary activity or by shivering as the temperature falls. Above T_C, in the first part of the physical zone, reflex changes in blood flow just below the skin surface alter the thermal insulation of the tissues, causing the transition between the lines of minimal and maximal non-evaporative heat loss. This is the comfort zone. As the temperature increases further (still within the physical zone), increased evaporation is caused by sweating or panting. The term 'thermoneutrality' is used by some authors to refer to the entire physical zone and by others just to the comfort zone; the 'zone of least thermoregulatory effort' has also been suggested to replace 'comfort zone' (Mount, 1974).

Among many deficiencies of this model is the fact that heat balance is only imperfectly achieved. T_B alters slightly and the temperatures of the limbs and of peripheral regions of the trunk alter considerably more. Periods of imbalance between heat production and heat loss give rise to temporary storage of heat in the body. The simple model also fails to take account of solar radiation. Solar heat load can be very considerable – even higher than the normal level of resting heat production. It can be included in the model by regarding it as an addition to heat production. To maintain heat balance, evaporative heat loss must be increased by a similar amount. These altered levels, consequent on solar radiation, are shown by dashed lines on the model. The net effect is a lowering of T_C and of temperatures in the comfort zone. Wind accelerates heat exchanges by reducing thermal insulation. The effect on the model is to make the slope of all lines steeper.

In addition to the reflex actions described above, animals (when free to do so) adopt behavioural patterns that influence heat exchanges. These include sheltering, huddling and curling up so as to limit heat losses in cold weather and standing in the wind or seeking shade when the weather is warm.

For small animals the comfort zone is very narrow, perhaps better described as a comfort point; for large farm animals it is only a few degrees wide. The table gives approximate critical temperatures (°C) for some farm animals exposed to neither solar radiation nor wind.

(JAMcL)

Critical temperatures (°C) for sheltered animals.

		Mature	
Species	Newborn	Maintenance fed	Lactating/laying
Cattle	14	7	–30
Sheep	29	–3	40
Pigs	32	23	14
Chickens	35	16	20

See also: Climate

Key reference

Mount, L.E. (1974) The concept of thermal neutrality. In: Monteith, J.L. and Mount, L.E. (eds) *Heat Loss from Animals and Man*. Butterworths, London, pp. 425–439.

Enzootic ataxia A gait disorder seen in young lambs, goat kids and deer, in Australasia and North America. It has also been seen in pigs. Swayback is a similar condition seen in lambs and goat kids in the UK: some breeds of sheep are much more susceptible than others. Both conditions are caused by copper deficiency and are associated with demyelination of the cerebrum or spinal cord. (WRW)
See also: Copper

Enzyme A protein (or sometimes more than one protein) that has the ability to catalyse a specific chemical reaction. Enzyme activity requires specific conditions of temperature, pH, substrate and co-factor concentrations, etc. Since enzymes act as catalysts they are not consumed while carrying out reactions. Enzyme activity can be reduced by enzyme inhibitors. (NJB)

Enzyme activity The potential of an enzyme, which may be one protein or a group of proteins, to carry out a reaction under idealized conditions. It can be measured using a purified protein or a sample of homogenized cells, tissue or organ. The system is optimized for pH, temperature, co-factor(s) and substrate concentration(s) and the reaction is assessed over a measured time. Results are expressed as a rate in relation to the amount of sample, e.g. μmol (min × mg protein)$^{-1}$. (NJB)

Enzymes as feed additives Enzymes are proteins that act as biological catalysts. They are produced by living cells and are intimately involved in essential transformations of substrates into products in biological systems. Many require non-protein co-factors. Enzyme activity depends on the co-factors present, the concentration and nature of substrate and enzyme as well as temperature and pH. The function of enzymes is critically dependent on their structure and they are therefore very susceptible to pH and temperature changes.

Enzymes are systematically named and each has an Enzyme Commission (EC) number which describes the reaction that it catalyses. The source of the enzyme (e.g. *Aspergillus niger*) is also frequently cited. Enzymes are often referred to as carbohydrases, proteases, lipases, phytases, etc., indicating that their major function is the degradation of carbohydrates, proteins, lipids and phytic acid esters, respectively.

Enzymes are produced commercially from microbes, fungi and yeasts in highly controlled conditions in fermentation plants. Their main uses are in the detergent and food industries but significant quantities are manufactured for use in animal diets. As feed additives, enzymes are mainly used in the diets of non-ruminants but are also added to ruminant diets. Their main purpose is to improve the nutritive value of diets, especially when poor-quality, and usually less expensive, ingredients are incorporated. It has been estimated that about 95% of intensively fed poultry are now given diets containing supplementary enzymes. In some circumstances enzyme supplementation can improve performance and nutrient utilization by as much as 20%. The efficacy of a feed enzyme depends on the nature and quantity of its substrate in the diet, the specific ingredients, the age of the animal and its nutritional and disease status. Enzyme supplementation has the greatest effect on the young animal.

The feeds of plant origin used in poultry and pig diets are often by-products of human food and of poor quality, with high concentrations of non-starch polysaccharides (NSPs) and oligosaccharides, as well as proteins that are resistant to digestion, and antinutrients such as tannins, trypsin inhibitors, lectins and phytates. Such feeds cause physico-chemical problems – increased digesta viscosity, water intake and moisture in the gut – that lead to reduced nutrient availability and increased endogenous losses. Nutrients are frequently enclosed in cells with indigestible cell walls, making them inaccessible to the animal's own digestive enzymes. Supplementation with the correct enzymes can increase the availability of nutrients and alleviate the adverse effects of antinutrients. In some instances, however, enzymes may actually release antinutrients.

Enzymes used as feed supplements are carbohydrases, proteases, phytases and, to a lesser extent, lipases. They may be used singly or in combination. The carbohydrases can be subdivided according to their substrate, whether starch or NSPs such as β-glucans, cellulose, hemicellulose, xylans, galacturonans and galactans. For use in the European Union, the enzyme preparations must be registered with the EU Scientific Committee on Animal Nutrition. The table gives a summary of the enzymes available and their sources.

In poultry, the residence time of digesta in the gastrointestinal tract is relatively short (4–6 h); it is longer in the pig (6–8 h) and longer still in ruminants. Thus exogenous enzymes have greater opportunity to function effectively in ruminants and pigs than they do in poultry; however, this also depends on pH, buffering capacity and other conditions in the gastrointestinal tract. Generally, the enzymes required for ruminants are different from those needed in diets for pigs and poultry. For ruminants, cellulases and hemicellulases are of particular interest, whereas the NSPs and phytases are especially useful in diets for non-ruminants.

Enzymes can be added to diets as powders, granules or liquids. The solid material is added during mixing while the liquid can be applied to pellets. The thermal stability of exogenous enzymes is extremely important in diets that are heated, either to reduce transfer of pathogenic microorganisms or when the diets are pelleted. Overheating can denature supplemental enzymes, reducing their potencies.

A benefit of supplemental enzymes in diets for non-ruminants has been in reducing the occurrence of wet, sticky faeces. This tends to reduce the incidence of dirty animals, products and litter; it also tends to decrease contamination of the animals with dangerous bacteria such as *Clostridium* spp. Supplemental enzymes frequently reduce the viscosity of digesta in the gastrointestinal tract. (TA)

Enzymes and the organisms from which they are obtained.

Enzyme	Main sources
Phytases	
3-phytase (EC 3.1.3.8)	*Aspergillus* spp., *Trichoderma* spp.
Phosphoric monoester hydrolase (EC 3.1.3.26)	*Aspergillus* spp.
Carbohydrases	
Endo 1→3 (4)-β glucanase (EC 3.2.1.6)	*Trichoderma* spp., *Aspergillus* spp., *Geosmithia* spp., *Penicillium* spp., *Humicola* spp., *Bacillus* spp.
Endo 1→4-β xylanase (EC 3.2.1.8)	*Trichoderma* spp., *Aspergillus* spp., *Geosmithia* spp., *Penicillium* spp., *Humicola* spp., *Bacillus* spp.
Alpha galactosidase (EC 3.2.1.22)	*Aspergillus* spp.
Polygalacturonase (EC 3.2.1.15)	*Trichoderma* spp., *Aspergillus* spp.
Alpha amylase (EC 3.2.1.1)	*Bacillus* spp., *Humicola* spp., *Trichoderma* spp.
Proteases	
Subtilisin (EC 3.4.21.62)	*Bacillus* spp.
Bacyllolysin (EC 3.4.21.62)	*Bacillus* spp.

Further reading

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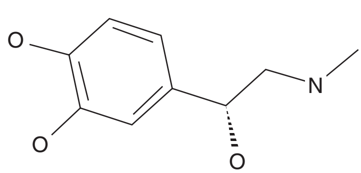
Enzyme inhibitors A term applied to both inorganic and organic substances that have a negative effect on enzyme activity. Inhibitors compete with the normal substrate(s) or co-factor(s) for the enzyme and decrease the rate of reaction. The effectiveness of the inhibitor is described in many cases by the amount of the inhibitor required to suppress the activity of the enzyme by 50%. This is referred to as the K_i and has units such as nmol l^{-1}. The smaller the value for the K_i, the more powerful is the inhibitor. Important examples of the role of enzyme inhibitors in nutrition are the trypsin inhibitors found in many foods, especially legume seeds.
(NJB)

See also: Feedback inhibition

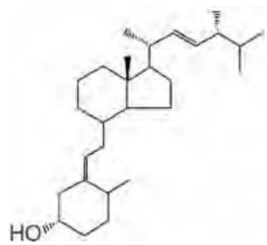
Epinephrine A catecholamine, also called **adrenaline**, produced in the adrenal medulla from the amino acid L-tyrosine. Epinephrine is released in response to both physical and physiological challenges. It causes the liver and muscle to increase the rate of glycogen breakdown, increases the release of fatty acids from adipose tissue and increases circulating lactate. An increase in metabolic rate is often noted in response to epinephrine.



(NJB)

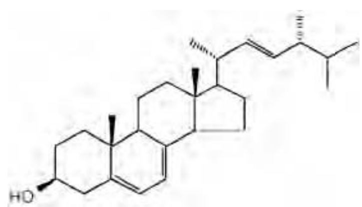
Epiphyses Separate, enlarged, terminal ossifications of long bones attached to a growth plate, but growing separately from the shaft and covered by a layer of articular cartilage.
(MMax)

Ergocalciferol A trivial name for vitamin D_2 or a specific vitamin D compound that possesses the ergosterol side-chain. It is one of the two common nutritional forms of vitamin D, the other form being cholecalciferol or vitamin D_3. Unlike vitamin D_3, this compound is not formed in the body but is produced by ultraviolet irradiation of ergosterol. The structure of ergocalciferol is:

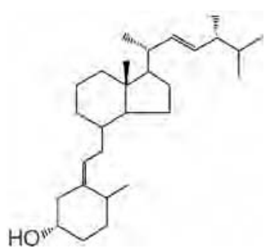


It can only be used in mammals. It has low biological activity in birds because it is rapidly metabolized. In mammals its activity is equal to that of vitamin D_3 or cholecalciferol.
(HFDeL)

Ergosterol A sterol found in plants, yeast and moulds having the structure:



Upon irradiation with sunlight or ultraviolet light it is converted to ergocalciferol or vitamin $D_{2,}$ having the structure:



(HFDeL)

Ergot Ergot alkaloids are produced by *Claviceps* fungi infecting grains and grass seeds, and by *Neotyphodium coenophialum* endophytic fungi infecting grasses such as tall fescue (*Festuca arundinacea*). *Claviceps purpurea*, *C. paspali* and *C. cinerea* are the three major fungal species. The fungus parasitizes the grass, attacking the ovary and replacing the developing seed with an enlarged, black structure in which fungal spores are contained in a resin that eventually hardens, forming the sclerotium or ergot body. The ergot body may be harvested with the seed head or consumed by animals grazing an infected pasture.

The fungus produces toxic ergot alkaloids, including ergonovine, ergotamine and ergovaline, which are derivatives of lysergic acid. The hallucinogenic drug of abuse, lysergic acid diethylamide (LSD), is an ergot alkaloid. Symptoms of ergotism include hyperthermia (elevated body temperature), vasoconstriction and gangrene of extremities (e.g. fescue foot) and behavioural effects such as hyperexcitability, convulsions and poor coordination. There are three main combinations of symptoms in livestock: the convulsive form, consisting of convulsions, laboured breathing, lack of coordination, excessive salivation and diarrhoea; the gangrenous form, producing dry gangrene of the nose, ears, legs and tail; and the reproductive form, consisting of abortion, agalactia and reduced neonatal survival. A major sign of tall fescue toxicity (summer fescue toxicosis) is ergot alkaloid-induced hyperthermia. Young poultry are also susceptible to ergotism, with the symptoms of severe toxicosis being poor feathering, nervousness, incoordination and gangrene of the foot and beak. Prevention of ergotism is only possible by removing animals from infected feed or removal of the ergots from the grain by screening. (DRG, PC)

Erucic acid A long-chain monounsaturated fatty acid ($C_{22}\Delta^{13}$, $CH_3{\cdot}(CH_2)_7{\cdot}CH{=}\ CH{\cdot}(CH_2)_{11}{\cdot}COOH$). Diets in which erucic acid forms a major part of dietary fatty acids are associated with fatty infiltration of the heart, with subsequent permanent damage. Erucic acid has also been associated with liver damage in rats when fed at more than 5% of diet, resulting in slower mitochondrial oxidation of substrates.

Erucic acid is found in large amounts in some rapeseed oils, mustard seed oil and also crambe, meadow foam, nasturtium and lunaria seeds. The erucic acid content of rapeseed oil is controlled by two genes and zero-erucic acid rapes are now available. The EU has set maximum levels for erucic acid in human foodstuffs at 2%. Erucic acid and its derivatives are used in industry, for example as lubricants. (EM)

Escherichia coli A Gram-negative bacterium which is a normal inhabitant of the gut of most mammals and birds. It is excreted in faeces and can survive in the environment for many weeks or even months. There are several different strains, most of which are not pathogenic. They can be distinguished and described by serotyping the O (cell wall), K (capsular), H (flagellar) and F (fimbral) antigens.

Pathogenic *E. coli* can cause enteritis or septicaemia in young animals, oedema disease in weaned pigs, mastitis, urogenital infections or toxaemia, depending on the strain and on the species of host animal.

Pathogenicity may depend on the presence of an antigen on the surface of the bacterium which allows adhesion to the intestinal wall or the ability to produce toxins. Toxins either act locally in the gut or are absorbed and target other cells. Many strains of *E. coli* are secondary or opportunist pathogens. Those that are pathogenic for one host species may not be for others; for example, *E. coli* strain 0157, which has caused major food-poisoning incidents in humans, is carried undetected in the gut of a small proportion of cattle and other species. There may be variations in susceptibility within species to different genotypes, e.g. in piglets to *E. coli* strain K88.

Specific strains of *E. coli* can be controlled by vaccination, either of the dam to provide passive immunity, or directly of the susceptible animal. Vaccine–antisera combinations are available for enteric disease and there is also a vaccine to aid in the control of *E. coli* mastitis in cattle. (EM)

Essential amino acids Those amino acids that the animal under consideration cannot synthesize at a rate adequate to achieve optimal performance. To meet physiological needs, these amino acids must be supplied in the diet or, in ruminants, by the rumen microflora. In contrast, non-essential amino acids can be synthesized in adequate quantities from simpler precursors, for example glucose or pyruvate together with an amino group. The non-essential amino acids are none the less components of protein and are therefore physiologically essential for body protein synthesis. The terms 'indispensable' and 'dispensable' are often considered preferable. The nine amino acids that are generally considered essential for all non-ruminant mammalian and avian species are lysine, threonine, methionine, leucine, isoleucine, valine, phenylalanine, histidine and tryptophan. *De novo* biosynthesis of these amino acids is essentially zero. Arginine is partially synthesized in mammals, but not at a rate sufficient for maximal growth. It is not synthesized at all by avian species and for them it is therefore an essential amino acid.

For maximal growth of broiler chicks and turkey poults, small quantities of glycine (or serine) and proline must be present in the diet. Biosynthesis of these amino acids occurs, but the quantities synthesized fall short of the total needs for these amino acids.

Tyrosine and cysteine are called semi-essential amino acids, because tyrosine can be synthesized in the body from phenylalanine and cysteine can be synthesized from methionine and serine. Taurine, a non-protein amino acid that is made from cysteine, is synthesized inefficiently by feline species and for them it is therefore considered an essential amino acid.

(DHB)

Essential fatty acids Essential fatty acids (EFAs) are 18- to 20-carbon unsaturated fatty acids having at least two double bonds. The term 'essential fatty acids' means that they are essential for life and must be provided in the diet to prevent death. These fatty acids are dietary essentials because animal systems do not have enzymes that can insert a double bond distal to n-9 carbon in a fatty acid. Experiments carried out in the late 1920s showed that fat or some component in the fat was required to support expected rates of growth and reproduction in laboratory rats. Previously it was thought that fat could be made from carbohydrate or the carbon skeletons from amino acids, thus fat itself should not be an essential dietary ingredient. Later, **polyunsaturated fatty acids** were shown to counteract the growth-depressing effects of a fat-free diet. This was the first indication of a dietary requirement for something that was classified as a fat. Of the three polyunsaturated fatty acids usually thought of as EFAs – linoleate (18:2 n-6), linolenate (18:3 n-3) and arachidonate (20:4 n-6) – the highest biopotency for growth is seen with arachidonate. **Arachidonic acid** is found predominantly in animal tissues whereas **linoleic acid** is distributed in plant oils. Arachidonic acid itself cannot be classified as an essential fatty acid since it is derived from linoleic acid in metabolism. The classical symptoms of EFA deficiency are growth depression, decreased reproduction, decrease in skin integrity (more evaporative loss), tissue membrane degradation, and changes in fatty acid concentrations in blood and tissue lipids. Humans given a fat-free diet intravenously had evidence of an EFA deficiency (altered triene:tetraene ratio) by 14 days and in some cases by 2 days. Ruminants seem to be unexpectedly resistant to similar treatments. A number of hormones are derived from the essential fatty acids. Each EFA is a precursor for a separate series of prostaglandins, thromboxanes and leukotrienes – hormones intimately involved in cell and tissue metabolism. A marker of EFA deficiency is the triene:tetraene ratio in plasma, erythrocyte or tissue lipid. A ratio less than 0.4 suggests the diet meets the EFA requirement. A decrease in the dietary availability of linoleate (18:2 n-6) results in lower concentrations of arachidonate (20:4 n-6) which normally suppresses the conversion of oleate 18:1 n-9 to 20:3 n-9. This results in a triene:tetraene ratio above 0.4, which is representative of a deficiency. The minimum requirement for linoleate lies between 1 and 2% of dietary calories for rats, pigs and infants. (NJB)

See also: Eicosanoids

Key reference

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Esterification The formation of ester bonds. For example, a carboxyl carbon R·COO$^-$ reacts with an alcohol R·COH to produce an ester R·CO·OCH$_2$·R. Examples are found in the triacylglycerol (triglyceride) molecule of a neutral fat when a fatty acid reacts with the alcohol group of glycerol or similar linkages in phospholipids. Another example is cholesterol esters in which unsaturated or saturated fatty acids react with the alcohol group $^-$OH of carbon 3 of cholesterol to form an ester bond. (NJB)

Ester An organic compound in which the replaceable hydrogen of an acid can be replaced by an alkyl radical. Esters can be made on carboxyl carbons of fatty acids, phosphate (PO_4^{2-}) in ATP, and sulphate (SO_4^{2-}) in heparin. Esters occur in neutral fats the fatty acid binding to the alcohol group of glycerol (·R·H$_2$CO·OC·(CH$_2$)$_{14}$·CH$_3$) and where a fatty acid binds to the alcohol group R·OH of cholesterol or α-tocopherol. The phosphate esters of ATP are R·O·P=O(OH)·O·R. The sulphate esters of heparin are glucosamine·O·SO$_3$H. (NJB)

Ethanol A monohydric primary alcohol (C_2H_5OH, molecular weight 46), most commonly produced by the fermentation of carbohydrates such as molasses and cereal grains by *Saccharomyces* yeast. (JKM)

Ether extract The residue obtained when a feed sample, or other material, is continuously extracted (4–16 h) with diethyl ether; in the proximate analysis of foods it is a measure of crude fat content. Water-soluble substances may first be removed from the sample by extraction with several portions of water; the sample is then dried and continuously extracted, in a Soxhlet apparatus, with anhydrous diethyl ether. The extract is weighed after evaporation of the ether. (CBC)

Ethoxyquin An antioxidant, dihydro-6-ethoxy-2,2,4-trimethylquinoline, $C_{14}H_{19}NO$, boiling point 123–125°C. A light yellow to brown liquid with an unpleasant, mercaptan-like smell. It is combustible (flash point 107°C) and incompatible with oxidizing agents. It polymerizes if heated. (MG)
See also: Antioxidant

Ethylenediamine tetraacetic acid (EDTA) (HOOC·CH$_2$)$_2$NCH$_2$·CH$_2$N(CH$_2$·COOH)$_2$. An excellent chelating ligand molecule which is hexadentate. It forms strong complexes that wrap around metal cations, reducing their biological activity. Chromium EDTA has been used as an indigestible fluid marker in digestibility studies (*see* **Feed evaluation**). EDTA may also be used to strip toxic metals from the body and facilitate their excretion (chelation therapy). (IM)

EU regulations Directives issued in Brussels by the European Commission regulate member states of the European Union on many issues. In the case of animal feeds these regulations include: target species; prohibition of feeds; feed processing requirements; feed contamination, composition and labelling; the marketing and management of animal foodstuffs; and licensing of mineral supplements, pharmaceuticals and feed additives. (JKM)

European sea bass (*Dicentrarchus labrax*) A eurythermal, euryhaline species living in coastal and brackish waters of the eastern Atlantic, ranging from Norway to the Mediterranean and Senegal. It is grown in brackish lagoons and sea cages. Sea bass is spawned in full sea water, the larvae being fed initially on live prey organisms such as rotifers and artemia enriched with amino acids, vitamins and n-3/n-6 polyunsaturated fatty acids, then switched to formulated micro-diets. A market size of 300–400 g is attained in 12–18 months at temperatures near 20°C. (RHP)

Evaluation, feed: *see* Feed evaluation

Evaporative heat loss Evaporation is a powerful means of dissipating heat from the animal's body to the environment, especially in warm climates. The heat required to convert liquid into vapour (the latent heat of vaporization of water) is approximately 2.2 kJ g^{-1}; this heat is drawn from the evaporating surface, which may be the skin, lungs or respiratory passages. There is a minimal rate of evaporation due to normal respiration and diffusion of water through the skin; these together normally amount to < 10% of the animal's resting rate of heat production and are unavoidable, even in cold weather. In hot weather, evaporative heat loss is increased reflexly as a result of sweating and panting and can rise to two or three times the resting metabolic rate. This is vitally important in hot environments where evaporation may be the only means of heat loss, especially if heat production is elevated due to work or by production of milk, eggs, etc., or by growth, and when the animal may additionally be subjected to solar radiation. To be effective as a means of cooling, sweat must be evaporated from the skin surface; sweat that runs off the skin and drips to the ground as liquid provides no cooling. Some animals, e.g. pigs, voluntarily increase evaporation by wallowing to wet the skin surface when water, mud or damp bedding is available to them. (JAMcL)

See also: Climate; Environmental temperature; Thermoregulation

Ewe A female **sheep** capable of breeding. Ewes are usually categorized by age. Those mated in their first year are referred to as ewe lambs; between 1 and 2 years of age they are called yearlings, shearlings or 'twotooths', and thereafter adult or mature ewes. (JJR)

Ewe feeding A priority in ewe feeding is to enable the ewe to achieve a predefined level of production with minimal risk to her well-being. In some sheep systems the aim of the feeding regimen is to promote full expression of the ewe's genetic potential for the production of specific products such as meat, wool or milk. In others the goal is lower levels of output commensurate with a reduced availability of food. The application of appropriate feeding regimes for specific systems is facilitated by setting targets for body weight and condition score during key stages of production. For example, ewes bred in their first year should have attained 60% of their estimated mature weight at mating. Thereafter their weight gains should be moderate (1–1.5 g kg^{-1} estimated mature weight day^{-1}) rather than excessive (three- to fourfold higher) as the latter leads to excessive partitioning of nutrients to the maternal body at the expense of the placenta and fetus.

For the second and subsequent breeding cycles, practical guides for mating weights are 80 and 100% of estimated mature weights. The **body condition** of the ewe, which is often easier to estimate than weight, is also a valuable index in the implementation of feeding strategies. It has the added advantage that for many sheep breeds there is a positive correlation between the number of lambs born and the body condition of the ewe at mating. Thus the level of lamb production and therefore the feed requirements for pregnancy and lactation can be controlled by manipulating body condition at mating. The estimation of body condition involves palpation of the ewe over the lumbar region and ascribing a score (based on a 0–5 scale) for the degree of fat cover over the transverse processes of the vertebrae (Russel *et al.*, 1969). For most breeds, maximum ovulation rate and therefore the potential for maximum lamb production occurs with a condition score at mating of 3–3.5. This level of body condition is characterized by transverse processes that have a smooth and rounded feeling; firm pressure is required to feel over their ends and the eye muscle areas are full with a moderate degree of fat cover. The ideal follow-up feeding strategy for ewes in this body condition at mating is one that maintains body weight and condition for the first month of pregnancy, followed by a gradual move to a mild energy deficit, equivalent to a loss of up to 0.5 units of condition score, from the end of the first to the end of the third month of pregnancy. In general this small energy deficit increases the size of the placenta, which is in its rapid growth phase at this time. Provided that the plane of nutrition during the remainder of pregnancy is increased to meet the nutrient requirements of the rapidly growing fetus or fetuses, the end result is slightly larger and more vigorous lambs at birth; the bigger placenta also enhances mammary gland development, thereby increasing the potential for milk production.

An important component of ewe feeding for the full expression of production potential

The application of appropriate feeding regimes is facilitated by setting targets for bodyweight and condition score during key stages of production.

relates to the adverse effects on ovulation rate of **undernutrition** approximately 6 months prior to mating. This corresponds to the time that ovarian follicles leave the primordial pool and become committed to growth. In many production systems it also corresponds with peak lactation and an associated negative energy balance in the ewe. Fortunately the adverse effect of this negative energy balance on ovulation rate can be avoided by a pre-mating increase in nutrition (flushing), which sustains ovulation rate by minimizing the number of gonadotrophin-responsive and -dependent follicles that are lost from the ovulatory pool through atresia.

Some nutritional effects are irreversible. For example, undernutrition during early fetal life disrupts the normal development of oogonia in the fetal ovary, thus providing an explanation for the reduction in adult reproductive performance in ewe lambs conceived and born in harsh nutritional environments. Similarly, adverse effects on adult wool production have been recorded as a result of undernutrition during the last trimester of pregnancy in breeds such as the Merino, which has high genetic potential for wool growth. Other examples of nutritional effects *in utero* on later performance involve trace elements. Enzootic ataxia or 'swayback' arises from copper deficiency *in utero*, while subclinical cobalt deficiency during early pregnancy results in the birth of lambs that are slow to stand and suck; they also have a reduced acquisition of passive immunity as measured by their low serum IgG concentrations (Fisher and MacPherson, 1991). During the later stages of pregnancy an inadequate intake of selenium by the ewe results in the birth of lambs with reduced vigour and a suboptimal ability to generate heat from their brown adipose tissue. Many of the trace element deficiencies become more prevalent following the increase in pasture production that occurs after land drainage, additional fertilizer nitrogen usage and increases in soil pH. The causal mechanisms are a reduced plant uptake of trace elements, the demise of pasture species rich in the elements and the higher trace element needs of ewes whose production potential has been stimulated by increased feed availability. Reduced maternal tissue mobilization arising from the general improvement in the energy and protein status of the ewe also contributes to the problem by inhibiting the release of essential mineral elements from the ewe's body reserves. Pre-lambing calcium deficiency (hypocalcaemia) provides another example of this phenomenon. Heavily pregnant ewes receiving adequate amounts of calcium in their diet are extremely susceptible to hypocalcaemia following a sudden drop in calcium intake. The reason for this is that the adjustments in gut absorption and mobilization of calcium from bone, which are needed to prevent a fall in blood calcium, do not occur quickly enough to maintain calcium homeostasis when dietary intake falls.

High-input systems maximize production potential with minimum dependence on body reserves; in contrast, low-input systems that are a feature of harsh nutritional environments involve major depletions of body lipid and mineral elements to sustain production. For these systems it is important that energy deficits in late pregnancy do not lead to excessive rates of body lipid mobilization and associated elevations in blood ketones (3-hydroxybutyrate concentrations) above 0.8 nmol l^{-1} (Russel, 1984), otherwise there is a high risk of pregnancy toxaemia with the loss of both ewe and lambs. To prevent blood ketones rising above this threshold means restricting average daily energy deficits to $\sim$ 25 kJ ME kg^{-1} body weight or $\sim$ 2 MJ for a 75 kg ewe bearing twins in which the daily metabolizable energy requirement 2 weeks before lambing is $\sim$ 18 MJ ($\cong 1.7 \times$ maintenance needs of the ewe pre-mating). For ewes at the limits of their energy deficit during late pregnancy there are major nutritional benefits in feeding a small amount (1 g kg^{-1} ewe body weight day^{-1}) of a protein supplement such as fish meal. This protein source is rich in essential amino acids that escape degradation in the rumen and are therefore available for absorption in the small intestine. Its presence in the diet allows body fat reserves acquired prior to mating to be utilized more efficiently and safely for pregnancy; it also enhances colostrum production and the ewe's ability to combat gastrointestinal parasites (Donaldson *et al*., 2001).

Output from extensive systems is often dictated by available feed resources (natural plus supplements) during late pregnancy and early lactation when nutrient demands are greatest. The magnitude of these demands is set by the plane of nutrition and body condition of the ewe at mating. Pre-mating improvements in nutrition (flushing) can increase the average litter size of ewes that are in poor body condition (score 1.5) from 1 to 1.3, while a one unit increase in condition score to 2.5 can increase it to 1.6. Thus the post-weaning to pre-mating nutritional management of the flock plays a central role in its productivity. (JJR)

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Ewe lactation The milk produced by lactating ewes may be used either for the production of lambs or, via milking, to provide milk and milk products (yoghurt, cheese and now pharmaceutical proteins) for human consumption. Milking usually follows a period (1–2 months) of suckling until the lambs can survive and grow on solid food alone. In some systems lambs are removed within 2 days of birth and ewes are milked for the next 6–7 months. Alternatively, following the first few days of suckling, ewes may be milked with the lambs restricted to daily sucking periods after milking until weaned at about 2 months of age, after which the ewes are milked for another 3–4 months. Durations of lactation therefore vary from approximately 3–4 months for lamb-rearing systems to 6–7 months for dairy systems, which use breeds such as the East Friesland and Awassi that are noted for their high milk yields.

In addition to ewe genotype, there are numerous other non-nutritional factors that affect milk yield. These include the positive effects of the number of lambs carried during pregnancy as well as the number reared. In the ewe, almost all of the udder's secretory tissue is laid down during pregnancy. Thus the effect on milk production of litter size during pregnancy arises from the increase in the size of the placenta and the accompanying stimulatory effect on mammogenesis of its associated greater production of hormones, notably placental lactogen. The effect on milk yield of the number of lambs reared is greatest between singletons and twins; milk intake by singletons is usually well below the ewe's production potential and thus ewes rearing twins produce about 40% more milk than those with singletons. Further increments in yield for triplets and higher multiples are generally much smaller (approximately 15–20%); they also occur early in lactation and gradually decrease so that by 12 weeks differences in yield due to the number of lambs suckled are negligible. At this point daily yields have declined from a peak of about 4 l to about 1 l. In contrast, for dairy breeds in which lamb suckling is replaced by twice-daily machine milking during the second month of lactation, the rate of decline is slower, with yields not falling to 1 l day^{-1} until 20–25 weeks of lactation.

Daily nutrient requirements during early lactation are the highest experienced by the ewe in her lifetime and are met through a combination of increased appetite and the mobilization of body tissues. The extent of the appetite increase depends on the body condition of the ewe: fat ewes have smaller increases, and lose more body fat reserves, that their thinner counterparts.

Estimates of the energy requirements for lactation can be obtained from the yields of milk constituents. For example, for meat-producing breeds AFRC (1993) used the experimentally derived relationship NE_l (MJ kg^{-1}) = 0.04194F + 0.01585P + 0.02141L, where NE_l = net energy requirement and F, P and L are the amounts (g kg^{-1}) of fat, protein and lactose, respectively. Typical values are 70 for F, 55 for P and 45 for L. CSIRO (1990) used the coefficients 0.0381, 0.0245 and 0.0165 for F, P and L, respectively, whereas INRA (1989) used the relationship NE_l (MJ day^{-1}) = 0.0588F + 0.265, in which F is in g l^{-1}. In converting net energy requirements for milk production to metabolizable energy (ME), all three feeding systems accept that the efficiency (k_l) of utilization of ME for milk energy production is influenced by the quality or metabolizability (q) of the diet, i.e. q = ME/GE where GE = gross energy. AFRC and CSIRO used the relationship k_l = 0.35q + 0.420 whereas INRA used k_l = 0.24q + 0.463, which gives slightly higher values for k_l than AFRC and CSIRO and therefore marginally lower estimates of the ME requirements for milk production.

With regard to the contribution that mobilized body tissue makes to energy needs for lactation, AFRC derived a dietary ME equivalent of 31.6 MJ kg^{-1} liveweight loss for a k_l of 0.63, i.e. a diet with an ME concentration of 11.5 MJ kg^{-1} dry matter (DM). The corresponding CSIRO value was 28 MJ kg^{-1} weight loss. In contrast, INRA linked the extent of body energy mobilization for milk production to a proportion of maintenance and adopted a value of approximately 70% of maintenance (equivalent to approximately 0.3 MJ of ME kg^{-1} $W^{0.75}$ day^{-1}) for early lactation, when the deficit between energy intake and requirements is at its maximum.

Protein requirements for lactation are expressed in terms of metabolizable protein (MP). In the case of AFRC (1993) they were based on the assumption that ewe's milk contains 48.9 g true protein kg^{-1} and its production from MP is achieved with an efficiency of 68%. Although other systems use different efficiencies (CSIRO 70%, INRA 58%, NRC 65%), example calculations (Sinclair and Wilkinson, 2000) indicate that differences between systems in the estimates of microbial protein and the contribution of recycled nitrogen to the rumen lead to remarkably similar crude protein requirements. These are 169, 160, 167 and 154 g kg^{-1} dietary DM when the AFRC, CSIRO, INRA and NRC systems, respectively, are applied to a 70 kg ewe producing 2.0 kg of milk, consuming 2.1 kg DM and 23.1 MJ of ME daily and maintaining a constant body weight.

During periods of body tissue mobilization, which is the norm in early lactation, AFRC (1993) assumed that each kilogram of weight loss contributed approximately 120 g of milk protein (enough for about 2.4 kg of milk) whereas CSIRO used the slightly lower value of 108 g. In relation to the amount of milk (approximately 4.3 kg) that can be produced from the energy in 1 kg of weight loss, mobilized body tissue is clearly deficient in protein. Ewes in negative energy balance therefore respond, in terms of extra milk production, to increases in dietary protein. In fact, it can be argued that the aim should be to prevent body protein catabolism by ensuring that sufficient extra dietary protein (316 g MP kg^{-1} weight loss) is given to meet completely the milk production contributed from mobilized body energy. This value is based on 1 kg of weight loss contributing enough energy for 4.3 kg of milk with a protein content of 5% and a 68% efficiency of use of MP for the synthesis of milk protein.

The requirements for the major mineral elements, calcium and phosphorus, are based on the same general principles as for energy and protein. Their respective concentrations in milk are 1.9 and 1.5 g kg^{-1} but conversion of these to dietary amounts, particularly in the case of calcium, is not straightforward in that there is an inverse relationship between intake and absorption; also mobilization of skeletal calcium and phosphorus is a normal occurrence during early lactation. AFRC (1991) provided a comprehensive set of dietary estimates for Ca and P in relation to ewe size, milk yield and the metabolizability (q) of the diet. For calcium, the recommended dietary concentrations for a 75 kg ewe consuming a diet for which q is 0.6 decrease from 0.38 to 0.27% in the DM as her daily milk yield declines from 3.0 to 1.0 kg and her associated daily losses in body weight decline from 100 g to zero. Corresponding recommendations for dietary phosphorus are 0.41 and 0.30%. Unlike calcium and phosphorus reserves, magnesium reserves in the ewe's body are trivial and there is little, if any, response in Mg absorption as requirements increase. The lactating ewe therefore requires a constant dietary supply, particularly in the first 6 weeks of lactation, when she is vulnerable to death from acute hypomagnesaemia, and particularly if she is grazing lush pastures that are high in potassium and low in sodium. A common dietary supplement is magnesium oxide given at a daily rate of 7 g to ewes producing 3–3.5 kg milk day^{-1}. (JJR)

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Ewe pregnancy Pregnancy in the ewe lasts from the time of fertilization of an ovum or ova in the oviduct until the resulting concepta leave the uterus. In a successful pregnancy live lambs, with their associated placentas, are born approximately 5 months after fertilization. The gestation length is normally between 144 and 152 days but is to some extent dependent on breed, nutrition and the number of lambs in the uterus.

Ewes usually ovulate between one and four ova at each oestrous period. The numbers vary according to the nutritional status of the ewe (*see* **Flushing**), age, season and breed. Some breeds commonly carry one or two lambs, whilst others, such as the Border Leicester, will often carry two or three lambs to term.

Immediately after fertilization, the ovum begin to divide, forming a solid cluster of cells or blastomeres known as a morula (from its mulberry shape). This process takes about 4 days, during which the embryo continues its passage down the oviduct and enters the uterus. From about day 5 after fertilization, the ovum hollows out to become a blastocyst, which consists of a single spherical layer of cells, the trophoblast, with a hollow centre and an inner cell mass at one edge. The inner cell mass is destined to form the embryo, whilst the trophoblast provides it with nutrients and will form the fetal component of the placenta. At about day 6 the blastocyst 'hatches' from its shell (the zona pellucida) and is elongating rapidly by about day 11. Meanwhile, the inner cell mass differentiates to form the germ layers, namely the ectoderm, mesoderm and endoderm. The ectoderm gives rise to the external structures such as skin, hair, hooves and mammary glands and also the nervous system. The heart, muscles and bones are eventually formed from the mesoderm whereas the other internal organs are derived from the endoderm layer. By day 45, formation of the primitive organs is complete.

The embryo is able to exist for a short time by absorbing nutrients from its own tissues and from the uterine fluids, but it ultimately becomes attached to the endometrium by means of its membranes through which nutrients and metabolites are transferred from mother to fetus and vice versa. The ewe placenta, unlike that of the cow, allows the passage of antibodies from the mother to the fetus, so that lambs can acquire immunity from their dams *in utero*. The attachment process is known as implantation and may begin as early as day 10, but is not complete until around day 30. If the ewe is carrying more than one lamb, the placentas and their blood supplies remain separate. Thus, unlike the cow, there is little or no danger of sheep producing freemartins.

Fetal growth is exponential throughout gestation, the rate increasing as pregnancy progresses. Fasting metabolism during pregnancy is higher than that in non-pregnancy and increases throughout pregnancy. This, together with the liveweight increase that should occur, leads to a gradual rise in the maintenance energy requirement. Thus, the requirement for energy in pregnancy is increased by far more than the calculated requirements for the storage of energy in the uterus. The fetus has a high priority for energy and can draw specific nutrients from the ewe's body reserves even if she is being underfed. Fetal lambs can, for example, be adequately supplied with iron even when the mother is anaemic, and a ewe can lose up to 14 kg of her own body weight during pregnancy and still give birth to normal lambs. The fetus can maintain higher blood sugar levels than those of the ewe, which can thus succumb to a hypoglycaemic condition known as pregnancy toxaemia. Ewes carrying more than one lamb are more prone to the condition, which is also called twin lamb disease. The problem is exacerbated by the fact that voluntary feed intake tends to be suppressed in late pregnancy when energy requirements are very high. It is good practice to scan ewes to detect the presence of more than one fetus, so that extra feed can be given during the last 2 months of pregnancy to ewes carrying multiple lambs as well as to those with lower body condition scores.

Severe underfeeding ultimately affects the unborn lambs as well as their mothers. The young may die *in utero* or have reduced viability after birth as a result of a lowered birth weight and a possible lowering of milk yield. Severe malnutrition in early pregnancy may simply reduce litter size. Protein, vitamin A and certain mineral and amino acid deficiencies can cause fetal death. In the case of vitamin A the lambs may be affected even though the ewe remains healthy. Vitamin deficiency may cause congenital deformities in fetal lambs that survive, while copper deficiency can cause 'swayback', which can severely affect the coordination of newborn lambs.

Increasing the energy intake of the ewe in the last 6 weeks of pregnancy can increase the birth weight of lambs (see table). (PJHB)

Reference and further reading

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Exercise: *see* Activity, physical

Exopeptidase A proteolytic enzyme that has the capability to hydrolyse the terminal peptide bonds in a protein. **Aminopeptidases** liberate amino acids consecutively from the N-terminus. In contrast, **carboxypeptidases** act from the C-terminus and may also liberate di- and tripeptides. (SB)

The effect of energy intake of ewes in the last 6 weeks of pregnancy on the birth weights of their twin lambs. Source: McDonald *et al.* (1995).

Group	Energy intake MJ/day	Liveweight change of ewes (kg)	Birthweight of lambs (kg)
1	9.4	–14.5	4.3
2	12.4	–12.7	4.8
3	13.9	–11.4	5.0
4	18.6	–5.4	5.2

Exophthalmia A common degenerative condition of the eye in which the globe is pushed out of the eye socket. In fish, it is typically related to the enlargement of the choroid gland of the posterior uvea or to degeneration of the ocular musculature. It has been linked to niacin deficiency. (DS)

Extensive livestock systems Livestock systems, often based on natural grazing or rangeland in dry areas, in which inputs and outputs are low. In large livestock operations, breeding is often carried out extensively, followed by intensive finishing of progeny for marketing. Extensive systems are not suitable for profitable smallholder livestock production. (TS)

Extracellular water Body water that is outside the cells, in contrast to intracellular water. Extracellular water includes that of blood, lymph, cerebrospinal and peritoneal fluids as well as interstitial water in the extravascular spaces within tissues. It can be estimated from the dilution of tracers that do not enter cells significantly during a short equilibration (e.g. bromide). Total body water is the sum of extracellular and intracellular water. (MFF)

Extract, ether: *see* Ether extract

Extraction, oil Oil is extracted from oil-rich vegetable seeds, such as **soybean** (20% oil), **oilseed rape** (46%) and **linseed** (39%), by first dehulling and then crushing the seed between rollers or a screw press and collecting the resultant oil. This process is known as expelling. The remaining solids are known as expeller or 'cake' and have variable oil contents of around 10%. Many are sold and used as animal feed ingredients in this state. The oil is a useful component of the material but it is susceptible to oxidation and therefore poses potential storage problems. Further oil may be removed by organic solvent extraction, which reduces the oil content of the final meal to 2–3%. The solvent is finally evaporated from the meal using heat. The resulting oilseed meals are valuable vegetable protein sources for animals of all species. (MG)

Extrusion A process in which conditioned meal is forced through an adjustable annular gap under high pressure. The high shear forces created rupture the cell structure, increase the temperature and gelatinize the starch. Extrusion takes place in a compression chamber of variable length, normally at least 2 m. The pressure is produced by feeding meal into the chamber at one end, whence it is moved along the chamber by a revolving screw conveyor before being forced through a die with many holes at the other end. The flow of meal is adjusted to keep the conveyor running full and obtain maximum pressure at the die. Steam is normally injected along the length of the barrel to aid the extrusion process. Extrusion can be used to condition before **pelleting**, but is more commonly used as a manufacturing process in its own right. Extruded products are commonly used as fish food, as the modification of starch greatly improves the swelling properties in cold water. They are also used for diets for young mammals and poultry, due to the improved digestibility of the starch. Most dried pet foods now contain extruded chunks, since shapes can easily be made by changing the shape of the hole in the die. (MG)

Exudative diathesis A disorder of poultry caused by selenium deficiency, usually as a result of consuming cereals with a low selenium concentration. It is characterized by a generalized oedema, which arises from abnormal permeability of the capillary walls. Usually the oedema first appears on the breast, wing and neck, with the greatest accumulation of fluid eventually forming under the ventral skin. Broilers are usually affected between 3 and 6 weeks of age, when they will lose weight, develop leg weaknesses and may die. Supplementary selenium or vitamin E will prevent the disorder. (CJCP)

Eye diseases The eye is well protected from variation in nutritional status but there are disorders of the eye that have nutritional connections. Vitamin A deficiency causes a dryness of the conjunctiva (xerophthalmia) and can lead to night blindness or complete blindness. Eyes are susceptible to cancer during excessive exposure to ultraviolet light, and foods with high levels of antioxidants protect against this. Diabetes mellitus, arising from chronic hypoglycaemia, can result in retinopathy, cataracts and glaucoma. In grazing animals, eye inflammation, or conjunctivitis, can arise from irritation from seeds, chaff, awns, etc. (CJCP)

F

Factorial method (for estimating nutrient requirements) A method by which the requirement for a nutrient is estimated as the sum of its components. Depending on the animal and the nutrient in question, these components may include growth, activity, gestation, lactation, egg production, wool growth, etc. Dietary nutrients are used with varying efficiency to meet these needs, and these efficiencies must be included in the assessment. For example, the energy requirement (R) of a growing animal is commonly considered to be the sum of its requirements for maintenance (M), protein accretion (P) and fat (lipid) deposition (F). Thus,

$$R = M/k_m + P/k_p + F/k_f$$

where k_m, k_p and k_f are the efficiencies with which dietary energy (usually metabolizable energy) is used for each process. It will be seen that the equation is used to derive a requirement for particular rates of protein and fat deposition; when these rates are inserted into the equation, an estimate of the intake required to support those rates is generated, though at some intake the animal's potential for protein or fat deposition will be reached and the linear responses will no longer apply.

Such a simple model implies that efficiency is constant at all intakes, which is often demonstrably untrue. More complex models allow for diminishing efficiency at higher intakes. The simple model also applies only to an individual, whereas in practice the need is usually to derive the response of a population (herd or flock) that comprises individuals with varying values for each of the terms. This requires a more complex set of equations.

(MFF)

Faecal flora: *see* Gastrointestinal microflora

Faeces Also called stool. Waste matter discharged from the intestines through the anus. The amount and composition of faeces vary between species and according to the diet consumed. Faeces originate from undigested feed and endogenous losses (gastrointestinal secretions and sloughed epithelial cells from the gastrointestinal tract) that have not been reabsorbed. A considerable portion of these may be transformed into microbial matter. A large part of the electrolytes present in the faeces are of metabolic origin.

Faeces of non-ruminant animals are dominated by bacterial cells, which may contribute up to 85%. Starch in faeces is indicative of inefficient milling of cereals or of retrogradation. Faeces of ruminants consuming mainly roughages are mainly cell wall components. The colour of faeces is derived from plant pigments and bacterially degraded bile pigments.

The water content varies considerably within a species but is generally higher in the faeces of cattle (75–85%) than that of pigs (65–75%) or even hens (70–75%), which secrete urine together with faeces via the cloaca. The pH varies with the composition of the diet and is generally below 7 in cattle and horses but above 7 in pigs, sheep and hens.

An abnormal water content of faeces is indicative of **digestive disorders**, in particular diarrhoea. **Steatorrhoea** is the excretion of fatty, bulky, clay-coloured stools resulting from impaired digestion and absorption of fat.

(SB)

Faeces collection Faeces are collected for many purposes, most commonly for measuring nutrient digestibility or for investigating effects on the microflora. Total collections are made by confining the animal in a metabolic cage or by a container fixed around the anus or cloaca, usually with a harness. Simple 'grab' sampling of the faeces can be used to measure digestibility if a **marker** is added to the diet and if faeces samples are collected systematically for a suitable period. Faeces are often collected from fish by stripping, i.e. pressing out the contents of the lateral intestine. In all digestibility studies a sufficiently long preliminary period, which depends on the transit time in the particular animal species, is essential. (SB)

Fasting metabolism Measurement of an animal's fasting metabolic rate is commonly used as an estimate of its **basal metabolism**. The animal must be pre-trained to the calorimeter and the actual measurement takes place over a prolonged period during which the animal is free to move within the confines of the chamber. The fasting period before the measurement begins should exceed that over which there is an observable heat increment following the last feed; in ruminant animals this is 48 h or more.

(JAMcL)

See also: Heat increment of feeding

Fat metabolism: *see* Lipid metabolism

Fat-soluble vitamins There are four fat-soluble vitamins: A, E, D and K. A deficiency of vitamin A results in defective night vision and keratinization of epithelial tissues, e.g. in the eye (xerophthalmia) which can lead to blindness. The lungs and gastrointestinal tract are also affected. A deficiency of vitamin D results in rickets and osteomalacia, which involve a derangement of calcium and phosphorus metabolism. A deficiency of vitamin E (an antioxidant) leads to tissue damage by reactive oxygen species produced during aerobic metabolism. A deficiency of vitamin K results in haemorrhage, because vitamin K is involved in the synthesis of the blood clotting factors. (NJB)

Fats Esters of fatty acids with glycerol. Simple fats are called triacylglycerols or triglycerides. Triacylglycerols with three saturated fatty acids of ten or more carbons are solid at room temperature. Those with fatty acids of less than ten carbons or fatty acids with one or more double bonds (unsaturated) are often liquid at room temperature and are called oils. Thus, fats and oils are similar in structure but are either solid or liquid at room temperature. Processed fat derived from pigs is called lard. Processed fat from cattle, sheep and horses is called tallow. Both of these are solid at room temperature.

To estimate the amount of fat in a feed or food, a sample is extracted for a specified time with a solvent such as ether. In some cases, where total fat in a tissue is required, a system based on a mixture of chloroform/methanol is used. In the Weende system of feed analysis, the fat component is defined as the ether-extractable material. The weight of material extracted from a known amount of sample is used to calculate the percentage of the sample weight that is made up of 'fat'. However, not all ether-extractable material is fat as defined above, because other lipid-soluble materials are extracted by ether. Fats used as food or feeds come both from animals and plants. Animal products generally contain more saturated fats while plant products contain more unsaturated fats. Fat is a significant source of food energy. The gross energy of fat is 37.7–39.7 kJ g^{-1} (9.0–9.5 kcal g^{-1}), 2.5 times that of glucose.

Fats used for animal feeding are extracted either from animal carcasses, e.g. tallow, or from plant seeds, e.g. palm oil. Beef tallow is no longer used since the occurrence of BSE. Coconut oil and palm kernel oil are rich in lauric acid (C12:0) and are sometimes referred to as the lauric acid oils. Palm oil and tallow are composed mainly of palmitic (C16:0), stearic (C18:0) and oleic (C18:1) acids. The melting point of fats is determined mainly by the chain length of the fatty acids and their saturation. Fats with short-chain fatty acids or unsaturated fatty acids have lower melting points than those with long-chain saturated fatty acids. Saponification value is an indicator of the chain length of fatty acids in a fat or oil. High values indicate shorter chain lengths. Iodine value is an indicator of the degree of unsaturation of a fat or oil; high values are associated with a high proportion of unsaturated fatty acids.

(NJB, JRS)

Fatty acid composition (%) and physico-chemical properties of common fats.

Lipid	Beef tallow	Lard	Coconut oil	Maize oil	Rapeseed oil	Palm oil
10:0			7			
12:0			47			
14:0	3	2	17			1
16:0	26	26	8	11	4	48
16:1	6	4				
18:0	17	14	4	2	2	4
18:1	43	43	5	24	56	38
18:2	4	10	2	58	20	9
Melting point (°C)	40–50	28–48	23–26			38–45
S/U ratio	0.85	0.72	13.29			1.13
Saponification value	190–200	193–200	251–264			196–202
Iodine value	32–47	46–66	7–10			48–56

S/U ratio = ratio of saturated to unsaturated fatty acids.

Fattening The term fattening (or 'finishing') is used to describe the process of bringing animals to an appropriate stage of body condition prior to slaughter for meat consumption. As the animal grows towards maturity the parts of the musculature that provide the most desirable cuts of meat tend to be late developing and the subcutaneous and visceral fat deposits increase more rapidly. The desired state of fatness (or 'cover') will vary with the culture and consumer demand. Furthermore, as the rate of protein deposition decreases and the rate of fat deposition increases, the **feed efficiency** declines to a point where it becomes uneconomic to grow the animal to a higher weight. In developed economies, where the consumption of animal fat is generally regarded as detrimental to health, there are usually grading systems in place with financial penalties for animals that are considered to be too fat. In the case of pigs, grading is usually based on one or more measurements of subcutaneous fat depth at specified points on the carcass. Systems for cattle and sheep relate to visual inspection of the extent and depth of subcutaneous fat cover on the carcass. With poultry there is little external fat and even the fat content of the meat tends to be low; the main source of fat is the abdominal fat pad, which is usually left in the eviscerated bird. (KJMcC)

See also: Carcass; Finishing; Meat composition; Meat production

Fatty acid synthase A multi-enzyme complex of seven enzyme activities responsible for the *de novo* synthesis of fatty acids. In biosynthesis of longer-chain fatty acids, two carbon units derived mainly from the catabolism of glucose and amino acids are added two by two (i.e. via malonyl CoA to acetyl CoA) to make palmitate, which is a 16-carbon saturated fatty acid, $CH_3{\cdot}(CH_2)_{14}{\cdot}COO^-$. In ruminants the source of the two carbon units is acetate from fermentative digestion in the rumen. The major site of fatty acid biosynthesis depends on the animal. In humans it is in the liver, in rats liver and adipose and in birds it is only in the liver. (NJB)

Fatty acid synthesis The process whereby fatty acids (for example, palmitate, $CH_3{\cdot}(CH_2)_{14}{\cdot}COO^-$) are synthesized, mostly from non-fat sources (carbohydrate and amino acids). Synthesis of fat is a means whereby excess energy from a meal can be stored in the body for later use. The *de novo* synthesis of fatty acids occurs in the cytoplasm of liver or adipocytes, depending on the species. Acetyl-CoA ($CH_3{\cdot}CO{\cdot}SCoA$), derived from carbohydrate or fat catabolism or from activation of acetate formed in intestinal fermentation, is the starting two-carbon unit for long-chain fatty acid biosynthesis. Another acetyl-CoA is converted to malonyl-CoA by acetyl-CoA carboxylase, $CH_3{\cdot}CO{\cdot}SCoA + CO_2 \rightarrow HOOC{\cdot}CH_2{\cdot}CO{\cdot}SCoA$ and added to the growing acyl-CoA chain as a three-carbon unit. After loss of CO_2 from the added malonyl-CoA a two-carbon unit has been added. To complete the process of adding a two-carbon unit to a growing fatty acid chain, two molecules of NADPH are used to reduce the unsaturated double bonds created in the biosynthetic process. The reducing equivalents (i.e. NADPH) are produced in the catabolism of glucose in the pentose cycle. The overall stoichiometry of the reaction is: 1 acetyl-CoA + 7 malonyl-CoA + 14 NADPH + $14H^+ \rightarrow$ $CH_3{\cdot}(CH_2)_{14}{\cdot}COOH + 7CO_2 + 6H_2O$ + 8 CoASH + 14 $NADP^+$. (NJB)

Key reference

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Fatty acids Compounds of carbon, hydrogen and oxygen with a functional group, a carboxyl carbon, $CH_3{\cdot}(CH_2)_n{\cdot}COOH$. They are either saturated or unsaturated (see tables opposite). Unsaturated fatty acids, which have at least one double bond, belong to one of three families. The 18-carbon n-9 (Δ^9) oleic family has at least one double bond between carbons 9 and 10. The 18-carbon n-6 ($\Delta^{9,12}$) linoleic family has at least two double bonds, one at 9–10 and one at 12–13. The 18-carbon n-3 ($\Delta^{9,12,15}$) linolenic family has at least three double bonds, one at 9–10, one at 12–13 and one at 15–16. When fatty acids are synthesized by an animal, the initial fatty acid unit may be either a two- or three-carbon fatty acid. When a two-carbon unit (acetate) is the starting unit, the fatty acids are even-chained because the fatty acid chain is elongated by two carbon units. If the starting unit is a three-carbon unit (propionate), the fatty acid will be an odd-chain fatty acid. All combinations of saturated, unsaturated, even- and odd-chain fatty acids would be expected in nature.

A unique series of fatty acids is the medium-chain fatty acids, C-6, C-7, C-8, C-9, C-10. In animal nutrition they play a important role in meeting the energy needs of newborn mammals. These fatty acids are usually located in the *sn*3 position of milk triglyceride. Fatty acids in this position are released by lingual lipase or pregastric esterase and are absorbed directly into the bloodstream, where they are transported as free fatty acids. After being taken up by cells these fatty acids do not require carnitine to be transported across the inner mitochondrial membrane to the matrix, their site of catabolism. Since their rate of metabolism is not controlled by transport, these fatty acids can be metabolized rapidly. In the mitochondrial matrix they are activated by one or more of the acyl-CoA synthases, which convert them to fatty acyl-CoA which can be degraded to two carbon units of acetyl-CoA and used as a source of energy. Because these medium-chain fatty acids (as triacylglycerols) can be taken up rapidly, they may be selected as a fuel when normal digestive processes have been compromised.

Long-chain fatty acids, with ten or more carbons, are released from dietary triacylglycerols in the lumen of the intestine by pancreatic lipase. In the presence of bile salts they diffuse into the mucosal cells as free fatty acids and monoglycerides where they are re-esterified into triglycerides (triacylglycerols) combined with cholesteryl esters, some phospholipid and protein. They are packaged into chylomicrons and delivered to the body via the lymphatic system. After being taken up by cells, the fatty acids are activated by one or more of the acyl-CoA synthases in the cytoplasm to acyl-CoA. In the cytoplasm these long-chain fatty acids and the acyl-CoA derivative must be converted to acylcarnitine before they can be transported across the inner mitochondrial membrane by carnitine palmitoyltransferase. Once in the mitochondrial matrix, fatty acids are reconverted to fatty acyl-CoA which can be degraded to two carbon units of acetyl-CoA and used as a source of energy for ATP production. (NJB)

Feather meal A light brown material obtained by hydrolysing, drying and grinding poultry feathers. Hydrolysis is achieved by steaming under pressure for 30–45 min at a temperature of about 145°C, which renders the proteins soluble. Care must be taken to avoid contamination of the meal with salmonella organisms that may be present on the feathers. Composition depends on the type and age of fowl used. Although the protein content is high, its quality is low and its availability is only about 50%. It is used as a pro-

Saturated fatty acids.

Common name	Systematic name	Structure	Source
Formic		$HCOOH$	Metabolic product of amino acid metabolism
Acetic	Ethanoic	$CH_3{\cdot}COOH$	Produced by fermentative digestion
Propionic	Propanoic	$CH_3{\cdot}CH_2{\cdot}COOH$	Produced by fermentative digestion
Butyric	Butanoic	$CH_3{\cdot}(CH_2)_2{\cdot}COOH$	Produced by fermentative digestion
Isobutyric		$(CH_3)_2{\cdot}CH{\cdot}COOH$	Produced from the catabolism of L-valine in the rumen bacteria
Valeric		$CH_3{\cdot}(CH_2)_3{\cdot}COOH$	Produced by fermentative digestion
Isovaleric		$(CH_3)_2{\cdot}CH{\cdot}CH_2{\cdot}COOH$	Produced from the catabolism of L-leucine by rumen bacteria
Caproic	Hexanoic	$CH_3{\cdot}(CH_2)_4{\cdot}COOH$	Produced by fermentative digestion, in milk fat, coconut oil
Caprylic	Octanoic	$CH_3{\cdot}(CH_2)_6{\cdot}COOH$	Milk fat, coconut oil
Pelargonic	Nonanoic	$CH_3{\cdot}(CH_2)_7{\cdot}COOH$	Coconut oil
Capric	Decanoic	$CH_3{\cdot}(CH_2)_8{\cdot}COOH$	Milk fat, coconut oil
Lauric	Dodecanoic	$CH_3{\cdot}(CH_2)_{10}{\cdot}COOH$	Milk fat, palm and coconut oil
Myristic	Tetradecanoic	$CH_3{\cdot}(CH_2)_{12}{\cdot}COOH$	Milk fat, palm and coconut oil
Palmitic	Hexadecanoic	$CH_3{\cdot}(CH_2)_{14}{\cdot}COOH$	Animal and plant fats and oils
Stearic	Octadecanoic	$CH_3{\cdot}(CH_2)_{16}{\cdot}COOH$	Animal and plant fats
Arachidic	Eicosanoic	$CH_3{\cdot}(CH_2)_{18}{\cdot}COOH$	Groundnut, rape, butter and lard
Behenic	Docosanoic	$CH_3{\cdot}(CH_2)_{20}{\cdot}COOH$	Groundnut, rape, milk fat, marine oils
Lignoceric	Tetracosanoic	$CH_3{\cdot}(CH_2)_{22}{\cdot}COOH$	
Cerotic	Hexacosanoic	$CH_3{\cdot}(CH_2)_{24}{\cdot}COOH$	
Montanic	Octacosanoic	$CH_3{\cdot}(CH_2)_{26}{\cdot}COOH$	

Unsaturated fatty acids.

Common name	Systematic name	Structure	Source
Palmitoleic	*cis*-9-Hexadecenoic	16:1 n-9 (Δ^{9})	Nearly all fats
Oleic	*cis*-9-Octadecenoic	18:1 n-9 (Δ^{9})	All fats
Elaidic	*trans*-9-Octadecenoic	18:1 n-9 (Δ^{9})	Hydrogenated fats, milk fat
Gadoleic	*cis*-9-Eicosenoic	20:1 n-11 (Δ^{9})	Brain phospholipid, fish liver oil
Erucic	*cis*-13-Docosenoic	22:1 n-9 (Δ^{13})	Rape, mustard seed oils
Nervonic	*cis*-15-Tetracosenoic	24:1 n-9 (Δ^{15})	Nervous tissue
Linoleic	all-*cis*-9,12-Octadecadienoic	18:2 n-6 ($\Delta^{9,12}$)	Maize, groundnut, cottonseed, soybean oils
γ-Linolenic	all-*cis*-6,9,12-Octadecatrienoic	18:3 n-6 ($\Delta^{6,9,12}$)	Some plants, limited in animals
α-Linolenic	all-*cis*-9,12,15 Octadecatrienoic	18:3 n-3 ($\Delta^{9,12,15}$)	Maize, groundnut, cottonseed, soybean, linseed oils
Mead acid	all-*cis*-5,8,11-Eicosatrienoic	20:3 n-9 ($\Delta^{5,8,11}$)	Animal fats, phospholipids
Arachidonic	all-*cis*-5,8,11,14-Eicosatetraenoic	20:4 n-6 ($\Delta^{5,8,11,14}$)	Animal fats, phospholipids
Timnodonic	all-*cis*-5,8,11,14,17-Eicosapentaenoic	20:5 n-3 ($\Delta^{5,8,11,14,17}$)	Fish oils, cod liver oil, mackerel, menhaden, salmon oils
Clupanodonic	all-*cis*-7,10,13,16,19-Docosapentaenoic	22:5 n-3 ($\Delta^{7,10,13,16,19}$)	Fish oils, phospholipids in brain
Cevonic	all-*cis*-4,7,10,13,16,19-Docosahexaenoic	22:6 n-3 ($\Delta^{4,7,10,13,16,19}$)	Fish oils, phospholipids in brain

tein concentrate but is more suited to the feeding of ruminants than monogastrics, due to the deficiency of essential amino acids, particularly lysine and methionine. Feather meal should be introduced into the diet gradually to overcome its low palatability. It can be used in the diet at inclusion rates of 7% for beef cattle, 3% for lamb and 2.5% for ewe and dairy cattle diets. The dry matter (DM) content of feather meal is 900 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 860, crude fibre 6, ether extract 65 and ash 40, with MER 12.6–14.1 and MEP 12.5–14.2 MJ kg^{-1}. (JKM)

Feed A source of nutrients for animals and an ingredient of diets. Feeds include grazed pasture, conserved forage crops, grains and seeds, crop residues and by-products. The word 'feed' usually refers to animal diets and the word 'food' to human diets. (JMW)

Feed additive: *see* Additive, feed

Feed blocks Molassed supplement blocks are particularly useful for feeding ruminant animals in remote or inaccessible areas. They vary in weight from 20 to 500 kg and generally withstand harsh weather conditions. They usually contain a balanced supply of nutrients, including minerals and vitamins, and may be medicated. In rough and remote areas where transporting high volumes of feed is impossible, this may be the only practical way that animals can be offered essential minerals and vitamins. Such nutrients are particularly vital before mating, during the last third of pregnancy and in lactation.

Raw materials in feed blocks include cereals, cereal by-products, distillery by-products, molasses, minerals and vitamins. Urea is sometimes added as a nitrogen source for ruminants. Blocks are designed for relatively low daily intakes, e.g. 175 g per head for sheep or 500 g per head for cattle. They may also be used to relieve the boredom of stalled animals such as pigs and horses. In addition, they have been innovatively used to administer medication to wild game birds, e.g. moorland grouse.

Feed blocks are usually made by grinding the raw materials, mixing with molasses and compressing with a hydraulic press in a mould to form a dense block. They may also include calcium oxide: the exothermic reaction between this and the molasses sets the material into a hard block. The block must be hard enough to avoid excessive intakes but not so hard that animals, particularly those with less secure teeth, cannot access the supplement. (MG)

Feed composition tables Tables listing the chemical composition and nutritional attributes of feeds, such as energy, protein and amino acids and their digestibility, are used in ration formulation and are included in computer ration formulation software. The following are those used most extensively in animal nutrition.

MAFF-ADAS (1986) *Feed Composition, UK Tables of Feed Composition and Nutritive Value for Ruminants*. Chalcombe Publications, Marlow, UK, 69 pp.
Givens, D.I. and Moss, A.R. (eds) (1990) *UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs*. Rowett Research Services, Aberdeen, 420 pp.
Ewing, W.N. (1997) *The Feeds Directory*, Vol. 1, *Commodity Products*. Context Publications, Leicestershire, UK, 118 pp.
Lonsdale, C.R. (1989) *Straights: Raw Materials for Animal Feed Compounders and Farmers*. Chalcombe Publications, Marlow, UK, 88 pp.
Agricultural Research Council (1976) *The Nutrient Requirements of Farm Livestock. No. 4: Composition of British Feedingstuffs*. HMSO, London, 710 pp.

Food composition tables are likewise used in human nutrition. A detailed account of these is given by Southgate (1993). (IM)

Key reference

Southgate, D.A.T. (1993) Food composition tables. In: Garrow, J.S. and James, W.P.T. (eds) *Human Nutrition and Dietetics*, 9th edn. Churchill Livingstone, Edinburgh, pp. 264–272.

Feed conversion: *see* Efficiency of feed conversion (FCE); Feed conversion ratio

Feed conversion ratio (FCR) The ratio of the weight of feed eaten by an animal to the weight of its productive output. The productive output of a growing pig or calf is its weight gain; the productive output of a laying hen is the weight of eggs produced and that of a dairy cow is the weight of milk produced. The cost of feed is the major cost in animal production and so the feed conversion ratio (FCR) has importance in describing the efficiency of an animal production system or enterprise.

Differences between animals affect the FCR on a standard feed. The proportion of nutrients required for body maintenance in relation to the amount then available for productive output can differ between species and strains, and between individuals within a strain. Higher FCRs result if a greater proportion of the nutrients is used for maintenance of body tissues and metabolism. Maintenance requirements are affected primarily by the body weight of the individual, the ambient temperature and the extent of physical activity. The composition of the productive output also affects the FCR. Productive outputs with high water contents (e.g. lean meat) result in a lower FCR (water intake is not considered part of the feed intake). The energy density of body fat is greater than the energy density of lean tissue and so the energy cost of depositing 1 kg of body fat is greater than that of depositing 1 kg of body lean. Body weight gains that have a high proportion of fat thus result in higher FCRs.

Differences in the composition of the feed can affect the FCR of a given population of animals. FCRs decrease with increasing nutrient density. Nutrient density can differ between feeds because of the water content of the feed, the types of nutrients supplied in the feed (high-fat feeds are more energy dense) or the availability of the nutrients. Many practical feedstuffs contain high proportions of non-starch polysaccharides (dietary fibre). These are largely unavailable to non-ruminants, especially poultry, and so increase the FCR of the feed. The availability of other nutrients, such as protein, may be reduced in practical feedstuffs and also give similar effects on FCR. The apparent FCR of a feed may also be increased if there is a large amount of feed wastage that results in feed being spilt on the floor and not being eaten.

Some people prefer to consider the ratio between feed intakes and productive output as an efficiency and so they express the relationship as a ratio of weight of productive output to weight of food intake. This is called feed conversion efficiency (FCE). (SPR)

See also: Efficiency of feed conversion; Feed:gain ratio

Key reference

Guenter, W. and Campbell, L.D. (1995) Comparative feeding programmes for growing poultry. In: Hunton, P. (ed.) *Poultry Production*. World Animal Science, C9. Elsevier, Amsterdam.

Feed dispensers: *see* Automatic feeding

Feed evaluation The process of determining the nutritional value of a feed. Feed evaluation can be conducted in a number of different ways. Practical feeding trials remain the best way to investigate any given feed, providing information not only on nutrient availability but also on voluntary intake or palatability of a feed when fed to the animal species of interest at the relevant stage of development. In these *in vivo* feeding trials nutrients are evaluated in terms of the proportion that is retained in the animal body or secreted as milk, and the proportion that is excreted in faeces, urine and, in some cases, gas. Such trials are energy or mass balance trials in which all of the feed inputs and excretory outputs are measured over a trial period and the mass (or energy) not lost in excreta is divided by the input to give the apparent digestibility. The partitioning of gross energy fed to an animal is conceptualized as shown (Fig. 1). An example of an *in vivo* feeding trial might involve six animals in metabolism cages that allow total collection of excreta. After a 2 week preconditioning period the animals are fed at maintenance level for an 8 day period during which total feed input and the outputs of faeces and urine are measured according to a defined protocol. Some energy is also lost as methane and hydrogen: to measure these losses it is necessary to enclose the animal in a respiration chamber equipped with gas analysers. Energy lost as urine and methane in ruminants can often be assumed to be relatively constant for most practical purposes. Weighed pellets of dry feed and faeces are combusted in an adiabatic bomb calorimeter.

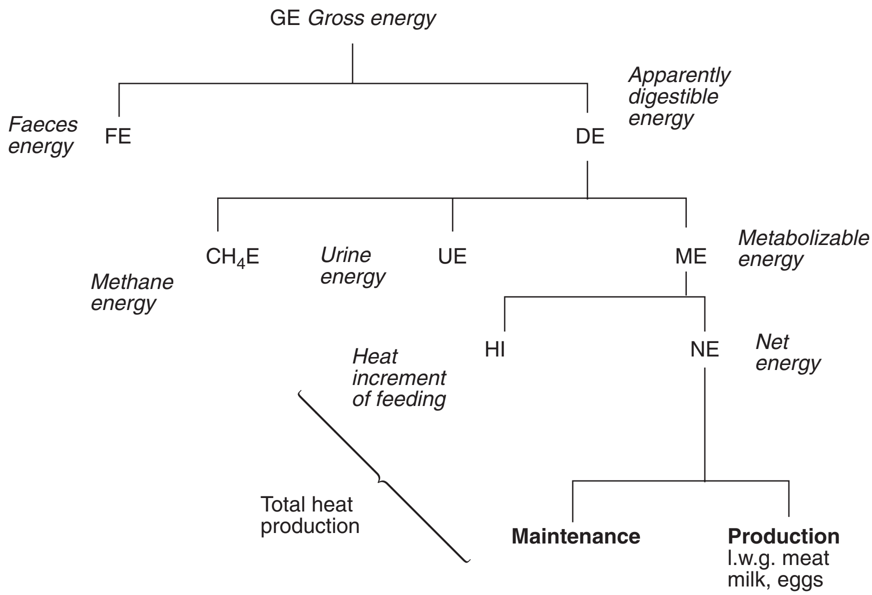

Fig. 1. Partitioning of food energy in animals.

The apparently digestible energy (DE) is obtained from the difference between feed energy input and faecal energy output. Metabolizable energy (ME) may be estimated from DE using assumed or measured values for energy lost as urine (UE) or methane (CH_4 E) in ruminants. ME is the energy absorbed by the animal and available for metabolism (anabolism and catabolism). Some of the ME is lost as heat in the form of the heat increment of feeding (HI) and the remaining fraction is described as net energy (NE). Part of the net energy is used in *maintenance*, which merely serves to keep the animal alive with no change in body mass, while the remainder of the net energy is used in *production*.

By using indigestible markers it is possible to evaluate feeds *in vivo* without total faecal collection. For this, the feed includes a known concentration of an inert marker substance such as chromium trioxide (Cr_2O_3). The concentration of the marker in 'grab' samples of faeces is determined by chemical analysis and the dry matter digestibility (DMD) can be determined from:

$$\text{DMD \%} = 100 - \left(\frac{100 \times \text{concentration of marker in feed DM}}{\text{concentration of marker in faeces DM}} \right)$$

Similar marker methods have been devised using endogenous substances naturally present in forage feeds, such as acid-insoluble ash, or cuticle wax *n*-alkanes (Mayes *et al.*, 1986). This method uses the ratio of naturally occurring odd chain-length *n*-alkanes to dosed synthetic even chain *n*-alkanes to estimate herbage intake.

So-called *in vitro* methods for the evaluation of feeds attempt to mimic digestion in the animal. These methods were devised mainly for forage evaluation for ruminants using the two-stage rumen-pepsin digestion devised by Tilley and Terry (1963) and subsequent modifications including replacement of rumen fluid by cellulase from *Trichoderma viride* (Jones and Hayward, 1975), or liquor from homogenized sheep faeces.

A more recent development of the *in vitro* rumen technique involves the gasometric technique (Menke *et al.*, 1979) in which a feed sample is digested in buffered rumen fluid in a 100 ml gas syringe. The rate of gas production vs. time gives a curve which can be interpreted to give the kinetics of degradation in a similar but more accessible way to the *in sacco* technique. The ***in sacco***, or nylon bag technique, isolates a small aliquot of feed in a porous nylon bag which can be suspended in the rumen of an animal and removed at intervals to monitor the rate of digestion. Alternatively nylon bags may be allowed to pass through the whole digestive tract to be recovered from excreta. The gasometric and nylon bag techniques permit study of the kinetics of degradation of cell wall material or protein by fitting equations to the observed degradation curve (Ørskov and McDonald, 1979). Both the rate and extent of digestion have a bearing on the nutritional value of feedstuffs, especially in ruminants. The degradation curve for a food (Fig. 2) shows that the soluble material is immediately lost from the nylon bag. This component is represented by **a**. Initially the most readily degraded fraction is hydrolysed rapidly with rate decreasing with time until a plateau in the degradation curve is reached where the curve becomes asymtotic, reaching the maximum extent of degradation represented by **a+b**. As the degradation progresses the slope of the curve **c** decreases. Such curves can be described by an equation of the form:

$$p = a + b(1 - e^{-ct})$$

where p is the per cent degradation at time t, and a, b and c are constants.

Laboratory methods of feed evaluation based on chemical analysis attempt to measure nutritional attributes and predict animal performance (*see* **Chemical composition**). Prediction equations which use laboratory chemical measurements as explanatory variables to predict animal performance have been devised for forages and compounded feeds. With the advent of computer-assisted near infrared (NIR) reflectance spectroscopy (Norris *et al.*, 1976), the prediction of chemical composition and animal performance can be done rapidly using NIR. (IM)

References

Mayes, R.W., Lamb, C.S. and Colgrove, P.M. (1986) The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. *Journal of Agricultural Science, Cambridge* 107, 161–170.

Tilley, J.M.A. and Terry, R.A. (1963) A two-stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society* 18, 104–111.

Jones, D.I.H. and Hayward, M.V. (1975) The effect of pepsin pre-treatment of herbage on the prediction of dry matter digestibility from solubility in fungal cellulase solutions. *Journal of the Science of Food and Agriculture* 26, 711–718.

Menke, K.H., Raab, L., Salenski, A., Steingass, H., Fritz, D. and Schneider, W. (1979) The estimation of the digestibility and metabolizable energy

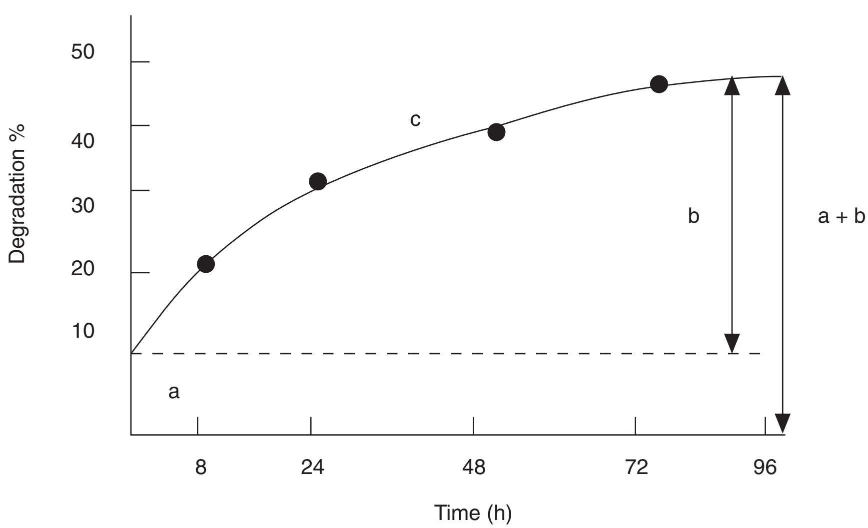

Fig. 2. Degradation of fibrous feeds derived from intra-ruminal incubations.

content of ruminant feedingstuffs from the gas production when they are incubated with rumen liquor *in vitro*. *Journal of Agricultural Science, Cambridge* 93, 217–222.

Ørskov, E.R. and McDonald, I. (1979) The estimation of protein degradability in the rumen from incubation measurements weighted according to rate of passage. *Journal of Agricultural Science, Cambridge* 92, 499–503.

Norris, K.H., Barnes, R.F., Moore, J.E. and Shenk, J.S. (1976) Predicting forage quality by near infrared reflectance spectroscopy. *Journal of Animal Science* 43, 889–897.

Feed formulation Traditionally, compound feeds were manufactured using standard formulae that were tried, tested and seldom varied. These feeds provided an excellent ration for livestock, although the balance of nutrients supplied fluctuated with natural variations in the quality of ingredients. These formulae could not be easily changed to take account of changes in the market prices of raw materials or to make best economic use of the resources available. In recent decades, the number of available raw materials has increased greatly. Given such a range of raw materials there can potentially be thousands of combinations that will satisfy the nutrient requirements defined in a feed specification. One of those combinations of raw materials will be the cheapest. The development of computing and particularly the introduction of linear programming allowed such least-cost solutions to diet formulation to be calculated. The first electromechanical machines, introduced in the 1950s, took up to an hour to calculate a single diet but today microcomputers can do the calculations in fractions of a second. Software can now provide least-cost solutions for raw material use and allocation not just for a single feed product but also across multiple products, manufacturing sites and periods of time.

To formulate an individual feed product the input data required are the price and nutrient values of each available ingredient, a product specification that defines the minimum and maximum concentrations of each nutrient and the minimum and maximum permitted inclusion of each available ingredient. The least-cost solution generated for a single feed product is dependent on the relative price and nutrient content of each available ingredient. It takes no account of the amounts of ingredients required to manufacture other feed products. However, it is not always possible to purchase enough of an ingredient to satisfy the demand created by a number of feed products that have been formulated independently of each other. Equally, an excess stock of an ingredient may have been purchased which it is necessary to use up. In these situations, linear programming can optimize multiple specifications and allocate ingredients most economically. The additional data required to build this economic model are maximum levels of scarce ingredients, minimum levels of surplus ingredients and the amount of each product, which is to be manufactured. In a similar way, linear programming can also be used to optimize the distribution of ingredients across multiple manufacturing sites and periods of time. Decisions can then be taken on when and where to buy, sell or use ingredients.

Linear programming is based on providing exact values for the input data. In practice, the nutrient contents of the feed ingredient are not known with certainty but are laboratory analytical mean values with standard deviations. Such values are stochastic rather than discrete. As a result the calculated nutrients in a formula are not known with certainty. Using average values, linear solutions will only meet nutrient requirements 50% of the time. When formulae need to be produced with a high probability of meeting nutrient levels, calculations must take into account the uncertainty in the nutrient content of each ingredient. For this purpose, stochastic formulation systems, using non-linear programming techniques, can be used.

(AM)

Feed:gain ratio A measure of the efficiency of converting feed inputs into productive output. It is also called feed conversion ratio. In growing animals it is the feed consumed per unit of body weight gain. It may also be used in other situations; for example, with laying hens, as feed consumed per unit of egg mass output; or in milk production, as feed consumed per litre (or gallon) of milk produced. (SPR)

See also: Efficiency of feed conversion (FCE); Feed conversion ratio (FCR)

Feed grains The cereal grains used for feeding livestock. They include wheat, maize, barley, oats, rye and triticale.

(ED)

Feed intake In broad terms, feed consumption is the amount of food required to provide the nutrients to allow the animal to fulfil its genetic programme. When food availability is unlimited (i.e. more food is provided than is required), the amount of food eaten is referred to as **voluntary food intake**. When food availability is limited, as during routine quantitative food restriction, feed intake is usually equal to the ration provided, because animals are chronically hungry and eat it all.

In general terms, food is consumed voluntarily in that amount which most closely meets the animal's needs, i.e. supplies the nutrients that allow it to fulfil its genetic programme. There are several reasons why animals might eat more or less than would be predicted from a knowledge of their 'requirements':

1. The 'requirements' specified by a particular feeding system might not be the same as the animal's needs. For example, a lactating cow's requirements for nutrients are conventionally calculated from the needs for maintenance and those for milk production; in fact the cow may be programmed to regain body reserves and/or to produce more milk than it is currently producing. In this case it will be driven to eat more than predicted from a 'knowledge of its requirements'.
2. There might be a physical restriction on intake, such as slow rate of eating or limited capacity for fibre in the stomach. For example, intakes of forages are likely to provide less nutrients than 'required' by either the feeding system in use or the animal's programme.
3. There might be metabolic imbalance. For example, if a food provides a lower ratio of protein to energy than required, the animal might increase its daily intake of that food in order to obtain sufficient protein. This would increase energy intake which, through various mechanisms, counteracts the drive to eat more food. Depending on the exact situation, nutrient imbalance can result in a higher (but usually lower) intake than predicted from nutrient requirements.
4. The animal might be suffering from an infectious or metabolic illness. This might change its 'requirement' for nutrients. For example, parasitic infection might increase protein requirements, which would stimulate intake, but in practice food intake might be reduced due to abdominal discomfort. Fever usually reduces food intake, while lameness can restrict the extent to which the animal is prepared to walk when grazing. A good stockperson is very aware of a reduction in voluntary food intake as an early sign of disease.

In practice, voluntary food intake is best predicted from observations of food intake in similar situations to those of current interest. Typical intakes of the major types of farm animal are outlined in the following paragraphs.

Growing broiler chickens

Intake increases steadily from hatching, to reach a plateau of around 160 g dry matter (DM) per day at about 6 weeks, under thermoneutral conditions. A major limitation to intake is high environmental temperature, especially at high stocking densities with heavy birds.

Laying hens

Food intake varies according to energy density of the diet, environmental temperature, rate of egg laying and body weight, and is around 120 g DM day^{-1} under many commercial conditions. Changes in the metabolizable energy content of the food cause compensatory changes in voluntary intake, but such compensation is not complete, resulting in higher weight gain and, sometimes, higher egg production, in hens given more energy-dense foods.

Growing pigs

Before weaning, piglets are often given access to 'creep' feed. Their intake of this is not usually more than a few grams per day. After weaning it can be expected that voluntary intake will be such as to meet the animal's energy requirements and therefore to be proportional to body weight and weight gain, and to be affected by the digestible energy concentration of the food. Under UK conditions the relationship between digestible energy intake (DEI, kJ day^{-1}) and body weight (LW) of growing pigs between 30 and 100 kg was found to be: DEI = 4000 LW$^{0.5}$. Thus, a pig of 50 kg is predicted to eat 29.4 MJ day^{-1} or, for a typical diet containing 13 MJ DE kg^{-1} DM, 2.26 kg DM day^{-1}. However, this is a simplification, as intake is influenced by potential to grow and fatten, amongst many other factors. In particular, during the first few days after weaning, intakes of both food and water increase slowly and weight gain does not normally resume until up to a week after weaning.

Pigs, pregnant and lactating

Pregnant sows will voluntarily eat about 6 kg day^{-1} of a concentrate feed, which results in extreme fatness. This is normally prevented by feeding about 2.5 kg day^{-1}. During lactation, intake increases up to about day 17 but then declines. A typical intake at the peak is 7.5 kg day^{-1} but this is influenced by environmental temperature, litter size and diet quality.

Growing cattle

The voluntary food intake of ruminants fed indoors varies over a wide range according to the quality of forage on offer (particularly its particle size, rate of digestion and crude protein content), the level (if any) of concentrate supplementation, and the genetic potential for growth and/or milk production. Under grazing conditions it is even more difficult to predict, complicated by effects of sward conditions, weather and social factors. Most of the equations for predicting the voluntary intake of food by ruminants are complex and outside the scope of this entry. A simple equation is: DMI (kg day^{-1}) = $0.172 \times$ LW$^{0.61}$.

Lactating cows

The following simple equation has been widely used in the UK:

$$\text{DMI} = 0.025\ \text{LW} + 0.1\ \text{MY}$$

where LW is body weight (kg) and MY is milk yield (kg day^{-1}); for a cow weighing 650 kg and producing 30 kg milk day^{-1}, a total intake of 19.3 kg DM day^{-1} is predicted. However, forage intake is depressed by concentrate supplements and there is typically a reduction of 0.4 kg forage DM intake kg^{-1} concentrate DM allowance. In addition, intake usually increases more slowly than milk yield after calving, leading to loss of body weight. This is replaced later in lactation, when intake remains high as yield falls.

Sheep

Intake of growing lambs depends to a great extent on the quality of the food available, as well as on their potential to grow and fatten. As with other classes of ruminants, prediction of intake is difficult and equations can only be used in situations close to those in which the data were collected from which the equation was derived. A lamb of a fast-growing breed at the point of inflexion of its growth curve would be likely to eat 2 kg DM day^{-1} of a pelleted food made from concentrates and dried grass.

During pregnancy, there is sometimes a slight increase in intake but often a marked decline in late pregnancy, especially in the last few days. A ewe of a hill breed weighing 50 kg might eat 1.5 kg forage DM day^{-1}, declining to 1.2 kg week^{-1} before lambing and to almost zero on the day of parturition. Intake increases in early lactation, reaching about 2.5 kg day^{-1} in the small hill ewe; suckling of twin lambs tends to increase the ewe's intake but also results in loss of more body reserves than in a similar ewe rearing a single lamb.

(JMF)

Feed mixing Feed is mixed primarily in order to provide a homogeneous composition to ensure that animals receive the intended quantity of each constituent ingredient. Failure to mix ingredients accurately can have a number of detrimental effects. Firstly, palatability may be adversely affected if one or more ingredients has a strong taint that would be masked if it was correctly mixed. This would almost definitely lead to large quantities of feed being rejected, which is not only wasteful but will also affect the animal's performance. Secondly, if the animal's intake of micro-minerals, vitamins and medication is variable due to inconsistent mixing, deficiency or toxicity symptoms may arise. Lastly, feed that is to undergo pellet pressing will have variable physical quality characteristics unless the raw materials are equally dispersed. Raw materials that have little or no starch and are not very pliable (e.g. mineral supplements) are difficult to press into a pellet capable of withstanding further handling and storage. A well-compounded mixed meal will bind these materials, forming a hard pellet, as opposed to a poorly mixed meal in which some material will not bind, resulting in a high and unacceptable proportion of dust.

Mixing is generally achieved with a mechanical mixer. Mixers fall into a number of different types, either horizontal or vertical, and mix a constant mass of material for a specific period of time. Vertical mixers have a central, vertical auger inside a cylinder. Material is taken from the bottom of the cylinder, transported up the centre of the drum inside the screw conveyor and dropped on the top. Horizontal mixers either rely on a spinning drum with internal bars to retain material, similar to a domestic washing machine, or use a rotating ribbon inside a fixed hopper. The ribbon is usually in the form of a double helix. Mixing times depend on the material being mixed and the equipment used but are generally between 30 and 300 s. A third mixer design is based on a chain and flight conveyor mounted at an angle of approximately 45°. Material is continuously fed into the bottom of a hopper and carried very slowly to the top, where it is then dropped back down to the bottom, mixed material being taken away from the top. (MG)

See also: Compound feed; Pelleted feed; Quality control in feed mills

Feed preferences: *see* Choice feeding

Feed roots: *see* Carrot; Cassava; Fodder beet; Jerusalem artichoke; Potato; Sugarbeet; Swede; Sweet potato; Turnip; Yam

Feed selection There are many situations in which animals show a preference for certain feeds, or feed constituents. Grazing animals may select particular pasture species and reject others; they may also avoid forage that is contaminated. Browsing animals may select leafy material. Stall-fed animals may reject hard stemmy material in hay and most animals reject mouldy feed. Poultry given mixed rations may select certain parts over others. Animals given a free choice between alternative feeds may select a mixture that reflects their nutritional needs. (MFF)

See also: Choice feeding

Feed supplements: *see* Supplement

Feed trough A trough, by definition, is a narrow, open container in which food or water for animals may be placed. With cattle and sheep a feed trough can be a large wooden or metal construction, usually of U- or V-shaped profile, on legs, which is kept permanently outside and is filled manually. In the case of pigs the trough is usually sited at a low level along one wall of the housing. As it needs to be very robust, it is often built in and lined with half-round glazed pipe. It can be filled manually, or mechanically by an auger or automated liquid feeding system. A variety of designs has been developed, such as single-space hoppers, wet-and-dry feeders (in which a nipple drinker is incorporated) or multi-space feeders where several animals can feed simultaneously. The most sophisticated systems are those used for cattle or pigs in which each animal carries an electronic tag that opens a gate to permit only one animal access to the trough. Trough feeding is less common today with poultry farmers than in the past due to the need for greater automation and to avoid feed wastage. However, it is still used with adult birds such as breeding stock, or with extensively housed laying hens. Older mechanical systems used a chain to drag the feed from a large hopper at one end of the house along a continuous trough that ran all through the house. This was adequate for birds fed *ad libitum*, but not for restricted-feeding systems for breeders. This problem has been overcome by the use of an auger in the bottom of the trough to give high-speed feed distribution. (KF)

Feedback inhibition The inhibition of the activity of an enzyme early in a metabolic pathway by the end-product of the pathway. This is in contrast to product inhibition in which the accumulation of a product inhibits its own production. (NJB)

Feeding behaviour Most animals are not born with an innate ability to recognize food (apart from a young mammal's innate knowledge of where to seek milk) but have to learn this through experience. Parents, usually mothers, guide the food choice of their offspring and young animals stay close to their mothers for the first days and weeks of life. In the absence of a mentor, the young have to learn from post-ingestional consequences which items that are swallowed provide positive feedback and which ones do not. For example, in the absence of their mothers, it took 3–4 days for chicks to learn to distinguish mash food from sand. In commercial conditions, the positioning of food, drinkers, lighting and heating in the first 2–3 days after hatching or weaning is intended to stimulate eating. Even so, observed variation in growth rate between individual animals in the first days and weeks of life may well reflect variation in development of feeding behaviour.

Feeding behaviour can be monitored by eye but it is very time-consuming to collect comprehensive data. Time-lapse video recording is useful but still requires time to analyse the recordings. Automation of meal monitoring is possible by fitting a transponder to each animal's collar or ear tag, to be detected when the animal puts its head into the feeder. If the weight of the feed container is also monitored by the computer connected to the identity system, comprehensive data on meal timing and weight can be collected.

It must be emphasized that food-directed activity (e.g. duration of feeding) and weight of food consumed at a meal are not always closely correlated, i.e. food intake cannot be predicted directly from time spent eating. This is because feeding efficiency (g food eaten min^{-1} feeding) varies greatly, not only with different food particle sizes but also between individuals, genetic lines, times of day, environments and even within meals. For example, animals in individual pens spend much more time eating than those in groups, because individuals spend more time playing with food without eating it, whereas those in groups have more distractions; both may eat the same amount of food per day. A possible explanation is that eating per se may be separately reinforcing from food ingestion and that, depending on environmental constraints, feeding is sometimes expressed in apparently inappropriate ways in response to a specific deficit in reinforcement. Another environmental influence on feeding is social facilitation (mutual stimulation of behaviour in groups of animals), which has been shown to act more on food-directed activity than food consumption.

Information about processes underlying short- and longer-term control of feeding can be obtained by studying ways in which feeding activity and/or food intake vary from minute to minute, hour to hour and day to day.

Minute-to-minute variation (meal eating)

Animals with free access to food generally concentrate their feeding in discrete meals, which can be defined by identifying a criterion for distinguishing interruptions within meals from inter-meal intervals. Frequencies of different-length gaps in feeding are usually distributed in a bimodal way, with many short pauses within meals and many long gaps between meals, with relatively few inter-meal intervals of intermediate length; the inter-meal interval at the nadir of this frequency distribution is used to define the critical inter-meal interval. By calculating correlation coefficients between the size of meals and either succeeding (postprandial) or preceding (preprandial) adjacent intervals, clues can be obtained about degrees of control that hunger and satiety mechanisms have over initiation and termination of meals. Both types of correlation are weak in farm animals, consistent with the randomness in spontaneous meal occurrence.

However, when meal sizes are manipulated artificially there can be close relationships, verifying the existence of short-term hunger and satiety mechanisms. Because such mechanisms appear to have only loose control over meal eating, it seems appropriate to think in terms of degrees of hunger and satiety, rather than 'set points', determining probabilities of feeding starting and stopping.

Although meal and interval lengths are usually distributed exponentially within animals, mean meal-eating variables tend to be distributed normally between animals. Thus, in any population, some habitually eat many small meals while others consume the same amount per day in fewer larger ones. Furthermore, short- and longer-term regulation of food intake can be considered in terms of adjustments in mean meal size, meal frequency, or both.

Hour-to-hour variation (diurnal rhythms)

There is usually a diurnal rhythm of feeding. Most domesticated species of mammal take more frequent and larger meals during the day than at night. In both birds and mammals there is more intensive feeding after dawn, as a result of hunger due to lower intake at night, and before dusk, in anticipation of a period of low intake. While chickens do not normally eat in the absence of light they will do so if the dark period is very long. In continuous light, domestic animals show periodicity in food intake if there are regular phase-setting stimuli for them to cue into, or if they have been kept previously on a cycle of light and dark. There is evidence that regulation of feeding behaviour from hour to hour depends more on changes in meal frequency than in mean meal size.

Longer-term variation

Generally, longer-term adjustments in feeding behaviour and food intake, over days or weeks, depend more on changes in mean meal size than in meal frequency. Such adjustments may be in response to changes in diet or physiological requirement. Changes in mean meal size are usually gradual, and may be associated with gradual changes in capacity of the part(s) of the alimentary tract where meal eating is controlled (*see* **Voluntary food intake**).

There is surprisingly large variation in the weight of food eaten on consecutive days by individual animals. Over a period of several days the highest intake can be as much as double the lowest intake. As progressively more days are averaged a plateau in variability is reached, at about 3 days in chickens, 4 days in lactating cows, and 6 days in growing cattle. This suggests that the control of intake is on a time scale of several days rather than meal-by-meal, or even day-by-day.

(JMF, JSav)

Feeding standards Recommendations, published mostly by expert committees, that describe acceptable nutrient contents of diets to be fed to different types and species of animals. The recommendations are guidelines for good practice and do not necessarily describe the most economically or biologically efficient nutrient composition of a diet for a particular animal or population of animals.

(SPR)

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Feedlot An enclosed area on a farm or ranch, most commonly in North America, where livestock, especially beef cattle, are fed prior to slaughter for meat. In hot climates the areas may be partially roofed to provide shade. Systems of mechanical feeding, frequently of maize, are generally employed.

(AJFR)

Fermentation The decomposition of organic substances by microorganisms, including the conversion of carbohydrates to alcohol by yeasts and to organic acids by (mainly) bacteria. Anaerobic fermentation occurs in the digestive tract of animals and in the preservation of crops by ensilage. Essentially, dietary carbohydrates, proteins and some fats are reduced to short-chain fatty acids with the production of carbon dioxide, methane and ATP. The short-chain fatty acids produced in the digestive tract are principally acetic, propionic and butyric acids, though occasionally lactic acid is also produced. The main fermentation product in silage is lactic acid.

The most important fermentation in the digestive tract of ruminants occurs in the rumen and reticulum, which account for more than half the total volume of the digestive tract. In other animals, fermentation occurs mainly in the large intestine. This is of significance in all species, but especially in herbivores such as the rabbit and the horse. The ruminant has a considerable advantage over other herbivores because it has effectively two separate digestion processes and two sites of absorption of the end-products of digestion – through the wall of the rumen, and through the wall of the large intestine.

The fermentation of plant cell walls is very important in the nutrition of herbivorous vertebrates, because the animals themselves do not produce enzymes capable of breaking down cellulose and hemicellulose, which are the main components of most plant cell walls. The end-products of fermentation in the rumen account for about 75% of the energy supply to the ruminant animal.

The most important bacteria involved in these fermentations are the cell-wall digesting or cellulolytic microorganisms. The concentration of bacteria in the parts of the digestive tract where fermentations occur is usually very high. For example, rumen fluid has about 10^{10} to 10^{11} bacteria ml^{-1}, most of which are attached to particles of food. The predominant species of bacteria varies with the type of fermentation, which depends on the principal substrates in the diet. Thus the major species of bacteria in the rumen of animals given a diet of grass are those that digest cellulose and hemicellulose, such as *Ruminococcus albus*, *R. flavefasciens* and *Bacteriodes succinogenes*. Other species, such as *Streptococcus bovis*, ferment starch to acetic acid and ethanol. This species, along with other *Streptococcus* spp., can produce lactic acid and is more tolerant of acid conditions than other species of rumen bacteria. Acidosis can occur if the diet of the animal is changed abruptly from cellulose to starch or sucrose. The population of bacteria in the rumen changes from cellulolytic to amylolytic as the pH falls. Lactic acid accumulates and accelerates the fall in pH. Even a small fall in the pH of the rumen from pH 7 to pH 6 is reflected in a reduction in cellulose digestion and a change in the population of the bacteria towards the more acid-tolerant species.

Proteins are degraded to a varying extent during the fermentation to their constituent amino acids. Some amino acids are used directly by bacteria and protozoa, but most are used as a source of energy and are broken down further to ammonia and volatile fatty acids. Ammonia is used as a substrate for the production of microbial protein, with the excess being absorbed into the animal's portal blood and converted to urea in the liver. The extent to which proteins are degraded during the fermentation in the rumen depends on their solubility, which is generally relatively high except in feeds that have been subjected to heat treatment during processing. Thus the degradation of protein in fish meal is only about 0.4, compared with 0.9 for fresh herbage. Protein degradation also depends on the time the material spends in the rumen, and is lower for diets that pass rapidly through the rumen (concentrates and feeds of small particle size) than for long forages, which are digested slowly.

Protozoa and fungi are also involved in fermentations in the digestive tract of animals. These organisms can digest cellulose, starch, sugars and fats to produce acetic acid, butyric acid, lactic acid, hydrogen and carbon dioxide.

The predominance of the weak acids (acetic, propionic and butyric) in the end-products of fermentation in the digestive tract highlights the importance of buffering agents to maintain the pH of the environment close to neutrality. Saliva, containing sodium and potassium bicarbonate and urea, is the most important buffering agent in the rumen, and the amount of saliva produced during eating and rumination is therefore crucial to the neutralization of the fermentation acids in the rumen. Long fibre is often included as a supplement to diets high in concentrates to stimulate chewing and rumination. The constant flow of saliva into and the outflow of digesta from the rumen, as well as the absorption of digested nutrients into the portal blood, ensure that in most nutritional circumstances the environment for fermentation remains relatively constant. However, digestive disorders can arise to disrupt the equilibrium. Toxins, produced by undesirable bacteria and from moulds present in foods, can damage the sensitive lining of the wall of the rumen and intestines and reduce the absorption of nutrients. Parasitic infections can also interfere with both fermentation and the absorption of nutrients. Sudden changes in diet can change the microbial population and result in the production of lactic acid in the rumen, with a consequent reduction in rumen pH. If the pH of the rumen falls below pH 5 and remains low, there is a risk of rumen stasis that can result in bloat because the animal can no longer eructate the gases produced by the fermentation.

Methane loss from the rumen is estimated to account for about 8% of the total gross energy eaten. Methane is also produced by fermentation in the large intestine, as well as some hydrogen. Methanogenesis can be reduced by ionophores and by changing the pattern of fermentation to increase the proportion of propionate and reduce the proportion of acetate. Reduced total gas production is desirable in hind-gut fermenting animals, such as the horse, because excessive gas production is associated with digestive disorders, including colic. Fermentation rate can be reduced by including in the diet a source of slowly digested or indigestible fibre, such as hay or straw. (JMW)

See also: Fermentation products; Rumen digestion

Fermentation products The end-products of fermentation by bacteria, protozoa and yeasts. Fermentations occur in the production of alcohol, in making silage, in the rumen of ruminant livestock, and in the large intestine of most animals. The major fermentation product in silage is lactic acid, which is produced from the fermentation of fructans and glucose by lactic acid bacteria that are either present in the crop at harvest or are added in an inoculant additive (*see* **Preservative**). Other fermentation products in silage include acetic acid, propionic acid, butyric acid, ammonia and amines. The concentration of individual fermentation products in silage reflects both the extent and the pattern of fermentation in the silo. The extent of fermentation is determined mainly by the concentration of moisture in the crop at the time of ensiling. The wetter the crop, the greater is the amount of fermentation. The pattern of fermentation is determined by the concentration of fermentable carbohydrate in the crop and the buffering capacity of the crop. The lower the amount of fermentable carbohydrate and the higher the buffering capacity, the greater is the likelihood of an unstable fermentation, with the production of mixed fermentation acids and degradation of amino acids to amines and ammonia. The extent of fermentation can be reduced by wilting to remove water before the crop is harvested. The pattern of fermentation can be controlled by the use of preservatives, such as formic acid, and inoculants designed to accelerate the production of lactic acid in the early stages of the fermentation in the silo.

The major products of fermentation in the rumen and large intestine are acetic acid, propionic acid, butyric acid and ammonia.

(JMW)

See also: Acetate; Amine; Ammonia; Butyrate; Fermentation; Lactic acid; Propionic acid; Rumen digestion

Ferredoxin A family of low-molecular-weight soluble proteins involved in electron transfer (oxidation/reduction) reactions. These highly evolutionarily conserved proteins are found in bacterial, plant and animal cells. Ferredoxins are iron–sulphur (Fe–S) proteins that function in photosynthesis and other reactions in bacteria, plants and animals. Fe–S proteins contain iron and acid labile (released) sulphide which together act as the co-factor for the protein. Ferredoxins are involved in the formation of Fe–S proteins in mitochondria where they donate electrons involved in formation of Fe–S clusters. (RSE)

Ferritin Iron storage protein of animals and plants. Ferritin-like proteins are also found in bacteria. In animals it has been found in all tissues examined. Ferritin stores iron in

a relatively safe and metabolically available form and also serves to sequester iron, reducing its toxic effects. Ferritin has 24 protein subunits of two types, H (heavy) and L (light), that form a hollow sphere with channels in its wall. The ferritin macromolecule can store up to 4500 iron atoms but is usually found with 2000–2500 iron atoms *in vivo*. Liver and spleen contain the highest amounts of ferritin and serve as an important reserve of iron for red cell formation when dietary intake is insufficient. An iron-poor serum form of ferritin can be a useful indicator of body iron stores and its abundance is directly related to body iron stores in many situations in humans. Serum ferritin is artificially elevated in inflammatory situations and is not a good indicator of iron stores in this case. (RSE)
See also: Haemosiderin

Fertility The ability to produce offspring. In the male, this signifies the ability to produce a sufficient quantity of normal, fertile semen, to be physically capable of depositing it in a natural or artificial vagina and to possess sufficient libido to be willing and able to do so. In the female, fertility depends on the efficient functioning of a series of processes: (i) the ovulation of viable ova; (ii) the efficient transport of the ova to the site of fertilization in the oviduct; (iii) the display of oestrous behaviour at the appropriate time; (iv) efficient sperm transport and fertilization of the ova; (v) timely transport of the fertilized ova to the uterus; (vi) implantation; and (vii) carrying the products of conception to the point of birth of one or more live young. All of these processes can be affected by extremes or imbalances of nutrition.

In males and females, the reproductive processes are controlled by the secretion of gonadotrophin-releasing hormone from the hypothalamus, which in turn controls the release of luteinizing hormone and follicle-stimulating hormone from the anterior pituitary. Severe underfeeding interferes with this control mechanism. In males, prolonged underfeeding with a sub-maintenance ration will eventually give rise to some reduction in fertility as a result of decreased output of spermatozoa or accessory secretions. Libido is also likely to be adversely affected by chronic starvation. In females, continued underfeeding suppresses ovarian function. This is a particular problem in high-yielding post-partum dairy cows. Negative energy balance leading to loss of condition can cause a considerable delay to the resumption of ovarian cycles or, less commonly, a cessation of cycles. Underfed females are less likely to display oestrus, even if they are cycling regularly. Acute energy deficiency has been shown to cause embryo mortality in farm animals. Underfeeding of young males and females can delay the onset of **puberty**.

Overfeeding can also cause reproductive problems. Obese males are less inclined to mount oestrous females and are more likely to cause injury to them if they do. Overweight females are likely to have difficulty in giving birth. This can lead to damage to the reproductive tract and subsequent infection and infertility. In ruminant animals, obesity can restrict the intake of feed when energy demands are at their highest. This can lead to rapid mobilization of body reserves with consequent metabolic disfunctions such as pregnancy toxaemia in sheep or ketosis in high-yielding dairy cows.

Nutritional imbalances can also cause infertility. Specific deficiencies of vitamins and minerals have frequently been blamed for fertility problems, although in many experiments their effects have been confounded with those of inadequate energy intake. Protein insufficiency can cause infertility but, in cows at least, there is also evidence that high concentrations of crude protein can cause infertility. A variety of factors, including nitrate or ammonia toxicity in the reproductive tract, a depression of carbohydrate content of the grass and nitrate effects on rumen microflora, has been blamed for poor fertility when cows are turned out to spring grass heavily fertilized with nitrogen. (PJHB)

Fetal growth The growth of the conceptus in the uterus from the end of differentiation until the time of birth. Each cell of the early embryo, formed by mitotic division after fertilization, is capable of forming any of the body tissues. Over the next few days or weeks, the cells differentiate, becoming specialized so that in future development they can only form specific tissues and organs.

Once this process is complete and the rudimentary organs are formed, the embryonic phase gives way to the fetal phase. Thereafter, fetal growth in all viviparous animals is exponential, the rate increasing as pregnancy progresses. The size and weight of the fetus, and thus its requirements for energy, protein and minerals, increase rapidly, especially during the last third of gestation. As the fetus grows, its associated placenta increases greatly in size and the uterus also enlarges to many times its non-gravid weight and size in order to accommodate the physical bulk of the fetus and placenta and to provide the large surface area necessary for nutrient and waste exchange between the fetal and maternal circulatory systems.

The mother's own maintenance requirements also increase during pregnancy, so that her overall requirements increase by more than simply the nutrients required for deposition in the uterus. Furthermore, the uptake of nutrients by the fetus and placenta is less efficient than that of the mother's body, further increasing requirements. The fetus takes precedence over its mother for most nutrients and, once the pregnancy is firmly established (at about 60 days in cows and 40 days in sheep), it is able to maintain higher sugar levels than in the maternal bloodstream and generally does not suffer from underfeeding of the mother unless this is chronic or severe. On the other hand, feeding the mother at levels above maintenance requirements, especially in late lactation, can increase the birth weight of the young.

Severe long-term underfeeding of the mother in earlier pregnancy may result in the death of one or more fetuses. In later pregnancy, severe malnutrition may result in the death of the young *in utero* or to reduced birth weights and reduced viability. There may also be congenital abnormalities, particularly as a result of specific nutritional deficiencies. Non-ruminants, such as pigs, have specific amino acid requirements for the development of the fetus. (PJHB)

Fibre: *see* Dietary fibre

Fibrin The single protein monomer resulting from the blood clotting process whereby the soluble plasma protein fibrinogen is converted into fibrin by the action of the plasma protease thrombin. The released fibrin monomers polymerize, cross-link and form an insoluble clot. (NJB)

Fibrinogen A soluble plasma protein that is cleaved by the protease thrombin to produce a single molecule of fibrin which polymerizes with other fibrin molecules to become a clot. (NJB)

Fig A member of the genus *Ficus* of the *Moraceae* (mulberry family). The common fig (*Ficus carica*) is grown for its valuable fruit. The seeds have laxative properties that limit the inclusion of fig seeds in animal diets. The leaves of the fig can be fed to cattle when harvested directly following fruiting and before the onset of senescence (see table). (JKM)

Finishing The process of bringing meat animals to a desired state of body condition prior to slaughter. For cattle this may be a period of some months. Non-ruminants are usually given a diet of lower protein content than that required for the earlier grower period. Normally for broilers, finishing represents the last one-third of life and is the time when the vast majority of the feed (often known as finisher feed) is consumed. For pigs the period from around 40 kg to slaughter is generally known as the finishing period. (KF)
See also: Fattening

Typical composition of figs and fig leaves (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ether extract	Starch and sugar	Ash
Fresh figs	120	13	22	2	6	–
Fresh leaves	340–350	140–145	170–175	55–60	–	160–170

Fish In the general vernacular, a fish can be almost any exclusively aquatic vertebrate or invertebrate (e.g. ‘shellfish’, ‘finfish’ and ‘jellyfish’). Scientifically, the word is restricted to aquatic, cold-blooded, water-breathing, craniate vertebrates and includes three major groups: (i) the Agnatha, primitive jawless fishes (e.g. lampreys and hagfishes); (ii) the Chondrichthiomorphs, jawed fish with cartilaginous skeletons (e.g. sharks, rays, ratfishes); and (iii) the Teleostomi, jawed fish with bony skeletons (e.g. catfish, trout, bass, perch, salmon). This group contains by far the greatest diversity of living fishes.

There are about 28,000 species of living fishes, which accounts for slightly more than half the total number of living vertebrate species. There are 482 fish families with known living species, of which eight families comprise one-third of all species. These are, in descending order: the Cyprinidae (minnows and carps); Gobiidae (gobies); Cichlidae (cichlids, such as tilapia); Characidae (such as the tetras of the aquarium fish trade); Loricariidae (armoured catfishes); Labridae (wrasses, such as the ‘cleaning wrasses’); Balitoridae (river loaches); and Serranidae (sea basses).

At least eight orders of ray-finned fishes contain species that have received some attention for commercial culture as food, and the number is considerably greater if fish cultured for the pet trade are included. These include: Acipenseriformes (sturgeons); Anguilliformes (freshwater eels); Perciformes (perches, sea basses, cichlids, etc); Salmoniformes (salmon, trout, whitefishes); Gadiformes (cods); Pleuronectiformes (flatfishes); Siluriformes (catfishes); and Gonorhynchiformes (milkfishes). (RHP)

Fish culture: *see* Aquaculture

Fish farming: *see* Aquaculture

Fish feeding On the basis of their feeding habits, fish are broadly classified as herbivores, omnivores or carnivores. Feeding habits are also associated with particular body forms and functional morphologies of skull, jaws and alimentary tract. Herbivores do not have teeth but instead possess fine gill rakers that sieve phytoplankton from water. They also lack a true stomach. Carnivores have well-developed teeth and possess stomachs and a shorter intestine. The alimentary system of omnivores is intermediate in form between herbivores and carnivores. Many herbivores lack the ability to ingest and digest materials other than plants and they consume large quantities of food and extract nutrients in their elongated guts (e.g. grass carp). Carnivores have a specialized gut which is related to the size of their prey, being larger in those that consume small aquatic animals.

Feeds and feeding of fish depend upon the type of farming system used: extensive, semi-intensive, or intensive. In the first two systems, fish derive all or a substantial part of their nutrients from natural food organisms in culture ponds. Fish and shrimp maintained in intensive fish culture systems (tanks, raceways and cages) are totally dependent on the provision of nutritionally complete diets produced in either a dry or a semi-moist form. Formulated feeds are produced either by steam or cold pressure pelleting or by an extrusion process in various physical forms and shape and of different buoyancies (floating, slow- or fast-sinking). For example, catfish, salmon and shrimp require floating, slow-sinking and fast-sinking feeds, respectively. Proper feed distribution is necessary to achieve a better feed efficiency.

The body temperature and metabolic rate of cold-blooded fish are commensurate with the water temperature. The amount of feed offered to fish per day has been based on feeding tables developed on the basis of a percentage of body weight and water temperature. Small fish, often called fry or fingerlings, require feed at a greater percentage of their body weight (> 5%) per day than large fish. Demand or *ad libitum* feeding is commonly used in hatcheries where demand feeders dispense small quantities of feed when activated by the fish. Automatic feeders or hand feeding are used to feed fish in tanks or sea cages and their feeding behaviour may be monitored by video cameras. Frequency of feeding is important: larval fish and fry are offered a small amount of feed more than 12 times per day and the frequency is gradually decreased to one to three times per day. More time is required to feed fish at low temperatures.

Since fish live in water, water quality affects their feed consumption, growth, survival and health. Overfeeding results in feed wastage and deterioration in water quality, particularly an increase in suspended particles and lower dissolved oxygen levels, which directly affects respiration. In pond culture, on days with little sunlight when there is no photosynthesis, coupled with an increased water temperature, less feed must be offered, even though fish eat avidly, because in these circumstances excessive feeding would deplete the dissolved oxygen. Generally, undigested protein or carbohydrate increases the suspended solids in the water and increases biological oxygen demand. The principal excretory end-products of protein catabolism, ionized and non-ionized ammonia, are excreted through the gills. The latter product is toxic to fish. Fat not properly retained in the feed may leach out, producing a thin film on the surface of the water and causing respiration problems.

Fish locate food either by their sensory characteristics or by sight, but the taste of the food determines whether it will be swallowed or rejected. Species-specific taste receptors for chemical cues have been identified in several farmed fish species. Feeding stimulants include amino acids, betaine, inosine, dipeptides and organic acids. Generally, carnivores show a positive response to alkaline and neutral substances such as glycine, proline, taurine, valine and betaine, whereas herbivores prefer acidic substances such as aspartic and glutamic acid. Appearance (size, shape and colour) and feel (hard or soft, moist or dry) of the feed also influence the feeding behaviour and food intake.

Feeding of larval fish requires special consideration, because their digestive system is not fully developed after hatching. Currently larviculture depends upon feeding live feed organisms, such as brine shrimp (*Artemia*), rotifers and other planktonic organisms, that have been enriched with specific nutrients (essential fatty acids, vitamins, amino acids etc.) to improve their nutritional value. Larvae are gradually weaned on to highly digestible water-stable micro-diets of appropriate particle size (~ 0.1–0.6 mm), colour and organoleptic properties. (SPL)

See also: Aquaculture; Fish; Fish larvae; Rotifer; Salmon culture; Zooplankton

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Fish larvae The development of most fish species passes through four general stages: egg, larva, juvenile and adult. The larval stage begins at hatch and ends with metamorphosis. Fish larvae are usually transparent, with only scattered pigment cells or patches. The notochord and myotomes are visible, the blood is frequently without haemoglobin, and the full complement of fins is rarely present. The mouth and jaws may or may not have appeared. The larval stage may be subdivided into a period of endogenous yolk utilization (yolk-sac or pre-feeding larva) and a period of exogenous feeding prior to metamorphosis (post-feeding larva). The larval stage is frequently a difficult one for culturists, particularly the transition from yolk utilization to exogenous feeding. Metamorphosis to the juvenile stage is associated with generation of scales and skin pigmentation. The swim bladder and lateral line may develop at this time. The minimum adult fin ray complement has developed. With flatfishes, the optic region of the skull rotates at metamorphosis so that both eyes lie on the same side. Transition from juvenile to adult stage is primarily concerned with development of sexual maturity (gonad maturation and acquisition of sexual characters such as heightened colour). (RHP)

Fish meal: *see* Fish products

Fish oil: *see* Marine oils

Fish pond A natural or artificial body of water used to culture fish. It may be up to 50 ha in expanse and generally at least 1 m in depth and may have a sump for facilitating harvesting and cleaning. A number of fish ponds may be linked in series or in parallel, ideally gravity fed and easily drained. Fish ponds may be earthen, concreted or lined. Earthen fish-pond culture is most commonly found in developing countries, often integrated with agriculture or animal enterprises such as duck and pig farming. (RMG)

Fish products The annual world catch of fish is about 70 million tonnes, of which about one third is not used for direct human consumption and may be considered as raw material for fishery by-products. Fish meal is the predominant product; probably about 95% of all raw material not used for direct human consumption is processed into fish meal, because it is a stable, high-protein concentrate that may be transported around the world without deterioration. Of world fish meal production, about 90% is produced from oily species such as anchovy, capelin and menhaden, and less than 10% from white fish such as cod and haddock. Only about 1% of meal is produced from other sources such as whales and shellfish.

Almost all fish meal is produced by the wet reduction method in which the principal operations are cooking, pressing, separation of the oil and water emulsion with recovery of oil, drying of the residual protein material and grinding. This is accomplished in machinery designed for this purpose. During the pressing operation the aqueous portion (stickwater) and the largest portion of the lipid component are removed from the raw material. The remaining portion is known as the press cake. The oil-and-water emulsion is then separated and the water portion partially condensed. It may or may not be returned to the press cake to make a whole fish meal. The oil is collected and may be further processed into specific products.

Fish meal is usually a brown powder that normally contains a high level of protein and appreciable quantities of fat and minerals. It contains a higher level of lysine and sulphur amino acids than oilseed meals. White fish meal has a lower oil content and slightly higher mineral content than other types.

There are fishery by-products other than fish meal but their commercial production is limited. Crab process residue meal (or crab meal) consists of the undecomposed ground dried waste of crab and contains the shell, viscera and part or all of the flesh. Condensed fish solubles and dehydrated fish solubles are obtained by condensing or dehydrating the stickwater. Condensed fish autolysate (fish silage) is the condensed enzymatic digest of clean undecomposed whole fish or fish cuttings, or both, using an enzymic autolysis process. Shrimp process residue meal (or shrimp meal) consists of the whole undecomposed ground dried waste of shrimp and contains parts of shrimp or whole shrimp. Krill meal consists of the whole undecomposed ground dried parts of krill.

The tables on pp. 221 and 222 give the chemical composition of various fish products. (JSA)

Fistulation Establishment by surgery, under general anaesthesia, of an opening (fistula) into some part of the digestive tract. Fistulae into the lumen of the gut (oesophagus, stomach or intestine) are normally fitted at surgery with a cannula, usually made of plastic, which is closed by a screw cap or plug. Within a few weeks the fistula heals by formation of an epidermis-to-epithelium junction. The procedure allows sampling of gut contents or introduction of materials into the gut in the conscious, normally fed animal. Re-entrant cannulae may be fitted into the intestine to allow sampling and direct measurement of the flow of intestinal content: the intestine is transected, each end is sewn up and cannulas are fitted into each end, passed through the body wall and connected externally so as to re-establish the flow of intestinal content. (RNBK)

Flaking The rolling of grains and seeds using wet heat. The steam process causes gelatinization of grain starch and is carried out either at atmospheric pressure or under pressure (pressure cooking). The cooked grains are then rolled between close-fitting steel cylinders. Flaking increases palatability and digestibility, and modifies starch and protein digestion characteristics. It results in a high proportion of starch being digested in the reticulo-rumen (e.g. 93% in wheat) and also improves microbial protein synthesis through reduced protein solubility in the rumen. The process is commonly applied to cereal grains such as wheat, maize and oats, and to seed

Chemical composition of various fish products.

Ingredient	International feed number	Dry matter %	Crude protein %	Ether extract %	Crude fibre %	Ca %	Total P %	Ash %
Crab meal	5–01–663	95.0	30.0	2.2	10.5	18.0	1.5	31.0
Fish meal, AAFCO	5–01–977	88.4	59.0	5.6	1.0	5.5	3.3	20.2
Fish meal, herring, Atlantic	5–02–000	93.0	72.0	10.0	1.0	2.0	1.0	10.0
Fish meal, menhaden	5–02–009	92.0	62.0	10.0	1.0	5.0	3.0	19.0
Fish meal, anchovy, Peruvian	5–01–985	91.0	65.0	10.0	1.0	4.0	2.9	15.0
Fish meal, sardine	5–02–015	92.0	65.0	6.0	1.0	4.5	2.7	20.0
Fish meal, white	5–02–025	91.0	61.0	5.0	1.0	7.0	3.5	24.0
Fish solubles, condensed	5–01–969	52.0	37.0	4.0	1.0	0.1	0.5	10.0
Fish solubles, dehydrated	5–01–971	93.0	40.0	6.0	5.5	0.4	1.2	12.5
Krill meal	——	91.0	57.0	11.0	8.0	4.0	2.0	15.0
Shrimp meal	5–04–226	88.0	39.9	3.2	12.8	7.9	1.8	27.2
Fish silage	——	29.0	15.5	10.0	1.0	1.0	0.5	2.5

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl %	His %	Val %	Leu %	Arg %	Phy %
Crab meal	5–01–663	0.50	0.20	1.40	0.30	1.20	1.20	0.50	1.50	1.60	1.70	1.20
Fish meal, AAFCO	5–01–977	1.72	0.57	5.17	0.67	2.49	3.64	1.53	3.26	4.69	3.73	2.68
Fish meal, herring, Atlantic	5–02–000	2.20	0.72	5.70	0.80	2.88	3.00	1.91	5.70	5.10	5.64	2.56
Fish meal, menhaden	5–02–009	1.80	0.60	4.70	0.72	2.34	2.83	1.44	3.43	5.00	3.23	0.28
Fish meal, anchovy, Peruvian	5–01–985	1.90	0.60	4.90	0.75	2.70	3.00	1.50	3.40	5.00	3.38	2.39
Fish meal, sardine	5–02–015	2.00	0.80	5.90	0.50	2.60	3.30	1.80	3.40	3.80	2.70	2.00
Fish meal, white	5–02–025	1.65	0.75	4.30	0.70	2.60	3.10	1.93	3.25	4.50	4.20	2.80
Fish solubles, condensed	5–01–969	0.45	0.19	1.46	0.11	0.70	0.70	1.09	1.00	1.60	1.37	0.70
Fish solubles, dehydrated	5–01–971	0.64	0.50	2.60	2.30	1.10	1.20	0.90	1.60	2.60	1.80	1.30
Krill meal	——	1.54	0.68	3.93	0.74	4.10	2.62	1.25	2.68	4.10	3.19	2.39
Shrimp meal	5–04–226	0.82	0.59	2.17	0.42	1.42	1.46	0.90	1.83	2.60	2.35	1.59
Fish silage	——	0.53	0.27	2.74	——	1.55	1.29	0.89	1.61	2.59	1.80	1.54

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Ribo ppm	Panto ppm	Biotin $\mu g\ kg^{-1}$	Folic $\mu g\ kg^{-1}$	Choline ppm	B12 $\mu g\ kg^{-1}$	Niacin ppm
Crab meal	5–01–663	—	—	—	7.5	6.6	—	—	2024	448	44
Fish meal, AAFCO	5–01–977	—	18.5	1.3	6.5	8.7	—	—	3510	250	60.8
Fish meal, herring, Atlantic	5–02–000	—	16.8	0.1	8.7	21.7	200	520	5240	588	141.6
Fish meal, menhaden	5–02–009	—	5.7	0.2	4.8	8.8	150	1000	3080	150	55
Fish meal, anchovy, Peruvian	5–01–985	—	5.6	0.1	7.5	20.3	200	220	5100	600	135
Fish meal, sardine	5–02–015	—	5.6	0.08	4.4	14.3	100		3880	300	100
Fish meal, white	5–02–025	—	5.6	1.51	4.6	4.7	—	—	4050	71	38
Fish solubles, condensed	5–01–969	2.2	—	5.5	14.5	35.4	200		4028	350	169
Fish solubles, dehydrated	5–01–971	—	—	6.8	16.5	48.4	490	726	3960	308	209
Krill meal	—	12	—	3	1	7	100	—	—	100	23
Shrimp meal	5–04–226	—	—	—	—	—	—	—	5500	—	—
Fish silage	—	—	—	—	—	—	—	—	—	—	—

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Crab meal	5–01–663	0.85	0.45	0.88	0.04	133.0	440	32.8	102	3.8
Fish meal, AAFCO	5–01–977	1.07	0.39	0.21	0.24	22.8	360	14.6	100	1.8
Fish meal, herring, Atlantic	5–02–000	0.73	1.50	0.18	0.62	3.8	82	4.5	100	2.0
Fish meal, menhaden	5–02–009	0.34	0.72	0.14	0.45	35.6	438	11.4	151	2.2
Fish meal, anchovy, Peruvian	5–01–985	0.88	0.90	0.27	0.54	9.3	226	9.2	100	2.0
Fish meal, sardine	5–02–015	0.18	0.30	0.10	0.30	24.9	300	20.0	105	1.8
Fish meal, white	5–02–025	0.97	1.10	0.22	—	9.7	80	8.0	80	1.8
Fish solubles, condensed	5–01–969	3.10	1.75	0.02	0.13	11.9	300	48.2	38	2.0
Fish solubles, dehydrated	5–01–971	0.40	2.50	0.27	0.45	10.0	948	20.0	76	2.7
Krill meal	—	1.80	0.40	0.80	—	7.4	280	70.0	74	—
Shrimp meal	5–04–226	1.50	0.80	0.50	—	29.0	102	—	28	—
Fish silage	—	0.15	0.20	0.05	—	—	—	—	—	—

legumes such as peas, beans and lupins. Because of the cost of processing its use is generally confined to feeds for weaners and young growing stock and horses. (ED)

Further reading

Givens, D.I., Clarke, P., Jacklin, D., Moss, A.R. and Savery, C.R. (1993) *Nutritional Aspects of Cereals, Cereal Grain By-Products and Cereal Straws for Ruminants*. HGCA Research Review No. 24. HGCA, London, 180 pp.

Flatfish Farmed flatfish species include Senegal sole (*Solea senegalensis*), turbot (*Scophthalmus maximus*), halibut (*Hippoglossus hippoglossus*) and Japanese halibut (*Paralichthys olivaceus*) while farming of other species is still at the initial stages (lemon sole, *Microstomus kitt*, and plaice, *Pleuronectes platessa*). These species have highly compressed bodies with symmetrical pelvic and pectoral fins, elongated dorsal and anal fins extending to the base of the caudal fin, asymmetrical pigmentation and cranial asymmetry with an ocular side. The flatfishes with sinistral (left) eye migration are the right-eye flounders (Pleuronectidae), including soles, halibut, turbot and plaice; the left-eye flounders (Bothidae) include Japanese halibut. All right-eye flounders and most left-eye flounders are marine species. All have the common feature of hatching as bilaterally symmetric pelagic larvae and undergoing a true metamorphosis before settlement as compressed asymmetric benthic juveniles.

The farmed flatfish spawn or are manually stripped for their pelagic eggs, which hatch to release small pelagic larvae; these live on their yolk reserves until they commence exogenous feeding or ‘first feeding’ on phytoplankton or zooplankton. The small size of the larvae and their relatively primitive development at first feeding initially necessitated commercial use of intensively cultured microalgae, small cultivated rotifers or *Artemia* (intensive culture) or filtered wild zooplankon (extensive culture) rather than inert formulated diets. The ‘green water technique’, using algae as a direct source of nutrition and other zootechnical benefits for rotifers, *Artemia* and fish larvae, has become common.

There is general agreement on the importance of the essential fatty acids eicosapentaenoic acid (20:5 n-3), arachidonoic acid (20:4 n-6) and docosahexaenoic acid (22:6 n-3), the latter having an undisputed importance for correct neural development in larvae. Marine fish larvae generally have a requirement for vitamins C and A, which impact on skeletal and retinal development, and stress and disease resistance. Flatfish may have additional special needs for correct metamorphosis.

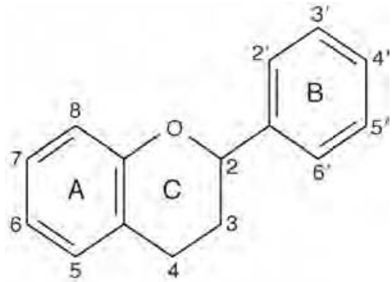
A special feature of flatfish farming is the need for volume prior to settlement (hatcheries for egg and larva stages) and the need for area after settlement. Common hatchery densities are 30 turbot larvae l^{-1} and < 10 halibut larvae l^{-1}. Rigorous hygiene is necessary and attention must be paid to water quality and renewal, as disease commonly strikes in intensive cultivation systems. The use of probiotics and microbial manipulation has potential, and most juveniles are vaccinated using commercially available vaccines against common bacterial diseases. Various technical systems have been employed for grow-out such as raceways, circular flat-bottomed tanks, submerged mesocosms and entire enclosed seawater ponds. Some refinements are subject to commercial confidentiality.

There is general agreement that broodstock management is essential to egg quality, though neither has been rigorously defined. Appropriate lighting (photoperiod, shading, intensity), temperature, oxygen and salinity, nutrition and husbandry affect broodstock physiology and thereby affect allocation of nutrients to eggs, spawning time or duration, fecundity and egg viability. Information on broodstock nutritional needs is sparse but commercial pelleted broodstock diets are available. (KP)

See also: Aquatic organisms; Fish larvae; Live fish food; Marine fish; Phytoplankton; Prey size; Rotifer

Flatus: *see* Gas production

Flavonoids A group of secondary plant metabolites based on substituted ring structures of the parent compound, flavan (see figure).



The subclasses of flavonoids are based on the substitution and state of oxidation of the C ring. There are at least 16 subclasses of flavonoids but flavonols, anthocyanidins and proanthocyanidins are the most abundant. The flavonoids are pigments in fruit, flowers and leaves. Their content in the leaves of higher land plants is highly variable but in some species may account for more than half the organic matter. (JDR)

Flavonols A subclass of flavonoids that are substituted with a ketone group at position 4, a hydroxyl group at position 3 and a double bond between positions 2 and 3 of the flavan C ring. The common flavonols are hydroxylated as shown in the figure.

The three most common flavonols are kaempferol (R and R′ = H), quercetin (R = OH, R′ = H), and myricetin (R and R′ = OH). Naturally occurring flavonols in plants are glycosylated. (JDR)

See also: Flavonoids

Flavour compounds Although birds have few taste buds compared with mammals, there is plenty of evidence that all have a good sense of taste. The domestic fowl has, on average, 340 taste buds located mainly in the palate and floor of the mouth while most mammals have hundreds of thousands. Flavour compounds are factors detected by taste buds, which can modify consumption of food or water, especially in the short term. Domesticated animals are sensitive to bitter, sweet, salt and acid flavours and they have an innate preference for sweet flavours. However, any flavour that is consistently associated with a food whose intake generates favourable metabolic consequences will become preferred, while sweet flavours can become aversive if paired with toxic or imbalanced foods. Foods can be flavoured in order to mask changes in the taste of their ingredients; for example, dairy cows exhibit neophobia for concentrate supplements with a novel flavour but this can be prevented by including a masking flavour in all supplements.

Flavours in common use in animal foods include aniseed, talin and plant oils. While saccharin is used as a sweetening agent in foods for young mammals, it is strongly aversive to chickens. (JSav, JMF)

Flour The product arising from the fine grinding of cereal grains or other starch-rich plant fractions. Flour is an important commodity in the manufacture of a wide range of food products worldwide, particularly baked products such as bread. Flour made from certain types of **wheat** grains is the one most closely associated with bread making. The production of flour involves the milling of refined grains in order to separate the starch-rich endosperm from the remaining fractions of the grain (kernel). The gluten of wheat flour has elastic properties which are utilized in baking and which help to trap air in the dough during bread making. Soft wheats (80–120 g crude protein kg^{-1} dry matter) produce flours that are suitable for products requiring minimal structure (e.g. cakes, biscuits, crackers) while hard wheats (120–150 g crude protein kg^{-1} dry matter) are more suitable for products requiring a stronger structure (e.g. breads). Wheat may be processed to produce a range of flours, including: (i) whole wheat (Graham) flour made from the entire wheat kernel and often unbleached; (ii) gluten flour, a starch-free, high-protein, whole wheat flour; (iii) all-purpose flour, refined (separated from the bran and germ), bleached or unbleached; (iv) cake flour, refined and bleached, with very fine texture; (v) self-rising flour, refined and bleached, with added raising agent and salt; (vi) enriched flour, refined and bleached, with added nutrients; and (vii) durum wheat flour, used for pasta manufacture.

Some by-products of the milling process (*see* **Milling by-products**) are suitable for animal feeding, including wheat bran, wheat middlings and wheat feed, which comprises fragments of the outer skins and broken particles of grains to which some endosperm is still attached. (ED)

Fluid therapy The replacement of fluids lost by a clinical condition, e.g. haemorrhage, or by overuse of normal routes, e.g. sweating, vomiting and diarrhoea, or arising from insufficient fluid intake. It may also be used to maintain a high rate of fluid throughput to wash out a toxin or noxious agent from the circulation; it may also provide a convenient route for the administration of a therapeutic agent over a prolonged period. The solutions used are isotonic, e.g. 0.9% sodium chloride, and may also include dextrose as a source of rapidly available carbohydrate. The acid–base status of the animal may be corrected by the addition of sodium bicarbonate in the case of an acidosis or ammonium chloride in the case of an alkalosis. The replacement of specific electrolytes, e.g. potassium ions lost during excessive diarrhoea, may be achieved in this way. (ADC)

Fluoride In very small amounts, fluoride increases the strength of bones and teeth. However, fluoride is generally regarded as toxic to domestic livestock, because in high amounts it accumulates in bone to an extent that actually weakens it, leading to lameness and increased wear of teeth. The teeth of fluoride-intoxicated cattle become mottled and stained and are eroded or pitted. Rock phosphates (fluorapatite, $Ca_{10}F_2(PO_4)_6$) can affect cattle when used in feed or when applied as a fertilizer without first being defluorinated. To qualify as defluorinated, feed-grade phosphates can contain no more than one part of fluorine to 100 parts of phosphorus. Other potential sources of fluoride include bone meal, deep-well water, and soil near volcanoes or aluminium processing plants. Soluble forms of fluoride, such as sodium fluoride, are rapidly and almost completely absorbed by cattle. Minor morphological lesions can occur in young cattle receiving as little as 20 ppm fluorine in their diets when their teeth are developing rapidly, but the relationship between these minor lesions and animal performance is unknown. (JPG)

Fluorine A halogen with an atomic mass of 19.00. Fluorine is found in nature as fluoride salts of various mineral elements. Excessive intake of fluorides from water, phosphate sources, or industrial pollution cause a disease called fluorosis. The syndrome is characterized by skeletal lesions and damage to developing dentition. (JWS)

Fluorosis: *see* Fluorine

Flushing A feeding strategy consisting of an increasing plane of nutrition in animals, usually applied before mating. It is particularly common in sheep, in which there is normally a period of several months between the end of lactation and the beginning of the breeding season, during which feeding levels provide for little more than maintenance requirements. Ewes that have been better fed during this period, and are thus in better body condition at the beginning of the breeding season, are more inclined to have multiple ovulations and hence to bear twins or triplets. The same effect can be achieved more economically by flushing, i.e. changing ewes from a maintenance ration to one that promotes liveweight gain 2–3 weeks before breeding begins. This can increase the lambing percentage (the number of lambs born per 100 ewes) by 10% or more.

Female pigs are commonly mated during and shortly after lactation, when their plane of nutrition is well above maintenance, so that flushing is superfluous. It may, however, be valuable in gilts at first mating.

It was once common to increase nutritional levels in order to promote liveweight gain in dairy cattle in the few weeks prior to calving, but it is now generally accepted that growth should be restricted, rather than encouraged, at this time in order to avoid the problems of calving too fat (*see* **Fertility**). (PJHB)

Foal A young horse of either sex up to 1 year of chronological age, or registered age. Registered Thoroughbred (TB) foals are conventionally aged from 1 January of the year in which they are born (in the southern hemisphere TB are aged from 1 August in the 12 months of their birth) and other breeds from 1 May, irrespective of their actual foaling date. Thus foals born just prior to 1 January (or 1 August) become 1 year of registered age immediately after those dates. Male foals are termed colt foals and females filly foals. (A hinny is the offspring from a stallion and a female ass, whereas a mule is the offspring from a male ass and a horse mare.)

Under natural environmental conditions in the northern hemisphere most foals are born between March and June, but with the use of artificial light and increased nutrition for the breeding mare the dates of conception and birth can be brought forward, so that foaling occurs in January. Foals are conventionally weaned from their dams at from 4 to 6 months of age, but for weaker foals weaning may be delayed. Healthy, strong foals commence eating significant amounts of grass at 3–5 weeks of age and it is possible, but not normally practicable, to wean foals with appropriate supplementary feed soon after they have received **colostrum**.

It is essential that the mare provides colostrum for her foal during the first 24 h following birth, before the foal receives other energy-containing feed. In the absence of this the foal should receive colostrum from another mare managed in the same environment, or, in the absence of both, a colostrum substitute. The foal receives γ-globulin from these sources, giving it some passive, or acquired, immunity to infection. The foal's active production of γ-globulin is detectable in the blood by 4 weeks of age in normally reared animals.

The large intestine of the foal is relatively small at birth and significant roughage consumption depends on the development of this region of the intestinal tract, though its development and expansion will be stimulated by roughage intake.

The foal gains rapidly in body weight during the first 6 months of life. A foal with a mature body weight of 500 kg may gain initially at the rate of 1.2–1.4 kg day^{-1}, the rate falling to 0.8 kg day^{-1} at 6 months and to 0.5 kg day^{-1} at 12 months. The weight increase is principally muscle and bone, hence the requirements for protein, calcium and phosphorus are high during the first 12 months. These needs are met by provision of mare's milk, but weaned foals need a high-protein cereal-based diet in order to achieve a normal growth rate. Alternatively,

Foals gain weight rapidly in the first 6 months of life. Their high requirements for protein, calcium and phosphorus are met by mare's milk.

vegetatively growing spring grass will meet the energy, protein and calcium needs of foals weaned at a normal age.

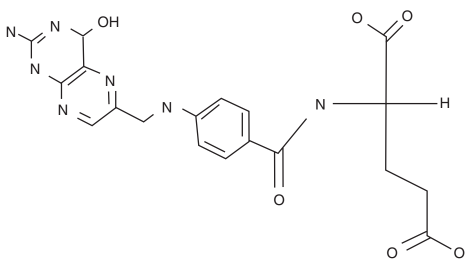
The normal neonatal foal has adequate iron reserves at birth to meet its requirements for this element until grazing commences, and supplements of **trace elements** will be required only if foals are weaned early and healthy pasture is unavailable. If the grazed pasture is deficient in **copper**, then copper supplementation of the pregnant mare is essential to ensure control of articular cartilage lesions in the young foal. Pasture deficiencies of **iodine** and **selenium**, and possibly of certain other trace elements, must be rectified by supplementation during pregnancy. For the minimum nutritional requirements of the foal, *see* **Horse feeding**. (DLF)

Fodder Crops and crop residues used as animal feeds. (JMW)

Fodder beet Fodder beet (*Beta vulgaris* L.) is a member of the *Chenopodiaceae*. It is sown from late March to June and the grey-white fleshy tubers are harvested from October to December. Fodder beet produces high yields of digestible nutrients. It is high in energy but low in protein, vitamins and minerals. Tops and roots can be used either fresh or as silage. Fodder beet tops contain toxic ingredients that can cause scour but wilting reduces this effect. The inclusion of high levels of fodder beet can cause digestive upsets, hypocalcaemia and death. As a consequence, dietary inclusion is limited in large ewes to 20% of the diet or < 2.5 kg day^{-1}, in beef cattle 20% of the diet or < 3.5 kg 100 kg^{-1} liveweight and in dairy cattle to < 1.7 kg 100 kg^{-1} liveweight in early lactation and < 3.0 kg 100 kg^{-1} liveweight in late lactation. Fodder beet can be fed to lambs at 15% and calves at 10% of the diet. The typical dry matter (DM) content of fodder beet is 160–180 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 63–70, crude fibre 60–65, ash 55–60, starch 20–22 and sugars 620–650, with ME 12–12.5 and DE 2.3 MJ kg^{-1} DM. (JKM)

Folate The B vitamin called folic acid, $C_{19}H_{19}N_7O_6$. The term folacin is used to describe the multiple metabolically active forms of folate. The vitamin is made of three components, having a pteridine linked to a *p*-aminobenzoic acid (PABA) linked to a glutamate. In its metabolically active form folate is involved in the metabolism of one-carbon units that have oxidation levels from the methyl, methylene, methenyl, formyl to the formimino forms. The vitamin has two nitrogen atoms that are intimately involved in its function in one-carbon metabolism. These are N^5 and N^{10} to which the one-carbon units are either linked one-to-one, such as N^5-methyl, or bridged across the two, as $N^{5\text{-}10}$-methylene. In order for folate to function in metabolism it must be reduced in two separate steps to tetrahydrofolate. In this form it is designated as tetrahydrofolate monoglutamate. The vitamin will function in this form but it is required in concentrations 70 times that of the pentaglutamate, which is the most abundant cellular form. The glutamate residues are added as the γ-glutamate. Cellular folates contain from one to seven γ-glutamyl residues attached to the tetrahydrofolate. The dietary form of folate is the tetrahydrofolate with multiple γ-glutamyl residues that must be hydrolysed before the vitamin can be absorbed as tetrahydrofolate monoglutamate. In metabolism, tetrahydrofolate polyglutamate is involved in catabolism of serine, glycine, the methyl carbons of choline, betaine, etc., as well as the single carbons of formaldehyde or formic acid. Folate intermediates (N^5-methyl, $N^{5\text{-}10}$-methylene, $N^{5\text{-}10}$-methenyl and N^{10}-formyl) provide one-carbon units critical to methyl-carbon metabolism via their role in methylation of homocysteine to form methionine (*see* **Methylation**). This methylation step provides a system by which methionine is regenerated. This methylation is critical to folate metabolism because of the production of tetrahydrofolate which can again participate in one-carbon metabolism. The intermediate forms of tetrahydrofolate ($N^{5\text{-}10}$-methylene, $N^{5\text{-}10}$-methenyl) are sources of carbons 2 and 8 of purine bases such as adenine. These are critical to the biosynthesis of nucleoside bases of DNA and RNA.

A deficiency of folic acid results in anaemia as well as other metabolic abnormalities. The anaemia is due to a lack of one-carbon units required for DNA and RNA biosynthesis and hence new erythrocyte formation. A deficiency of vitamin B_{12} also results in anaemia because it is critical to the use of N^5-methyltetrahydrofolate as a methyl source in methylation of homocysteine to form methionine. The deficiency results in the available tetrahydrofolate being tied up as N^5-methyltetrahydrofolate so that less is available for other reactions, in effect creating a folate deficiency. This accumulation of folate intermediates as N^5-methyltetrahydrofolate is known as the 'folate trap'.



(NJB)

Key references

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Herbert, V. and Das, K.C. (1994) Folic acid and vitamin B_{12}. In: *Modern Nutrition in Health and Disease*, 8th edn. Lea and Febiger, Philadelphia, pp. 402–425.

Folic acid: *see* Folate

Food allergies Adverse reactions to foods that invoke an immune response. Examples include allergies to specific proteins in soybean and groundnut products. In livestock, the main concerns are with soybean antigens in calves and piglets given soya-based milk replacers. The soya proteins glycinin and conglycinin are resistant to digestion in unweaned animals and can be absorbed into the intestinal mucosa, eliciting an immune response. When soya products are used in milk replacers or creep diets for piglets and calves, the lymphoid tissue (Peyer's patches) in the gut produces the immunoglobulins IgA and IgM. These **antibodies** are secreted into the gut and react with the soya **antigens** to prevent them from being absorbed. Antigens that escape antibody detection initiate an inflammatory response in the mucosa, causing the villi and microvilli to be damaged. The villi become shortened and broader, the microvilli are stunted and dysfunctional and the crypts of Lieberkuhn become deeper (crypt hyperplasia).

When calves or baby pigs are first exposed to soya products, and if absorption of the antigenic proteins occurs, the animals become sensitized to them. Subsequent exposures result in intestinal lesions, causing malabsorption, increased gut motility, growth of opportunistic pathogens and diarrhoea. Conventional heat processing of soya products does not inactivate the antigenic proteins but they can be removed by extraction with hot, aqueous ethanol. Alkali treatment with sodium hydroxide inactivates the proteins and can be used to prepare non-allergenic soya products for use in piglet and calf diets. Giving small amounts of soya products before weaning may sensitize young animals to later exposure to the antigens. A high intake of soya products before weaning has the opposite effect of inducing immune tolerance, which is achieved when the system no longer has the capacity to express a cell-mediated or humoral immune response.

Food allergy is a problem in dogs, causing atopy and pruritus (skin itching). A food elimination diet is used to isolate the offending food. Feeding sources of unsaturated fatty acids is helpful (*see* **Skin diseases**). (PC)

Food and Agriculture Organization An agency of the United Nations, with responsibility for the development of agriculture and food supply in UN member states. FAO publishes statistics on many aspects of world food production, and specialized publications on the nutrition of animals and humans. (MFF)

Food chain The living part of the ecosystem in which a living community depends on each member and its surrounding environment. The primary producers utilize the non-living matter such as minerals and gases from their environment to support life. Planktons and plants are at the beginning of the food chain. Many aquatic organisms, such as snails, mussels, shrimp, jellyfish and sea star, consume these plants. Small fish feeding on plankton become food for larger fish, e.g. tuna and mackerel, which are in turn eaten by larger fish and animals, such as shark and dolphin. Other organisms such as fungi and bacteria that feed on dead plants and animals reduce their remains to minerals and gases. Each level of consumption in a food chain is called a trophic level. (SPL)

Food intolerance An adverse reaction to foods that does not involve the immune system. For example, lactose intolerance occurs in individuals lacking adequate production of the lactose-digesting enzyme, lactase. Lactase deficiency results in fermentation of lactose in the gut, causing dehydration, diarrhoea and flatulence. Food intolerance also includes bacterial food poisoning and pharmacological reactions (caffeine, food preservatives, food colours, monosodium glutamate, aspartame). Food intolerance in livestock primarily involves adverse responses to lactose in milk products (e.g. whey) in weaned animals. (PC)

Food wastes: *see* Bakery products; Kitchen waste; *see also* individual crops and vegetables grown primarily for human consumption

Foot diseases Diseases affecting the hooves include ulcers, white line disease and laminitis, in which excessive carbohydrate and protein may be causal factors. Those affecting the skin of the foot include foul, digital dermatitis and foot rot, which are primarily caused by pathogenic organisms. Ergot poisoning causes gangrene of the feet. (WRW)
See also: Ergot; Hooves; Lameness; Laminitis

Forage The vegetable food of grazing or browsing animals. It includes both indigenous plants (e.g. grasses, forbs, shrubs, trees, lichens and mosses) and crops cultivated specifically as animal fodder (e.g. sown grasses, legumes, cereals, turnips, kale and rape), whether grazed or cut and fed. (AJFR)

Forage crop A crop harvested in its entirety as a feed for animals. Forage crops are commonly preserved as silage or hay. (JMW)

Foraging The act of harvesting forage by grazing or browsing. (AJFR)

Forb A feed that animals eat by browsing, including shrubs and small trees or herbs in grazed pasture. (JMW)

Force feeding Artificial cramming of dry or wet food into the oesophagus or crop, via a funnel with a rigid tube (long enough to reach the crop) and ramrod, or a syringe and flexible tube (for wet food in paste form). It is often used for experimental measurements (e.g. of digestibility or true metabolizable energy) when precisely known amounts of food are to be given. It is also used commercially (for *foie gras* production, when it is known as gavage). It is potentially harmful and, to avoid injury and impaction, must be done carefully, with limited amounts of food. Also called tube feeding. (JSav)

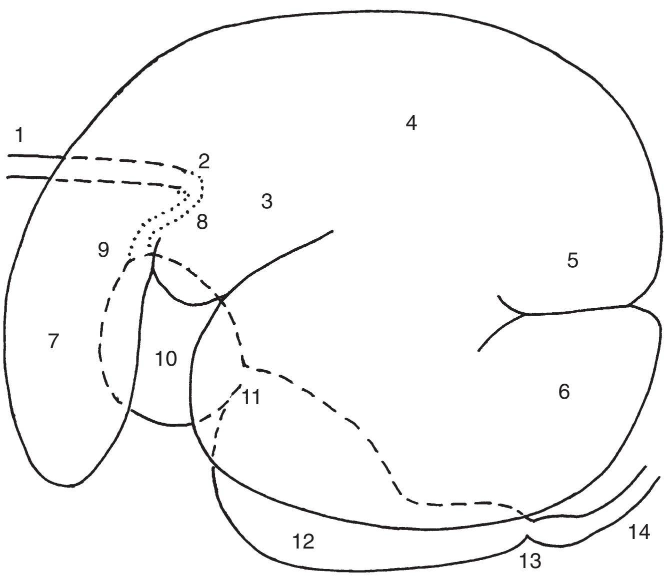
Foregut In common parlance, that part of the digestive tract lying anterior to the pyloric sphincter, i.e. stomach, oesophagus, pharynx and mouth. (RNBK)

Forestomach The compartments of the ruminant stomach (rumen, reticulum and omasum) lying anterior to the abomasum and the equivalent gastric compartment(s) in non-ruminant herbivores practising fermentative digestion (see figure overleaf). (RNBK)
See also: Omasum; Reticulum; Rumen

Further reading

Hofmann, R.R. (1973) *The Ruminant Stomach.* East African Literature Bureau, Nairobi, Kenya.

Forestomach development At birth, the abomasum of the ruminant is well developed but the **forestomach** is small. Once solid food is taken, all the compartments of the forestomach (**rumen**, **reticulum** and **omasum**) start to enlarge. The whole stomach reaches its adult proportions (forestomach 0.8, abomasum 0.2, by weight) when weaning is complete at about 8 weeks of age. Bulky roughages encourage an increase in forestomach volume; digestible roughages and the volatile fatty acids arising by microbial fermentation encourage papillary growth. Animals retained on a milk-only diet fail to show this development of the forestomach. (RNBK)



1 Oesophagus
2 Cardiac orifice of oesophagus
3 Cranial sac of rumen
4 Dorsal sac of rumen
5 Caudodorsal sac of rumen
6 Caudoventral sac of rumen
7 Reticulum
8 Ruminoreticular groove
9 Reticulo-omasal orifice
10 Omasum
11 Omasoabomasal opening
12 Abomasum
13 Pyloric orifice
14 Duodenum

The four-chambered stomach of the ruminant (based on the sheep), seen from the left.

Further reading

Warner, R.G. and Flatt, W.P. (1965) Anatomical development of the ruminant stomach. In: Dougherty, R.W. *et al.* (eds) *Physiology of Digestion in the Ruminant*. Butterworths, London, pp. 24–38.

Formaldehyde A simple aldehyde, CH_2O. It is used to preserve silage by inhibiting the fermentation process. It has been shown to reduce protein degradation in silage and to provide a more palatable feed. Aerobic deterioration of silage during feed-out may be problematic due to oxidation of residual sugars. A 40% solution of formaldehyde is commonly used as a sterilizing agent known as formalin. (RJ)

Formic acid Formic acid, HCOOH, is both produced and consumed in metabolism. It can be produced in the metabolism of the methyl group of methionine and can be metabolized as a folate one-carbon unit initially as N^{10}-formyltetrahydrofolate to provide carbon for methylation of homocysteine and for purine biosynthesis. As an acid, formic acid has many uses in manufacturing and as both the acid and calcium salt it has been used as a feed preservative. It is volatile and an irritant. The salt may be less effective as a preservative. (NJB)

Formiminoglutamic acid (FIGLU) An intermediate in the normal catabolism of L-histidine. Under the influence of the enzyme glutamate formimino transferase, formiminoglutamate and tetrahydrofolate are converted to N^5-formiminotetrahydrofolate. Thus, formiminoglutamate is important from a nutritional perspective because its excretion in urine is a unique and specific indicator of a folic acid deficiency. (NJB)

Fowl feeding: *see* Hen feeding

Fractionation, green-crop A process in which green crops, most commonly grass in

Western Europe, are separated into their component parts. There are two extraction concepts: (i) protein extraction for human consumption, with the fibre being fed to ruminants and the 'whey' to pigs and poultry, used as a fertilizer or growth substrate for microorganisms; and (ii) separation into a thick, protein-rich green juice for non-ruminants and a fresh or ensiled fibre-rich fraction for ruminants.

To obtain maximum protein, three crop factors need consideration: (i) rapid plant growth such that cells divide quickly and produce maximal protein; (ii) harvest before the plant is too mature, when protein content decreases and fibre content increases (the latter decreases the efficiency of extraction); and (iii) the crop must grow over a long season and re-grow quickly following defoliation.

The extraction process, commonly carried out by pulping, involves: (i) pulping the crop with metal beaters; (ii) compressing the pulp into layers 1 cm thick for a minimum of 7 s to allow the protein- and carbohydrate-rich fractions to flow from the fibre; (iii) filtration of the juice, followed by protein precipitation by heating (80–90°C) or acidification (pH 4.0–4.5); (iv) separation of the coagulated protein 'curd' (dry matter 10%) from the carbohydrate-rich 'whey' (dry matter 2–3%) by centrifugation; (v) washing and pressing the curd into a cake with the texture of cheese (dry matter 30–40%); and (vi) conservation and storage of the cake by acidification (pickling), salting, canning, high-temperature drying, freeze-drying or freezing at -10°C. The product must be maintained in a dark, oxygen-free environment and under these storage conditions it will keep for up to 1 year. (DD)

Free fatty acids (FFAs) Also called non-esterified fatty acids (NEFAs), fatty acids that are not esterified to glycerol or another alcohol such as choline or cholesterol. In blood plasma or serum, FFAs are really not free but bound to plasma albumin. (NJB)

Free radical Any compound that contains one or more unpaired electron. Free radicals are usually short-lived highly reactive compounds that react with a wide range of cellular molecules and macromolecules. They have a strong tendency to react with other compounds in order to gain or lose an electron, thereby becoming less reactive. Free radicals are produced in three ways, either to fulfil some purpose in the cell, as by-products of normal metabolic processes or in response to certain pathological insults. Some of the common free radicals in the body are those derived from oxygen such as superoxide anion, singlet oxygen and hydroxyl radical or nitrogen-derived species like nitric oxide and peroxynitrite (a very short-lived radical formed from nitric oxide and superoxide anion). Free radicals can be based on other atoms such as hydrogen, sulphur, carbon or minerals. Superoxide anion is generated by macrophages as a part of the immune response. In addition, macrophages and certain other cell types generate nitric oxide (NO·), which is a free radical. NO· can be a signalling molecule or it can be used to help to kill cells, as in the case when macrophages attack tumour cells or bacteria. They can also be generated as part of the reaction mechanism of certain enzymes and in these cases they remain bound to the enzyme. One example of this is the enzyme ribonucleotide reductase, which generates the substrates for DNA synthesis. Some enzymes produce free radicals as one product of their reaction mechanism. These include xanthine oxidase, amino acid oxidase and the ferroxidase centre of the H subunit of the iron storage protein ferritin. Superoxide anion is also produced by mitochondria during the process of ATP formation: it is estimated that between 1% and 5% of the oxygen consumed by this organelle is not completely reduced to water in the process of ATP formation. Free radicals are also produced in certain pathological situations such as those that occur in response to iron or copper overload. When present in excess, iron in the reduced state, Fe^{2+}, can react with hydrogen peroxide in the cell in a process referred to as the Fenton reaction. This leads to production of a highly toxic free radical, the hydroxyl radical. Free radical production increases during ischaemic events (e.g. strokes) when blood supply to an organ is reduced or cut off. Oxidants including free radicals are produced in response to certain drugs and to defoliants such as paraquat. Excessive production of free radicals is thought to result in increased incidence of some diseases. (RSE)

Freeze-drying A process of drying, also known as lyophilization, in which food and other heat-sensitive products (e.g. blood plasma) are rapidly frozen and dehydrated under high vacuum. The ice sublimes off as water vapour without melting under the low pressure. Freeze-dried materials are undamaged or little changed and there is less loss of flavour and texture of food than with other drying methods. For accelerated freeze-drying, controlled heat may be applied to the process without melting the frozen material. Freeze-dried products are porous and often rehydrate rapidly. (SPL)

Freezing The water temperature of aquatic habitats reaches close to freezing point in fresh water at 0°C and sea water at −1.86°C. The serum of a typical marine vertebrate freezes at −0.7°C and fish are at risk of freezing at this water temperature (DeVries, 1982). Several Antarctic and Arctic fishes can tolerate freezing temperature due to the presence of proteinaceous antifreeze unless they are exposed to ice below −2.2°C. Antifreeze proteins may be present in concentrations up to 10 mg ml^{-1}, which may account for as much as 3% of the total serum protein. Cod and Atlantic salmon are farmed in sea water but the latter does not produce antifreeze proteins. Most farmed fish are essentially isothermal with their aquatic environment and cope with the problem of variable body temperature (poikilothermy) by a diversity of biochemical mechanisms. Generally, food consumption ceases at freezing temperatures and handling of fish is minimized to improve survival. (SPL)

Key reference

DeVries, A.L. (1982) Biological antifreeze agents in coldwater fishes. *Comparative Biochemistry and Physiology* 73A, 627–632.

Fresh water Water that is not salty, i.e. with < 1 g dissolved solids l^{-1}. Most naturally occurring fresh waters are within the range of 50–300 mg total dissolved solids l^{-1}, the average of all rivers being 100–150 mg l^{-1}. The dominant inorganic constituents of typical fresh water are carbonates and bicarbonates of calcium and magnesium. In soft, acid waters, sulphate may be the dominant anion; while near sea coasts, sodium and chloride may be elevated by sea spray contribution. (RHP)

Freshwater fish Freshwater fish inhabit a variety of aquatic ecosystems, including streams, rivers and lakes. In these various environments, fish display diverse feeding habits – herbivorous, omnivorous or carnivorous. These can provide insights into a fish's nutritional needs when subjected to artificial conditions in aquaculture.

Protein is an extremely important component of fish diets. Satisfying a fish's dietary requirement for protein with a balanced mixture of amino acids is critical to ensure proper growth and health of the fish. Providing excessive levels of dietary protein is both economically and environmentally unsound, because protein is the most expensive dietary component and levels above that needed to satisfy requirements will result in elevated nitrogenous waste excretion into receiving waters. Most herbivorous and omnivorous fish evaluated to date have been determined to require crude protein at 25–35% of diet; carnivorous species may require crude protein at 40–50% of diet. This difference appears to be related to the limited use of carbohydrate for energy by carnivorous species, which in turn are very proficient at using dietary protein for energy. The efficient use of protein for energy is largely attributable to the way in which ammonia from deaminated protein is excreted via the gills with limited energy expenditure. Although protein requirements are generally expressed as a percentage of the diet, feed intake must also be considered in determining the amount of protein needed to satisfy metabolic requirements. Energy density of the diet and the ratio of energy to protein in the diet may also influence dietary protein requirements.

Quantitative dietary requirements for ten indispensable amino acids – arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine – have been determined for several freshwater fish species. Of the ten other dispensable amino acids that commonly make up protein, two are particularly important for their ability to replace partially or spare indispensable amino acids. Tyrosine can spare approximately 50% of phenylalanine in meeting the total aromatic amino acid requirement of fish species; cystine generally can replace a similar amount of methionine as part of the total sulphur amino acid requirement.

Carbohydrates are not specifically required in the diet of fish but may provide a rather inexpensive source of energy. The ability of fish to utilize dietary carbohydrate for energy varies considerably, with most carnivorous species having more limited ability than herbivorous or omnivorous species. The amount of soluble carbohydrate included in prepared diets for carnivorous species is generally less than 20% while diets for omnivorous species generally contain from 25 to 40% soluble carbohydrate. Carnivorous species tend to use lipid preferentially and use it more effectively than carbohydrate. Non-starch polysaccharides such as cellulose and hemicellulose are essentially indigestible by fish and do not make a positive contribution to their nutrition. Crude fibre in fish diets is typically restricted to < 7% to limit the amount of undigested material entering the culture system.

Lipid, in the form of triglycerides, is an important dietary component because it provides a concentrated source of energy that is typically well utilized by aquatic species. Carnivorous and omnivorous species both utilize dietary lipid efficiently for energy. Dietary lipid also supplies essential fatty acids that cannot be synthesized by the organism. Whereas marine species appear to have very limited ability to elongate and desaturate short-chain fatty acids, many freshwater fish have been shown to meet their essential fatty acid requirements with dietary linoleic acid or linolenic acid. Dietary lipids also serve as precursors of steroid hormones and prostaglandins in fish as well as providing a vehicle for absorption of fat-soluble vitamins. Lipid from the diet, deposited in the fish, may affect the flavour and storage quality of edible products derived from the fish.

Minerals are required by fish for tissue formation and other metabolic functions just as they are required by terrestrial animals; however, waterborne minerals also play a role in osmoregulation of fish and may contribute to meeting metabolic requirements. In terms of osmoregulation, freshwater species lose ions to the hypotonic environment and therefore suffer from hydration; thus, these organisms generally do not drink water but excrete large quantities of excess water as dilute urine. Dissolved minerals in the aquatic environment may contribute to satisfying the metabolic requirements of fish and interact with dietary requirements. In particular, fresh water of moderate hardness (~ 50 mg l^{-1} as $CaCO_3$) has been shown to provide fish with adequate calcium to sustain metabolic functions in the presence of very low levels of dietary calcium. In the presence of low levels of waterborne calcium, however, the essentiality of dietary calcium has been established for various freshwater species. Chloride, potassium and sodium are other minerals that may be present in fresh water at concentrations sufficient to assist in meeting metabolic requirements of fish.

Dietary deficiencies of most of the macrominerals generally have been difficult to produce with fish species because of the presence of these minerals in the water. Supplementation of phosphorus in fish diets is usually the most critical, because its presence in the water and utilization by fish are limited. A phosphorus deficiency can cause reduced growth along with other specific deficiency signs in a relatively short period of time. The availability of phosphorus from feedstuffs also may vary considerably; thus, supplementing diets on the basis of available phosphorus is important.

Of the microminerals, selenium and zinc have been demonstrated, in some fish species, to be most important as supplements in diets due to low levels in feedstuffs or to interactions with other dietary components that may reduce their bioavailability. Although supplementation of practical diets with other microminerals has not been shown to be necessary in most instances, an inexpensive trace mineral premix is typically added to most nutritionally complete diets to ensure adequacy.

Most vitamins that have been established as essential nutrients for terrestrial animals have also been demonstrated as being essential for various fish species. Dietary deficiencies of almost all of these vitamins have been shown to cause reduced growth and other specific deficiency signs in fish. Quantitative dietary requirements for as many as 15 vitamins have been determined for freshwater species such as the channel catfish, common carp and rainbow trout. These requirement values have been used to provide guidelines for vitamin supplementation of diets for these and other fish species. (DMG)

See also: Aquaculture; Catfish; Common carp; Rainbow trout

Further reading

National Research Council (1993) *Nutrient Requirements of Fish*. National Academy Press, Washington, DC, 114 pp.

Frog meal The rendered by-product from the frog leg industry. The meal is produced from the remaining parts of the frog (forelimb, head, body, entrails, etc.) after the hindlegs have been removed. On an average, these portions constitute about 65% by weight of the whole frog. Yield of the meal varies from 18% to 22% of the fresh frog waste. Meals prepared from frog waste conform to standards prescribed for fish meal and can therefore be used for supplementation of animal feeds.

Chemical composition of frog meal.

Proximate composition	(%)
Dry matter	93.00
Crude protein (CP)	64.55
Crude fibre	0.80
Ether extract	14.00
Ash	12.50
Amino acids (% of CP)	
Methionine	4.40
Lysine	8.95
Tryptophan	1.07
Leucine	7.81
Isoleucine	6.50
Valine	6.90
Arginine	4.12
Histidine	5.50
Phenylalanine	6.70
Threonine	3.20
Minerals	
Ca (%)	9.20
P (%)	4.60
Mg (%)	0.55
Fe (%)	0.01
K (%)	1.30
Na (%)	1.10
S (%)	0.70
Mn (mg kg^{-1})	68.00
Zn (mg kg^{-1})	70.00

(JSA)

Fructans Polysaccharides of β-D-fructofuranose residues, with a non-reducing terminal D-glucopyranose, synthesized from sucrose. Common fructans include inulin and levan (phlein). The predominant linkage in inulin is (2→1) fructosyl-fructose, and in levan it is (2→6) fructosyl-fructose. Fructans are widely present in the grasses, but in high concentration only in the northern grasses (subfamily *Pooideae*). Fructans are the principal storage carbohydrate in several of the *Alliaceae* (onion bulb and garlic clove), *Asterales* (chicory root, Jerusalem artichoke tuber, edible burdock root, endive root) and bulbs of several ornamental plants (hyacinth and dahlia tubers), and they are produced by some bacteria. Inulin is a linear fructan. Inulin in roots of Jerusalem artichoke, chicory and garlic consists of about 70 sugar residues. Levan in higher plants is a relatively small, usually highly branched polymer. Bacteria synthesizing fructans include the Enterobacteraceae, Streptococcaceae and Bacillaceae. Bacterial fructans are of the levan type, except for inulin formed by certain strains of *Streptococcus mutans*, a major component of dental plaque. Inulin from chicory may have health benefits through an increase in the proportion of bifidobacteria in the colon of non-ruminants. (JAM)

See also: Carbohydrates; Fructose; Oligosaccharides; Storage polysaccharides

Fructosamine An amino sugar, $C_6H_{13}NO_5$, molecular weight 179, in which the hydroxyl group on carbon 2 of fructose is replaced by an $-NH_2$ group. It may occur in the urine of individuals with diabetes mellitus. (JAM)

Fructose A hexose, $C_6H_{12}O_6$, molecular weight 180, also called levulose, with an anomeric carbon atom at position 2 which can be in furanose or pyranose (levulose) ring form. One of the two monosaccharides in sucrose, it is found in fruit juices and honeys, and is the sole constituent of inulin. (JAM)

See also: Carbohydrates; Fructans; Monosaccharides

Fruit The edible product of a plant or tree consisting of its seed or envelope, especially the latter when juicy or pulpy as in the apple, orange, plum, olive, etc. Fruit may be available for animal feeding both as waste whole fruit or as the by-products of processing. These materials are mostly bulky and wet and are therefore best suited to immediate use in a Lehmann system, but they may be a semi-dry pomace or dried into pulp. Fruits and fruit by-products require supplementation with protein, vitamins and specific minerals.

Citrus fruits (oranges, grapefruits, etc.) and apples are frequently grown for human consumption but surplus fruits and by-products may be used as animal feeds. Cattle can consume < 40 kg fresh fruits day^{-1} with no apparent harmful effects. Fresh oranges can produce higher milk yields than clover pastures but they should be offered following milking to avoid flavouring the milk. Fresh citrus fruits contain little protein, calcium or phosphorus and should be fed with protein and mineral supplements. Pigs prefer oranges and tangerines to grapefruit and limes. To avoid the danger of whole citrus fruits getting stuck in the gullet, they should be sliced. Fresh fruits can be included in the diet up to the following levels: calves and lambs 20%, dairy cattle 25%, ewes and beef cattle 30%, grower and finishing pigs and breeder and layer chickens 5%, sows 10% and broilers 2.5%. The dry matter (DM) content of whole citrus fruit is 319 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 113, crude fibre 42.3, ash 66, ether extract 94 and NFE 304 (McCann and Stewart, 2000). (JKM)

See also: Apple; Citrus products; Kiwifruit; Olive; Orange; Winemaking residues

Key reference

McCann, M.A. and Stewart, R. (2000) Use of Alternative Feeds for Beef Cattle. Cooperative Extension Service/The University of Georgia College of Agriculture and Environmental Services. http://www.ces.uga.edu/pubcd/1406-w.htm (29/01/2002).

Fucose A deoxy sugar, 6-deoxy-L-galactose, $C_6H_{12}O_5$, molecular weight 164, created by substitution of a hydrogen for the hydroxyl group of carbon 6 of galactose; found in oligosaccharide components of glycolipids, e.g. gangliosides, and glycoproteins, e.g. mucins (mucoproteins) and immunoglobulins. (JAM)

See also: Carbohydrates; Deoxysugar; Galactolipids; Mucin

Fuel: *see* Energy

Fumaric acid A dicarboxylic acid, HOOC·CH=CH·COOH, one of the intermediates in the tricarboxylic acid (TCA) cycle in which it is derived from succinate and is in equilibrium with malate. Fumaric acid is used as a feed additive to reduce digestive disturbances, especially in young pigs. (MFF)

See also: Acidification; Tricarboxylic acid (TCA) cycle

Fumonisins Mycotoxins produced by the fungus *Fusarium moniliforme*, also known as *F. verticillioides*. Fumonisins cause species-specific pathologies such as leukoencephalomalacia in horses, pulmonary oedema in pigs, liver lesions in ruminants, and possibly oesophageal cancer in humans. Poultry are resistant to the toxic effects. There are several fumonisins, including B1, B2, B3, B4, A1 and A2. They are structurally similar to sphingosine, a constituent of sphingolipids. Fumonisins inhibit sphingosine biosynthesis. Pathology is related to defective sphingolipid biosynthesis in nerve tissue and cell membranes. Fumonisins are primarily a problem in maize. (PC)

Functional food A food that benefits one or more functions in the body in addition to supplying nutrients. The benefit usually relates to an improved state of health and well-being or to a reduction in the risk of disease. (MFF)

See also: Nutraceutical; Pharmafood

Fungal diseases Fungal diseases (mycoses) are caused by inhalation, ingestion or traumatic introductions of fungi into the animal body. Pathogenic fungi establish in apparently healthy hosts, causing diseases such as histoplasmosis, coccidiomycosis and blastomycosis. Opportunistic fungi establish in a host that is debilitated or immunosuppressed, or following prolonged administration of antibiotics. Other examples of mycoses include aspergillosis, candidiasis, chromomycosis, cryptococcosis, entomophthomycosis and histoplasmosis. Treatment involves administration of specific antifungal agents.

(PC)

Fungi Eukaryotic microorganisms. Eukaryotes have a nucleus and other subcellular structures, in contrast to prokaryotes, which have no nuclear membrane. They exist in unicellular (yeast) and filamentous (mould) forms. Fungi can cause disease (mycotoxicoses) or can produce toxic metabolites (mycotoxins); they are also the source of antibiotics. Rumen fungi have a role in fibre digestion, and some yeasts (e.g. *Saccharomyces cerevisiae*) are used as feed additives to enhance rumen fermentation. Various fungi (moulds) may grow on moist feedstuffs, producing adverse odours and reducing feed palatability. Spores released by moulds growing on feeds or bedding may cause respiratory disease. (PC)

Furanose The five-member ring structure of a monosaccharide created by the reaction of the alcoholic hydroxyl group on carbon atom 5 with the carbonyl group at carbon atom 2, or by the reaction of the oxygen of the hydroxyl group on carbon atom 4 with the carbonyl group on carbon atom 1.

(JAM)

See also: Arabinose; Carbohydrates; Xylose

Futile cycles Futile cycles or substrate cycles involve the repeated interconversion of a substrate and product with the loss of a discrete amount of energy in each precursor–product cycle. An example would be production of glucose-6-phosphate from glucose + ATP followed by its hydrolysis to glucose. Each cycle involves the loss of one ATP equivalent of energy. Futile cycles may be regarded as energy wastage (inefficiency) but may also be a means of producing heat.

(NJB)

G

Gadoleic acid *cis*-9-Eicosenoic acid, a 20-carbon monounsaturated fatty acid, 20:1 n-11 (Δ^9), $CH_3 \cdot (CH_2)_9 \cdot HC{=}CH \cdot (CH_2)_7 \cdot COOH$, found in very low concentrations in brain phospholipids and fish liver oils. (NJB)

Gain:feed ratio A measure of an animal's efficiency in converting feed inputs into productive output. It is also called feed conversion efficiency (FCE). In growing animals it is the body weight gained per unit of feed consumed, i.e. the inverse of feed:gain ratio. It can also be applied to other production situations, such as laying hens (the weight of eggs produced per unit of feed consumed) or milk production (the weight of milk produced per unit of feed consumed). (SPR)
See also: Efficiency of feed conversion (FCE); Feed conversion ratio (FCR); Feed:gain ratio

Gait disorders Gait disorders can be caused by neurological disorders, associated with leg weakness or ataxia, or by a muscular abnormality or a systemic illness leading to lameness, leg weakness or tetany. Gait can be assessed by observing an animal moving on a firm non-slip level surface, and several systems for scoring locomotion have been devised (Ward, 1998; Whay and Main, 1999). Neurological gait disorders with nutritional causes include enzootic ataxia and swayback (copper deficiency) and rye-grass staggers (mycotoxin from *Neotyphodium lolii*, a fungus growing on rye-grass). Lameness of nutritional origin includes acute laminitis and sole ulcer (excess starch or protein).

Abnormal gait associated with muscular abnormality includes nutritional muscular dystrophy or white muscle disease (selenium/vitamin E deficiency). Gait disorders associated with systemic illness include milk fever or parturient paresis (hypocalcaemia), grass tetany (hypomagnesaemia), azoturia in horses (excess carbohydrate relative to work load), porcine stress syndrome (selenium deficiency), splay-leg in pigs (selenium deficiency and genetic predisposition) and muscular dystrophy in cattle and sheep (selenium/vitamin E deficiency). (WRW)
See also: Ataxia; Calcium; Foot diseases; Lameness; Leg weakness; Magnesium; Muscular diseases; Selenium; Starch; Vitamin E

References

Ward, W.R. (1998) Standardisation of gait analysis in cattle. In: Lischer, Ch.J. and Ossent, P. (eds) *10th International Symposium on Lameness in Ruminants*. University of Zurich, Switzerland.

Whay, H.R. and Main, D.C.J. (1999) The way cattle walk: steps towards lameness management. *Cattle Practice* 7(4), 357–364.

Galactan Homopolysaccharide of β-linked galactose residues, usually D-galactose, in either pyranose or furanose ring form. Carrageenan in red algae (seaweeds) and galactocarolose in the mould *Penicillium charlesii* are linear polymers. Molecular weight 1500–20,000. (JAM)
See also: Carbohydrates; Dietary fibre; Galactose; Gums; Storage polysaccharides

Galactolipids The three major classes of these derivatives of ceramide are cerebrosides, gangliosides and ceramide oligosaccharides. Cerebrosides, abundant in myelin sheaths of nerves, consist of a sphingosine, a fatty acid and either glucose or galactose; hence they are also called glucolipids or glucocerebrosides and galactolipids or galactocerebrosides, respectively. Gangliosides, also in nerves and spleen, are cerebrosides with additional molecules of carbohydrate as amino

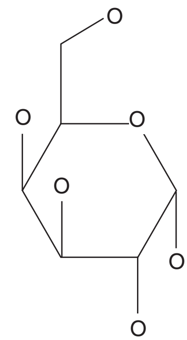
sugars and sialic acid. The ceramide oligosaccharides are ceramide derivatives containing one or more molecules of carbohydrate and termed ceramide mono- (or di-, tri- etc.) saccharides. A fourth class comprises galactosylacylglycerides, which are present in small amounts in plants. (JAM)
See also: Carbohydrates; Galactose

Galactomannans Heteropolysaccharides consisting of linear chains of 1→4-β-D-mannopyranose with αβ-D-galactopyranose side chains, varying widely in molecular weight and in the proportion of galactose. Found in plant cell walls and endosperm. Most seed galactomannans are water soluble and viscous in aqueous solutions, making them important food texture modifiers, e.g. gums of locust bean, carob bean, guar. The form and linkage of mannose and galactose in fungal and lichen galactomannans differ from those in plant sources. (JAM)
See also: Carbohydrates; Dietary fibre; Galactose; Gums; Mannose; Storage polysaccharides

Galactopoiesis Milk formation.
See: Lactation; Milk

Galactosamine An amino sugar, $C_6H_{13}NO_5$, molecular weight 179, in which the hydroxyl group on carbon two of galactose is replaced with an $-NH_2$ group. Almost always occurring as the *N*-acetylated compound, *N*-acetyl-D-galactosamine, it is a component of cartilage, chondroitin sulphate, several glyco- and galacto-sphingolipids and in secreted and surface glycoconjugates of the intestinal epithelium. (JAM)
See also: Carbohydrates; Monosaccharides

Galactose A hexose, $C_6H_{12}O_6$, molecular weight 180, usually found in pyranose form. An epimer of glucose in which the bond of carbon four, containing the hydroxyl group, is inverted. It is linked with glucose in lactose and is also a component of plant hemicelluloses and of cerebrosides. (JAM)
See also: Carbohydrates; Galactolipids; Glucose; Hemicelluloses; Monosaccharides



Galactosidase Glycolytic enzyme (α-galactosidase; melibiase; α-D-galactoside galactohydrolase; EC 3.2.1.22), in the brush border of mucosal cells of the small intestine, which specifically hydrolyses bonds with α-D-**galactose** (as in lactose). It does not hydrolyse bonds with β-D-galactose, as in the oligosaccharides, raffinose, stachyose and verbascose: these can be hydrolysed by microbial β-galactosidase, primarily in the large intestine. (SB)

Galactouronans Heteropolysaccharides of α-D-galacturonic acid residues in pyranose form with L-rhamnopyranose interspersed in the linear chains and with side chains of neutral sugars. The carboxyl groups are frequently present as the methyl ester, and the hydroxyl groups may be acetylated. Found in seeds, flowers, leaves, bark, roots, fruits and vegetables as structural or storage carbohydrates. (JAM)
See also: Carbohydrates; Dietary fibre; Pectic substances; Rhamnogalactouronans; Storage polysaccharides

Galacturonic acid A major constituent of pectins, HOOC·(CHOH)$_4$·CHO. D-Galacturonic acids are also found in plant gums and bacterial cell walls. Galacturonic acid is widely distributed in the plant world, functioning as a structural polysaccharide frequently in close association with cellulose, and as a storage polysaccharide. In the rumen it is fermented to the short-chain volatile fatty acids. (NJB)

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Gamma-amino butyric acid (GABA) γ-Aminobutyrate ($H_2NCH_2 \cdot CH_2 \cdot CH_2 \cdot COO^-$) is formed by decarboxylation of L-glutamate by L-glutamate decarboxylase primarily in the grey matter of the central nervous system. γ-Aminobutyrate is an inhibitory neurotransmitter. It is catabolized by γ-aminobutyrate transaminase to succinate semi-aldehyde which is converted to succinate. (NJB)

Gamma-linoleic acid (GLA) An 18-carbon n-6 unsaturated fatty acid, all-*cis*-6,9,12-octadecatrienoic 18:3 n-6 ($\Delta^{6,9,12}$). γ-Linoleic acid is parent fatty acid of the n-6 family. After a two-carbon addition and insertion of an additional double bond, γ-linoleic acid becomes arachidonic acid, 20:4 n-6 ($\Delta^{5,8,11,14}$). (NJB)

Gas production Gas is produced within the digestive tract of herbivorous animals both by microbial fermentation and by release of carbon dioxide from secreted bicarbonate. The rate of production in ruminant animals is very rapid, e.g. about 30 l h^{-1} in the reticulorumen of cattle. This gas is eliminated mainly by belching (unless it is trapped as a froth, as it is in animals suffering from bloat) and also by absorption and exhalation from the lungs.

Rumen gas typically contains about 65% CO_2, 27% CH_4, 7% N_2, 0.6% O_2, 0.2% H_2 and 0.01% H_2S. Part of the CO_2 and the CH_4, H_2 and H_2S represent end-products of microbial metabolism. Some CO_2 also arises from salivary bicarbonate in amounts dependent on secretion rate and on rumen pH and CO_2 tension. The N_2 and O_2 are either swallowed with food or diffuse in from the blood.

Gas arises similarly from the fermenting content of the large intestine, especially in hindgut fermenters (pig, horse, rabbit), and is eliminated as flatus or by absorption and exhalation.

Considerable volumes of gas may be swallowed as froth during bottle-feeding of young animals and some is propelled into the small intestine. (RNBK)

Further reading

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Gas–liquid chromatography Gas–liquid chromatography (GLC or GC) uses the general principle of chromatography to separate a mixture of compounds (solutes) in a sample. The sample is vaporized and injected on to a chromatographic column which has an immobilized stationary phase. It is separated into individual components by the flow of an inert carrier gas such as helium, hydrogen, argon or nitrogen. GLC separation occurs when the analyte partitions between the gaseous mobile phase and the liquid phase immobilize on the column as the stationary phase. Unlike certain other types of chromatography, the gaseous mobile phase does not interact with molecules of the analytes. A detector monitors the carrier gas as it emerges from the column and generates a signal in response to variation in its composition due to eluted components. Four of the most widely used detectors for gas chromatography are the thermal conductivity detector (TCD), electron-capture detector (ECD), flame ionization detector (FID) and nitrogen–phosphorus detector (NPD). Gas chromatography can also be coupled with other selective techniques, e.g. in GC–mass spectrometry (GC–MS) and GC–infrared spectroscopy (GC–IR). These methods provide powerful tools for identifying the components of complex mixtures.

GLC is widely used for the analysis of fatty acids, amino acids, carbohydrates, pesticides and herbicides in feedstuffs and animal tissues. Prior to GC analysis of oil samples, the triglycerides must be split up and the individual fatty acids converted to their methyl esters (FAMEs). Phospholipids are treated similarly to oils and wax esters can be studied as such or the fatty acids can be analysed as FAMEs and the alcohols as acetate esters. For other materials to be analysed by GLC, there can be acid hydrolysis of proteins followed by esterification (N-propyl esters) and silylation of carbohydrates to produce volatile samples for fatty acid, amino acid and sugar analysis, respectively. (RGA)

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Gastric emptying Gastric emptying is achieved by a concerted action between the antrum, pylorus and upper duodenum in which contraction of the antrum is followed by sequential contraction of the pyloric region and the duodenum. The gastric contents are squirted a little at a time into the small intestine. Only the liquid phase and small particles can be evacuated by the pylorus. Therefore, solid aggregates (several millimetres) present in the food must be crushed by strong muscular contractions that mash and homogenize the digesta. Meals rich in dietary fibre can delay gastric emptying.

Several mechanisms control gastric emptying in order to permit adequate time for digestion in the small intestine. These include neural signals from receptors that respond to hyper- and hypo-osmolarity and to high hydrogen ion concentration in the duodenum. They also include endocrine signals from receptors responding to peptides and lipids in the duodenum, which trigger the release of **cholecystokinin** (CCK), and from receptors that respond to lipids in the jejunum, which trigger the release of gastric inhibitory polypeptide. (SB)

Gastric juice: *see* Acidity of the gastrointestinal tract; Stomach

Gastric ulcers Gastric ulcers are open lesions in the wall of the stomach, usually in the pars oesophagea, due to erosion of the epithelial tissue by hydrochloric acid and peptic enzymes in gastric secretions. They are most common in pigs, where a prevalence of about 1% can occur. About 4% of neonatal deaths can be attributed to gastric ulcers. Normally the stomach wall is protected by its thick mucous secretions but these can become lessened by certain conditions, including prolonged stress. Chronic lesions may occur in either the glandular or squamous-lined regions of the stomach. The disease is multifactorial but stressful housing conditions are the commonest cause. Fine grinding of cereal (especially wheat) diets can also increase the incidence of ulcers in the oesophageal region of the stomach of growing pigs. Associated causes in pigs include swine fever, fungal infections of the gut that are acquired from infected bedding, and some parasitic infections. (JMF)

Gastrin A 34-, 17- or 14-amino acid polypeptide hormone secreted by cells in the fundic region of the stomach. The 17-amino-acid peptide is the major form with regard to gastric acid secretion. Gastrin increases the secretion of pepsin (a proteolytic enzyme) by the stomach and increases the growth of the mucosa of the stomach and intestines. It also increases gastric motility. (NJB)

Gastroenteritis: *see* Digestive disorders

Gastrointestinal disease: *see* Digestive disorders

Gastrointestinal hormones A number of peptide hormones that contribute to the regulation and optimization of the digestive processes in the gastrointestinal tract (GI). According to a close sequence homology they can be grouped into families, i.e. secretin family: secretin, glucagon, vasoactive intestinal polypeptide (VIP) and gastric inhibitory peptide (GIP); and gastrin family: gastrin and cholecystokinin (CCK). Other GI hormones are somatostatin, gastric releasing peptide (GRP) and substance P. GI hormones also regulate the further metabolism of absorbed nutrients by stimulation of the secretion of insulin from the pancreas. (SB)

Gastrointestinal microflora The gastrointestinal tracts of farm animals are inhabited by large populations of microorganisms. The host animals and their gut microbes form an integrated and mutually beneficial ecological unit. The density of microbial colonization and their species diversity vary with region of the gut, tending to be greatest in the stomach (reticulorumen, crop) and in the large intestine (caecum and colon). The microorganisms of the alimentary tract can be split into two groups: those occurring in the gut lumen, either free living or intimately associated with digesta particles; and those associated with the gut's mucosal epithelium. Ruminants such as cattle, sheep, goats and camelids are principally foregut fermenters (although some fermentation does occur in the hindgut), whilst non-ruminants such as pigs, horses and rabbits are largely hindgut fermenters. Several factors, such as diet, age, season, time of day, geographical location, temperature, pH, osmolarity, dissolved gases, digesta flow rates, metabolic inhibition and predation, are known to affect the numbers and diversity of gastrointestinal microbiota.

The digestive tract of the unborn mammalian fetus is sterile: microbial colonization of the gut commences during birth. The neonate acquires microorganisms successively from the mother's vagina and faeces, and then from food, other animals and the environment. Microbial colonization of the alimentary tract is a fast and complex process, and may reach completion within 48 h in non-ruminants. Although the neonate is exposed to many microorganisms of a very diverse species composition, it is the gut conditions such as the availability of growth factors and pH that determine the particular strains that establish successfully and eventually form the commensal gut microflora, whilst others fail.

Commensal gastrointestinal bacteria are known to enhance immune competence by increasing the resistance of the gut to colonization by pathogens. However, the main role of alimentary tract microorganisms is digestion. Mammalian enzymes are unable to hydrolyse β-linkages between glucose or pentose units of plant structural carbohydrates; cellulases of gut microbes impart this capability. Bacteria of the rumen, caecum and colon are capable of synthesizing a variety of vitamins, especially vitamins B and K. Rumen bacteria confer additional advantages to their hosts. They synthesize microbial protein of high biological value from poor quality nitrogen sources such as urea; they can degrade ingested antinutritional factors and toxins; and they recycle endogenous nitrogen. Nevertheless, rumen microbes also have adverse effects. The production of gases (hydrogen and methane) during microbial fermentation represents an energy loss. Some ingested proteins of high biological value, which do need to be fermented, are degraded and used to produce microbial protein, which may be of lower quality. Microbes may also produce toxins from non-toxic precursors.

The reticulorumen environment is highly variable, due to its sensitivity to the nature, type and amount of feed consumed and its requirement for a complex buffering mechanism for the maintenance of optimum pH in order to keep the fermentation working efficiently. On the other hand, the hindgut environment is more constant and less influenced by diet, since the source of nutrients for caecal and colonic bacteria is undigested dietary polysaccharides, sloughed epithelial cells and endogenous secretions.

Ruminants

In cattle, sheep and goats the reticulorumen contains vast numbers of bacteria, ciliate protozoa, phycomycete fungi and bacteriophages. Its bacterial population (Table 1) is about 10^{10}–10^{11} cells ml^{-1} rumen fluid, and its protozoal population some 10^5–10^6 cells ml^{-1}. There are more than 125 morphological types of bacteriophages in the rumen, which outnumber rumen bacteria by two- to tenfold. Rumen fungi (Table 2) can constitute up to 8% of the microbial biomass. The rumen environment is anaerobic, hence virtually all rumen microbes are strict anaerobes or facultative anaerobes.

Rumen protozoa fall into two main groups. The holotrichs, which are ovoid organisms and covered with cilia, include the genera *Isotricha* and *Dasytricha*. The entodiniomorphs include many species that

Table 1. Major groups of rumen bacteria (source: Hespell *et al*., 1997).

Group description	Species
Gram-positive or Gram-variable, straight or curved rods or coccobacilli	*Methanobrevibacter ruminantium, Methanobacterium formicicum, Lachnospira multiparus, Lactobacillus vitulinus, Lactobacillus ruminis, Eubacterium limosum, Eubacterium ruminantium, Eubacterium cellulosolvens, Eubacterium xylanophilum, Clostridium aminophilum, Clostridium pfennigii*
Gram-negative coccus-shaped	*Megasphaera elsdenii, Veillonella parvula, Methanomicrobium mobile, Anaeroplasma abactoclastium, Syntrophococcus sucromutans, Magnoovum eadii, Quinella ovalis*

Table 2. The common genera and species of rumen fungi of sheep and cattle (source: Hespell *et al*., 1997).

Genus	Species
Neocallimastix	*frontalis* *patriciarum* *hurleyensis*
Orpinomyces	*bovis* *joyonii*
Anaeromyces (*Ruminomyces*)	*Anaeromyces mucronatus* *Ruminomyces elegans*

vary in shape, size and appearance, and include the genera *Entodinium*, *Epidinium*, *Diplodium*, *Eudiplodium*, *Ophryoscolex* and *Polyplastron*. Holotrichs utilize sugars and other soluble feed components, whilst the entodiniomorphs depend on particulate food sources such as fibrous particles and bacterial cells.

In ruminants, substantial fermentation of nutrients also occurs in the hindgut (caecum and colon). However, the microflora of their hindgut is not as well understood as that of the rumen. Caecal fermentation in sheep may account for up to 13% and 17% of total methane and volatile fatty acid production, respectively. Under conditions of high cellulose intake, the numbers of cellulolytic bacteria in the caecum of sheep can exceed those of the rumen (Mann and Ørskov, 1973). In Mann and Ørskov's study, the caecal bacterial flora tended to be dominated by Gram-negative rods belonging to the genera *Bacteroides*, *Butyrivibrio* and *Fusobacterium*, with a small proportion of *Streptococcus bovis*, *Streptococcus faecalis* and also bacteria from the genera *Peptostreptococcus*, *Micrococcus* and *Selenomonas*.

Domestic fowl

The alimentary tracts of domestic fowl also harbour an extensive microbiota (Table 3). In general the crop has a preponderance of lactic acid-producing bacteria with no strict anaerobes such as *Bacteroides* species. The proventriculus and gizzard are quite inhospitable environments to microorganisms, due to their low pH (ranging from 1 to 4), therefore microbial proliferation in this region is mainly influenced by their acid tolerance (Mead, 1997). Nevertheless, *Lactobacillus* spp. (up to 10^8 cells g^{-1}) and small numbers of *Escherichia coli*, *Streptococci* and yeasts have been reported. The duodenal and ileal microflora are similar, comprising a mixture of anaerobic and obligate anaerobic bacteria. In the caecal and colonic lumen, mainly obligate anaerobes proliferate, whilst yeasts, moulds and protozoa are rarely found. Poultry have a short colon and it is therefore impossible to differentiate its microflora from those of the caecum. The main factors affecting numbers and species composition of the alimentary tract of chickens are age, diet and the use of microbial feed additives.

Table 3. Microbial species distribution in the regions of the poultry gut (sources: Mead, 1997; Ewing and Cole, 1994).

Alimentary tract region	Genus/species
Crop	*Lactobacillus* (*L. salivarius*), *Streptococcus* spp., *Staphylococcus, Escherichia coli,* yeasts
Duodenum and ileum	*Lactobacillus*, *Streptococcus, Staphylococcus*, *E. coli*, *Clostridium, Eubacterium*, *Propionibacterium, Fusobacterium*
Colon and caecum	*Eubacterium, Clostridium, Fusobacterium, Bacteroides* (*Prevotella*), *Methanogenium, Eubacterium, Bifidobacterium, Gemmiger, Peptostreptococcus*

Pigs

Some of the bacterial species that have been identified in the pig's gut are listed in Table 4. According to Stewart *et al.* (2001), *Lactobacilli* predominate in the pig's stomach and small intestine, whilst *Bacteroides* species tend to be absent from these sections. By contrast, there are similar numbers of *Lactobacilli* and *Bacteroides* in the pig's colon. However, the pig caecal microflora is dominated by *Prevotella ruminicola*, *Selenomonas ruminantium*, *Lactobacillus acidophilus* and *Butyrivibrio* (Stewart *et al.*, 2001). Some cellulose-fermenting strict anaerobes such as *Fibrobacter succinogenes* and *Ruminococcus flavefaciens*, normally found in large numbers in the rumen, have also been isolated from the pig's large intestine. According to Stewart *et al.* (2001) not all known species of gut anaerobic bacteria have been isolated from pigs. *Streptococci* are the main faecal bacteria of pigs, constituting over 25% of all isolates. (SC)

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Table 4. Principal microorganisms isolated from the pig's gut and faeces (sources: Ewing and Cole, 1994; Stewart, 1997; Stewart *et al.*, 2001).

Alimentary tract region	Species
Stomach	*E. coli, Lactobacillus, Streptococcus*
Small intestine	*E. coli, Lactobacillus, Streptococcus*
Caecum and colon	*Eubacterium, Bacteroides (Prevotella), Ruminococcus, Selenomonas, Lactobacillus, Butyrivibrio, Streptococcus, Peptococcus, Peptostreptococcus, Megasphaera elsdenii*
Faeces	*Streptococcus, Lactobacillus, Eubacterium, Fusobacterium, Bacteroides, Peptostreptococcus, Bifidobacterium, Selenomonas, Clostridium, Butyrivibrio, Escherichia, Ruminococcus, Succinivibrio, Veillonella, Propionibacterium*

Stewart, C.S., Hillman, K., Maxwell, F., Kelly, D. and King, T.P. (2001) Recent advances in probiosis in pigs: observations on the microbiology of the pig gut. In: Wiseman, J. and Garnsworthy, P.C. (eds) *Recent Developments in Pig Nutrition 3*. Nottingham University Press, Nottingham, pp. 51–77.

Gastrointestinal tract The gastrointestinal tract (GIT) is a long tube-like structure that extends from mouth to anus (see figure). The inside of the GIT can be considered as outside the body proper. Before food substances can enter the body, they must be broken down into smaller entities by physical, chemical and enzymatic processes collectively called **digestion**. The digested end-products then cross the intestinal epithelium and enter the body: this is called **absorption**.

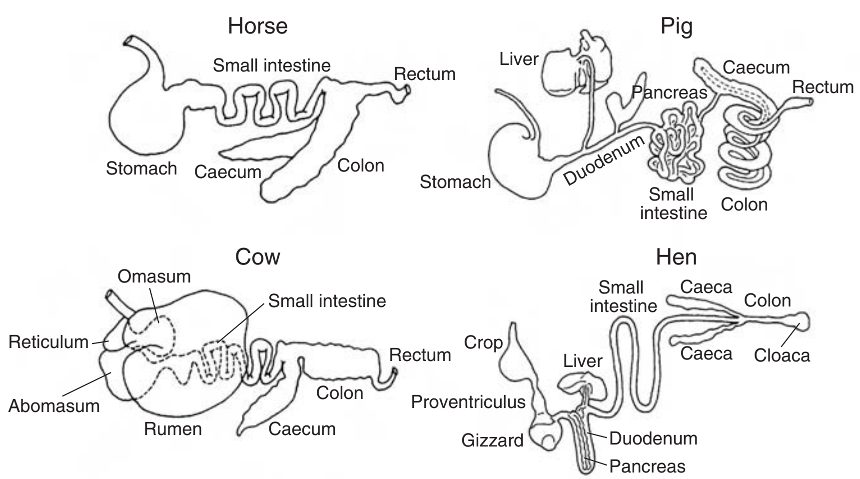
The GIT consists of several compartments and associated organs (**pancreas** and liver) and a large number of different glands. These include the salivary glands in the mouth, glands for producing HCl, pepsinogen, mucus and gastrin in the stomach, glands for producing HCO_3^- , digestive enzymes (or their precursors) and hormones in the pancreas, glands for producing **bile** (solution of bile salts, bilirubin, cholesterol, lecithin and electrolytes) in the liver, and glands for producing HCO_3^- (Brunner's glands) in the duodenum and mucus (**mucin**) throughout the intestines.

The principal parts of the GIT are the mouth (including teeth, tongue and pharynx), oesophagus, stomach, small intestine (sequentially duodenum, jejunum and ileum) and large intestine (sequentially caecum, colon, rectum) and anus. This organization describes the GIT of simple-stomached animals, e.g. the pig.

In ruminants, a **forestomach** (of three parts: reticulum, rumen and omasum) serves as a large fermentation chamber before the food enters the true stomach, called the abomasum.

In avian species, a forestomach (the **crop**) serves as a storage organ. The true stomach is called the **proventriculus** and is followed by another compartment called the **gizzard**. The small intestine ends at the ileocaecocolic junction, from where the digesta can pass into the two caeca or (as can also happen in mammals) directly into the colon. Birds also differ from mammals in that urine is excreted in semi-solid form along with the faeces (with N incorporated in uric acid rather than in urea).

In fish, the morphology varies widely among species. Some species (e.g. Cyprinidae) have no stomach (agastric); however, most species have a stomach, often J-shaped and consisting of a descending cardiac or fundic region and an ascending pyloric region (e.g. Salmonidae). In the eel a gastric caecum extends caudally, whereas in other fishes (e.g. Acipenseridae) the pyloric region is modified into a muscular gizzard-like region which has a special grinding function.



Gastrointestinal tract in various farm animals including the horse (non-ruminant herbivore), the cow (ruminant), the pig (non-ruminant omnivore) and the hen). Adapted from Moran (1982).

The organization and dimensions of the individual compartments have evolved in various ways according to the physical nature and chemical composition of the feed to which the particular animal has become specialized. The adult pig has a stomach of 6–8 l and a relatively long small intestine of 15–20 m. The stomach is only about 4% of body weight whereas in sheep and cattle it is about 25%.

The degradation of nutrients in the GIT is always accompanied by **fermentation from a resident** gastrointestinal microflora, and the development of the GIT has been strongly influenced by this action. Because the host animals can utilize the microbial degradation products from dietary fibre which cannot otherwise be utilized by the animal itself, the microflora has a symbiotic function. This is particularly important for herbivores and omnivores and less important for carnivores. Mammalian farm animals can be separated into the following groups according to their fermentation activity:

1. Pregastric fermenters
a. Ruminants (cow, sheep, goat)
2. Hindgut fermenters
a. Caecal fermenters (rabbit)
b. Colon fermenters
  (i) Sacculated colon (horse, pig)
  (ii) Unsacculated colon (mink)

The relative capacity of the different compartments varies considerably between the different species (see table).

The **digestion** of the food is initiated in the mouth where it is disintegrated by chewing or mastication. Birds have no teeth but may use their beak (and claws) to reduce the size of food components. Furthermore, the action of strong muscles in the wall of the gizzard, often with the help of small stones that are swallowed, reduces particle size and thus compensates for birds' lack of mastication.

During the process of mastication, saliva is added, primarily from three pairs of glands: the submaxilliary, at the base of the tongue; the sublingual, underneath the tongue; and the parotids, below the ear. Some species also have other smaller salivary glands. In the saliva of many animals an α-amylase initiates the enzymatic degradation of starch, and in young (sucking) animals a lipase initiates the degradation of milk lipids. In ruminants the saliva provides a significant source of N (from urea and mucoproteins), P and K which, together with bicarbonate, are essential for the microorganisms in the rumen.

In ruminants, in contrast to most other animals, the ingested food is fermented by microorganisms before it is exposed to the typical processes of digestion, which occur in the true stomach and intestine. The metabolites resulting from fermentation can be absorbed in the rumen. The reticulum functions to move ingested food into the rumen or into the omasum and in regurgitation of ingesta during rumination. The omasum helps to control the passage of digesta into the abomasum.

Some herbivorous non-ruminant animals such as horses and rabbits have a sacculated stomach with quite intensive microbial activity. In the crop of poultry, microbial fermentation may occur together with a continued action of salivary amylase on starch degradation.

In the true stomach (in birds, the proventriculus), HCl and pepsin are secreted, proteins are denatured and partially degraded and microorganisms are killed. Mucus is produced for protecting the gastric wall against the action of HCl and pepsin. Pepsin is secreted in an inactive form and activated by pepsin and HCl. In young sucking mammals rennin, rather than pepsin, is secreted. Rennin, which is also secreted in an inactive form and activated by HCl, coagulates milk by specific cleavages of milk proteins.

Approximate relative capacity of the compartments of the gastrointestinal tract of different farm animals.

	Stomach	Small intestine	Caecum	Colon
Cattle, sheep, goat	70	20	2	8
Horse	10	30	15	45
Pig	30	35	5	30
Dog, cat	65	20	–	15

Shortly after passing through the pylorus into the duodenum, the digesta are mixed with pancreatic juice. This is alkaline and neutralizes the acid digesta from the stomach. It also contains a variety of digestive enzymes from the pancreas, including amylase, proteases, lipases and nucleases for digesting starch, proteins, lipids and nucleic acids. At this point also the hepatic duct brings bile from the liver; bile salts are important for lipid absorption. In the sheep, the pancreatic duct is joined to the hepatic duct.

The surface for absorption in the small intestine is enlarged enormously by folds and by **villi**, which are fingerlike extensions of the gut wall covered with epithelial cells. These cells in turn have microscopic fingerlike extensions called microvilli, which form the **brush border**. It is through these membranes of the epithelial cells that absorption occurs. In the brush border are specific enzymes for hydrolysing oligomers and saccharides into monomers, and other enzymes for hydrolysing oligomer peptides. Dipeptides and tripeptides are mostly absorbed as such and hydrolysed to amino acids in the cytoplasm of the epithelial cells. In each villus is a blood capillary that drains into the portal system which goes directly to the liver.

The morphology of the small intestine is affected by the gut microflora. Small intestines are heavier in conventional than in **germ-free** chickens. The brush border is wider in germ-free birds and the area per unit of gut is greater.

The large intestine consists of caecum, colon and rectum. Dimensions vary greatly, depending on diet. Non-ruminant herbivores generally have a capacious large intestine. Horses and ostriches have a large colon whereas rabbits have a relatively large caecum. Often animals with a big caecum, e.g. the rabbit, practise coprophagy (or more accurately caecotrophy), which is a redigestion of soft faeces, which are excreted during the night and which have a high content of microbial protein and vitamins, with less fibre than the hard faeces excreted in the daytime. The caeca of birds are two blind sacs which have some fermentative capacity but this is often of little nutritional importance.

The main site of cellulose breakdown in horses is the colon, as well as the stomach. Horses and ruminants differ from most other species of mammals in their capacity to absorb nutrients through the epithelium of the large intestine. (SB)

Further reading

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Gavage: *see* Force feeding

Geese: *see* Goose

Gelatin A protein prepared from bones, skin etc. It is devoid of tryptophan. (MFF)

Genotype The term genotype refers to a combination of genes that are found within a species, giving rise to consistent identifiable breed characteristics. The Global Databank contains information on almost 4000 breeds within 28 domesticated animal species. There is enormous genetic diversity within species, affecting a wide range of traits related to body size and conformation, physiology, biochemistry, disease resistance etc. For example, over 350 breeds of pig have been identified, of which almost half originated in Asia. One of the most obvious characteristics is colour and at least 25 different colour-related alleles have been identified within the pig population. In poultry, sex-linked genes creating yellow and a variety of red, brown and black patterns in the down of day-old chicks allow colour-sexing in brown-feathered layers and some broilers. Coat colour and length (or, in the case of birds, feather colour and cover) can be important adaptations to particular environments. For example, in domestic poultry a major gene reduces body feather cover by 25–30% and is useful in enhancing broiler performance in hot climates.

Within species certain breeds have particular production traits, which have been exploited by genetic selection. Cattle are used mainly for production of meat, milk or both, although they were traditionally used as draught animals and still are in developing economies. Certain breeds, e.g. Charolais, are more suited to fast lean growth and reach high mature weights and are thus particularly suitable for beef production. Others, such as Holstein and Ayrshire, are less suitable for meat production but produce high milk yields and the small dairy breeds (Jersey and Guernsey) are noted for high contents of butterfat in the milk. Within the cattle population there are two main subspecies, *Bos taurus*, the main source of domesticated breeds in Europe and North America, and *Bos indicus*, source of many breeds in Asia and Africa. *Bos indicus* has a very different body shape from *B. taurus*, with a shoulder hump, pendulous dewlap and a higher number of sweat glands which help the animal to survive much better in hot conditions.

Commercial domestic fowl have been selected, especially over the last 40 years, for either egg or meat production. Most egg-laying strains produce eggs with white or brown shells. The world market is split almost equally between white and brown shells. Egg-laying breeds of low mature body weight have been intensively selected to increase egg numbers while keeping the **maintenance** energy requirements low to improve production efficiency. On the other hand the larger breeds have been selected for high food intake leading to fast efficient growth. The skin of the majority of chickens is white or yellow. Some markets prefer a meat chicken with a yellow skin and this can be enhanced by feeding a diet high in xanthophylls or other yellow pigments.

Mature size differences are a common feature in all species. For example, many of the hill sheep breeds are small, thus reducing energy requirements in times of food shortage; lowland breeds may be twice as large. Similarly, within the horse species, there is a range of pony breeds on the one hand in contrast to the large draught horses such as Shire, with stallions weighing up to 1000 kg.

One danger arising from intensive selection of a few breeds with particular production traits is the possibility of losing breeds and thus diminishing the genetic pool. This has been particularly noticeable with pigs and domestic chickens, where breeding programmes tend to be dominated worldwide by a handful of breeders. One good example of the economic benefit of maintaining genetic diversity is in the increasing use of the Chinese Meishan pig in crossbreeding programmes to introduce improved prolificacy and mothering qualities into the more efficient Landrace breeds that have dominated because of fast, efficient production of lean meat.

(KJMcC, KDS)

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Genotype–nutrition interaction The performance of a trait by individuals or groups of animals of one breed or strain – the phenotype – is determined by the response of the genotype to the environment. Environment in the broadest context includes all aspects of husbandry and management from conception or incubation, and includes nutrition. The performance of an individual is an example of an interaction between a specific genotype and nutrient intake from a specific feed formulation. When a flock or herd of one breed or strain is considered there is variation in the genotype, because even siblings are not clones. Each individual has a unique assembly of genes. Given a situation in which all other aspects of environment are the same, groups of animals receiving the same nutrient intake may be expected to differ in performance; this is the result of an interaction between the genotype and the nutrients consumed. Given that there will be variation in the nutrients in different samples of feed (i.e. the samples that individuals consume each day) the interaction between the genotype and feed can be considered as the normal variability of performance. The practice of nutrition – formulation, feed compounding and feed distribution – attempts to minimize the variability of nutrient intake between individuals and the contribution it makes to phenotypic variance. These types of interaction are often referred to as micro-environmental. The subject is the individual, whose experience of the nutritional conditions is independent of conditions encountered by other members of the flock or herd.

Important genotype–nutrition (G × N) interactions occur when large genotype differences are combined with large differences in nutrient supply. The changes in nutrient supply do not directly change the response of each genotype in the same manner. The change in performance is not predictable from the average genotype and nutritional effects; in other words the effects are non-additive and an interaction has occurred. The interaction demonstrates how gene expression may be changed by differences in nutrient supply. The following discussion will focus on poultry to provide examples of the types of interaction that occur; however, similar interactions occur in mammalian species and indeed the phenotypic variations are at least as large, due to the fact that mammalian females give birth to only one or up to 12 offspring at a time.

Horst (1985) examined 181 experiment reports, over the period 1938–1981, for various genotype × environment (G × E) interactions in laying hens. Of these experiments, 81 involved genotype and feeding and 37 (about 50%) reported the presence of an interaction. The traits showing interactions were body weight, age at sexual maturity, egg production, egg weight, albumen quality, shell quality, fertility and hatchability and mortality. These traits cover a wide range of heritability levels but the magnitude of the interactions was generally greater in traits with lower heritability. Thus there is a negative association between a high G × E interaction and a lower heritability. However, since heritability is a ratio between additive variance and phenotypic variance, a large G × E interaction would indicate a high non-heritable variation rather than a lack of heritable variation (Cahaner, 1990). Equally important is the fact that important economic traits – body weight, egg production, egg weight, age at first egg, and albumen quality – demonstrate a change in performance that may not be predicted by known input–output relationships.

There are numerous complex relationships involved and three are highlighted below.

Carcass quality

Integrated broiler production and processing companies have the opportunity to use breed packages (parent stock from the same breeding company) or to choose male and female parents from different breeding companies, in order to maximize profits from the products they supply to the various markets. Extensive breed and breed-cross evaluation trials are conducted by some integrators. Breed choice decisions are based on live performance of parents and broilers and the end-product yields and quality. G × N interactions have been demonstrated in studies on **carcass** meat yields involving breeds and breed crosses. After producing a short list of breeds or crosses, following extensive screening of breed candidates, further evaluation of feed nutrient levels is required to tailor the feeding programmes. The least-cost feed formulations can then be targeted to achieve optimum performance in the final product, be it whole carcass, pieces or a meat product. Increasingly, decisions on feed formulations to optimize feeding of commercial broilers are based on computer modelling. Awareness of G × N interactions is therefore crucial to the reliability of decisions based on the model technique.

Immunoresponsiveness

In general, selection for faster growth has reduced immunoresponsiveness to pathogens. Responses by different genotypes indicate that resource allocation to general fitness has decreased as that to growth has increased. Various G × N interactions, such as those between feeding methods and broiler genotypes (post-inoculation lesion scores to *Escherichia coli* challenge; Boa-Amponsem *et al.*, 1991) and feed nutrient content and broiler versus layer genotypes (antibody titres to sheep red blood cells, and heterophil:lymphocyte ratios; Praharaj *et al.*, 1995), indicate that feeding regimes need to be tailored to optimize disease resistance (the phenotype) for specific genotypes. Deviations from the optimum nutrition would predispose susceptible genotypes to adverse thermal and gaseous environmental and infectious agent challenges.

Feed intake

There are differences among breeds of laying hens in the response of **feed intake**, and therefore **energy intake**, to changes in dietary energy content. In general, lighter breeds are able to adjust feed intake to maintain a constant energy intake whereas heavier breeds have a lesser ability for adjustment and show an increasing energy intake as dietary energy content increases. At a basic level of least-cost formulation of feeds it is important to establish the feed intake characteristics of a commercial layer. This relationship is then included in the formulation constraints and the outcome is least-cost feeding rather than least-cost per weight of feed. This is possible in cage operations where feed delivery is mechanized, often quantitatively accurately, for the expected performance of a layer. Extensive production systems, where layers are expected to scavenge for a portion of their daily requirements, may not be suitable for layers bred for cage systems. Those with a small appetite may not be able to consume adequate nutrients for production and maintenance of an efficient immune system. Laying hens bred for cages have under-performed in scavenging situations and have been out-performed by scavenging breeds (e.g. Sørensen, 1999). (WKS)

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Gentiobiose Disaccharide (molecular weight 342) of two β-linked (1→6) glucose units, in pyranose ring form; it is an enzymatic or chemical degradation product of 1→6 β-linked D-glucose side chains of β-linked-D-glucans. Gentiobiose is found in brown marine algae, cereals, moulds, yeasts, lichens and bacteria. It is not metabolized by endogenous enzymes of non-ruminants. (JAM)
See also: Carbohydrates; Oligosaccharides

Geophagia A fixated appetite for soil, common in some farm animal species, particularly cattle, but with high individuality. Although the intake of elements from ingested soil can be significant, their availability is often low due to the elements being chelated in the soil matrix. Indeed, addition of certain soils to the diet, and in particular zeolites, can reduce the absorption of some toxic elements. Health risks exist when soils with potentially pathogenic microorganisms or toxic metals are consumed. Many pathogenic bacteria survive in soil for considerable periods of time, sometimes in a dormant state, until consumed by a suitable host. Soil around metal workings or smelters is likely to contain potentially lethal concentrations of heavy metals, in particular lead. (CJCP)

Germ-free animals Animals raised entirely free of microorganisms. Animals are normally sterile whilst in the uterus or the egg but acquire their first microorganisms during birth or hatching. To maintain a germ-free status, mammals are delivered by caesarean section or delivered naturally with special sterile precautions. Birds can more easily be reared germ-free by disinfecting the outsides of the eggs and hatching them in a sterile incubator. After birth or hatching, germ-free animals are kept continuously in a sterile enclosure, with filtered air and water and sterilized food, passed in through an air-lock. The main uses of germ-free animals are in disease research but they are also used in nutrition studies when the influence of the **gastrointestinal microflora** is to be studied. As a result of their lack of commensal gut flora, the gastrointestinal tracts of germ-free animals tend to be enlarged and anatomically different from those of conventional animals. (MFF)

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Germination Seed germination requires moisture, oxygen and a suitable temperature (optimum 30°C). Seeds absorb water, raising the moisture content from 10% to 40%. Protein and nucleic acid synthesis increase. Proteases and amylases catalyse the breakdown of the endosperm for translocation of nutrients, with starch in the endosperm being converted to dextrins, maltose and other sugars. Germination increases the lysine and sugar contents but decreases the starch and fibre contents of the seeds, with no other major change in composition. In malting, seeds are germinated for the purpose of brewing. The by-products, which include malt culms, brewers' grains, brewers' yeast and draff, are used for animal feed. (JKM)

Gestation: *see* Cow pregnancy; Ewe pregnancy

Gestation period The time (usually expressed in days) from conception to giving birth in viviparous animals. The gestation periods (in days) for farm animal species are:

Cattle (*Bos taurus*):	279–290
Cattle (*Bos indicus*):	282–292
Sheep:	144–152
Goats:	144–151
Pigs:	112–117
Horses:	310–365
Red deer:	225–245
Buffalo:	310–330
Bactrian camel:	370–440
Dromedary:	355–390
Llama:	330–340
Rabbit	30–32

(PJHB)

Gills Organs whose primary purpose is to obtain dissolved oxygen from water. They may also transfer inorganic ions or excrete wastes. They are filamentous processes of the pharynx of fishes, but aquatic invertebrates possess a variety of functionally analogous structures (e.g. ctenidia in the molluscan mantle cavity). In teleosts, gill filaments radiating laterally from the pharyngeal arches bear 10–30 interdigitating lamellae where respiratory exchange occurs. The gill area may range from 150 to 2000 $mm^2\ g^{-1}$ body weight. (RHP)

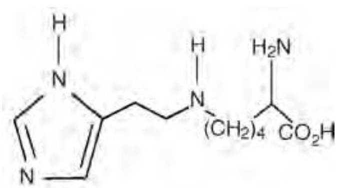
Gilt A young female pig. In the growing phase, gilts have a protein deposition rate and feed intake which is intermediate between those of castrates and entire males. The term gilt is also commonly used for young breeding sows during their first pregnancy and lactation. During this time, an additional allowance of nutrients must be made for their continuing growth. (SAE)

Gilthead sea bream (*Sparus aurata*) A species that ranges from the Mediterranean and Black Sea to the eastern Atlantic Ocean from the southern part of the British Isles to Senegal. Sea bream is farmed in several Mediterranean countries; Greece, Turkey and Spain are the major producers. Juvenile fish (1–5 g) are stocked in either sea cages or land-based tanks and earthen ponds. They

reach a market size of 400–500 g over a period of 12–14 months. Gilthead sea bream are hermaphrodites and develop as males during the first year. After the spawning season, the males begin to develop ovaries until early autumn. At this stage, fish either develop as females or absorb the ovarian tissues and redevelop male gonads. (SPL)
See also: Marine fish

Gizzard Sometimes known as the muscular stomach or ventriculus, present in birds but also found in some fish and invertebrates, the gizzard is a large, bulbous, muscular organ located adjacent and distal to the proventriculus, lying partially between the lobes of the liver in the upper left-hand side of the abdominal cavity in birds. When the gizzard is empty, food and grit pass directly through the crop to the proventriculus. In adult domestic fowl, the gizzard measures about 5 cm in diameter and 2.5 cm in thickness and has a smooth, nonstriated musculature rich in myoglobin. The inner aspect of the gizzard is of a hardened keratinoid membrane with a cuticle occasionally referred to as the 'koilin layer'. The asymmetrical arrangement of the muscles in the gizzard rotates as well as crushes and grinds the food like mill-stones. Aided by the gastric secretions from the proventriculus, this ground food passes through the pyloric valve into the first section of the small intestine, the duodenum. The characteristic green or yellow colour of the gizzard is caused by regurgitation of bile from the duodenum via the pylorus. Some studies suggest that the gizzard may be under diurnal rhythm control, with activity being reduced during darkness. (MMax)

Gizzerosine $C_{11}H_{20}N_4O_2$, molecular weight 240. A dipeptide-like compound of histamine and lysine, formed by Maillard browning reactions during the heating of proteins, notably fish meal.



Gizzerosine causes gizzard erosion in poultry, characterized by necrosis of the lining tissue with ulceration of the muscle wall. Gizzard erosion may also be caused by consumption of grains contaminated with mycotoxins. (DRG)

Globe artichoke *Cynara scolymus*, a member of the *Compositae* family. Globe artichokes are grown for the immature flower buds, which are used as human food. The fleshy bases of the flower bracts and the receptacle to which the bracts are attached are known as the 'heart'. Commercially produced fresh globe artichokes are commonly found on the market all year round. They may be available for animal feed due to oversupply or inferior quality. They can be fed to dairy and beef cattle at 30% and to ewes at 20% of total diet. The dry matter content of globe artichokes is 150 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 32.7, crude fibre 54, ether extract 1.5, ash 11.3 and starch and sugar 105, with GE 197 MJ kg^{-1}. (JKM)

Globulins One of the three major classes of plasma proteins (albumin, globulin and fibrinogen). The globulins are further subdivided into four identifiable forms: α_1, α_2, β and γ. The γ-globulin proteins comprise the well-known antibody fraction of plasma proteins. (NJB)

Glucagon A polypeptide hormone of 29 amino acids synthesized by α cells in the islets of Langerhans of the endocrine pancreas. Glucagon is the major metabolic hormone that is released in response to low concentrations of blood glucose. It acts through a cyclic-adenosine monophosphate (cAMP)-mediated intracellular pathway to stimulate the breakdown of glycogen in liver, thereby elevating blood glucose levels. (GG)

Glucanase A class of enzymes that hydrolyse glucans involving either one or several types of linkages. Typical glucanases include 1,3-β-D-glucanase, 1,4-β-D-glucanase, 1,6-β-D-glucanase, 1,3-α-D-glucanase, 1,6-α-D-glucanase (dextranase), cellulase and lichenase. Different enzymes vary markedly in their substrate specificity, some being highly specific for a particular bond, others actively hydrolysing several different bonds. They are produced by bacteria, yeast and fungi. (NJB)

Glucans Homopolysaccharides of linear or branched glucose residues, α- or β-linked, with molecular weight 20,000–1,000,000. The β-linked D-glucopyranose polymers are found as constituents of fungi, algae and higher plants, such as cellulose, callose, curdlan, laminaran, lichenan and β-glucans in cereals; α-linked D-glucopyranose polymers are found as constituents of moulds, yeasts, lichens, bacteria, higher plants and animal tissues and include amylose, amylopectin, glycogen, pullulan and dextran. Animals have endogenous α-amylases but not β-amylases, but β-glucans are degraded by intestinal bacteria. (JAM)
See also: Carbohydrates; Dietary fibre; Starch

Glucoamylase A glycolytic enzyme (exo-1,4-α-glucosidase; 1,4-α-D-glucan glucohydrolase; EC 3.2.1.3) that cleaves glucose from maltose, maltotriose and other polymers of glucose in α(1–4)-linkage. A number of industrial enzymes with this activity, purified from microorganisms, are called amyloglucosidase. (SB)

Glucocorticoids Steroid hormones that are made from cholesterol in the adrenal cortex. In the rat, corticosterone is the glucocorticoid that promotes gluconeogenesis. In humans, cortisol is the glucocorticoid that promotes gluconeogenesis. Glucocorticoids increase gluconeogenesis most likely because they increase protein breakdown and amino acid catabolism, making the amino acid carbon available to the liver for glucose production. (NJB)

Glucofructans Includes fructo-oligosaccharides, both naturally occurring and those produced from fructans such as inulin. All naturally occurring fructans are really glucofructans, because the reducing end of the fructose chain is glycosylated to the reducing end of a glucose molecule. (JAM)
See also: Carbohydrates; Dietary fibre; Fructans; Raffinose

Glucokinase One of two enzymes involved in converting glucose to glucose-6-phosphate in the cytoplasm. Glucokinase is housed in the liver while hexokinase, the other enzyme, is in muscle. Both of these enzymes are involved in sequestering glucose into the cell by converting glucose to glucose-6-phosphate, which lowers the potential loss of glucose from the cell by diffusion because it is no longer glucose. The k_m of glucokinase for glucose is such that variations in the activity of the enzyme change with glucose concentration in the physiological range. Thus, short-term regulation of the activity of the enzyme is built into the system by the k_m and changes in the amount (activity) of enzyme are not dependent on changes in its synthesis or degradation. (NJB)

Gluconeogenesis The process whereby glucose is biosynthesized from products derived from glucose (lactate), from sugars that are not glucose (e.g. ribose), from the glycerol portion of triacylglycerols, from some amino acids or from breakdown products that provide four (propionate, aspartate) or five (glutamate) carbon intermediates to the citric acid cycle. Gluconeogenesis occurs in both the liver and kidneys. It is normally a cyclic process that occurs after consumption of a meal when substrates enter the body faster than they are catabolized. Thus, some of the extra energy can be stored in glucose that can then be incorporated into glycogen (a glucose polymer) in liver and muscle. Amino acids can provide carbon for gluconeogenesis in starving animals because visceral and muscle protein is being used as a fuel and some of the amino acids provide carbon for glucose production. Amino acids that can provide pyruvate carbon (serine, glycine, alanine, cysteine, threonine, tryptophan) can be net producers of glucose because pryuvate can be converted to a four-carbon intermediate (oxaloacetate) which is a net producer of glucose carbon. Methionine, valine, isoleucine, phenylalanine and tyrosine are gluconeogenic because they provide other four-carbon intermediates (fumarate and succinate). Glutamate, histidine, proline and arginine are gluconeogenic because they can provide carbon for a five-carbon intermediate (α-ketoglutarate). The process of gluconeogenesis provides a means whereby in starvation a steady supply of glucose can be provided for tissues that require it by conversion of amino acids derived from protein breakdown into newly formed glucose. (NJB)

Glucose $C_6H_{12}O_6$. D-Glucose is a central metabolite in animal metabolism. It is a primary metabolic fuel and can be stored as glycogen in the liver (1–5% of the wet weight) and muscle (~ 1% of the wet weight). It is the major energy substrate used by the brain and in cases where glucose becomes limiting can lead to serious physiological consequences. In cases where glucose catabolism is slowed, and fat catabolism increased, animals such as the lactating cow are often found to have ketosis, a metabolic problem which can be fatal.

Glucose can provide carbon for all the organic molecules in the body with the exception of essential fatty acids, essential amino acids and vitamins. The glucose in starch makes up more than one-half the gross energy of grains. The other glucose polymer in plants, cellulose, is a structural element in the cell walls of grasses and grains. Starch can be digested and used by ruminant and non-ruminant animals. Cellulose can be hydrolysed to glucose by some rumen bacteria and then used as a source of energy by many bacteria. Cellulose can be partially digested and used by non-ruminants via fermentation in the caecum and large intestine. Horses and rabbits may digest 40% or more of some forms of cellulose in the lower intestine. The end-products of fermentation (acetate, propionate and butyrate) are taken up by the liver and activated to their CoA forms. In this form they are able to contribute to the energy budget of the animal. Absorbed glucose is a major source of food energy in non-ruminant animals. A unique metabolic capability in animals (anaerobic glycolysis) allows glucose, unlike other metabolites, to provide a limited amount of energy (8 mol ATP mol^{-1} glucose) when oxygen becomes limiting. The lactate produced is returned to the liver where it is reconverted to glucose (*see* **Cori cycle**). When oxygen is available in sufficient amounts, glucose can be totally oxidized to carbon dioxide and water ($C_6H_{12}O_6 \rightarrow 6\ CO_2 + 6\ H_2O$) yielding a total of 38 mol ATP mol^{-1} glucose catabolized. Glucose metabolism via the pentose phosphate pathway meets a number of other essential needs in animal metabolism. First, it is a source of D-ribose or 2-deoxy-D-ribose, the sugar(s) required for the nucleosides incorporated into both RNA and DNA, as well as the D-ribose required for vitamin co-factors such as NAD, NADP, FAD, CoA and B_{12}. Secondly, ribose is part of ATP, a critical co-substrate in cellular energy metabolism. Glucose carbon, via serine, glycine and betaine, can be a source of the one-carbon units in the folate system. Glucose carbon can provide the glycine required for the biosynthesis of purine bases needed for *de novo* synthesis of RNA and DNA. The other important product from the pentose phosphate pathway is NADPH, which is used as to reduce the double bonds produced in the *de novo* biosynthesis of fatty acids. The carbon in glycerol in triacylglycerols is derived totally from glucose. Thus, the reducing equivalents (NADPH) and carbon used in *de novo* synthesis of fat are totally derived from glucose. Glucose can provide the carbon skeleton for the dispensable amino acids serine, glycine (via serine), alanine, cysteine (via serine), aspartic acid, glutamic acid, proline and ornithine (via glutamic acid), arginine (via ornithine) and the methyl carbon of methionine. Glucose can provide all of the carbon for the steroid hormones, some of the carbon for peptide hormones but none of the carbon for hormones derived from the essential amino acids, histidine, tyrosine (via phenylalanine), tryptophan or the essential fatty acids. Glucose is the carbon source for creatine and for part of carnitine. (NJB)

Glucose tolerance The response of plasma glucose concentration to an oral bolus of glucose. In 70 kg non-ruminant animals doses of 50–75 g of glucose are used. In a non-diabetic animal plasma glucose concentration reaches a peak about 30 min after the bolus and then returns to the original concentration by 2 h. Diabetics have basal blood glucose levels that may be 1.5 times normal: in response to a bolus, glucose concentration may double by 1.5–2.0 h and then only slowly return to the original elevated level. (NJB)

Glucosidase A general class of hydrolytic enzymes that cleave glucose units from oligosaccharides, polysaccharides and a vast array of non-carbohydrate substrates. The term does not distinguish between those enzymes that hydrolyse glucose connected via α- or β-linkages to the hydroxyl group on the other molecule. Enzymes in this broad group are produced by essentially all living animal and plant matter and include digestive enzymes and lysosomal enzymes. (NJB)

Glucosides Derivatives of glucose produced by the condensation of the anomeric hydroxyl group of glucose with the hydroxyl group of another carbohydrate molecule or non-carbohydrate moiety, thereby linking the two by an ether bond. (NJB)

Glucosinolates Thioglycosides that yield isothiocyanate, nitrile or thiocyanate upon hydrolysis of the aglycone. Glucosinolates occur in many cultivated plants and in particular the genus *Brassica* (cabbage, broccoli, kale, rapeseed, mustard and turnips); these may be referred to as glucobrassicans. Other examples of glucosinolate-containing plants are *Amoracia* (horseradish), *Crambe*, *Limnanthes* (meadowfoam), *Nasturtium* (watercress), *Raphanus* (radish) and *Thlaspi* (stinkweed). The most important source of glucosinolates in animal nutrition is rapeseed (*Brassica napus*).

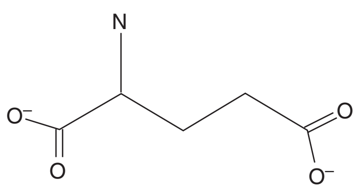
Glucosinolates are hydrolysed by enzymes known as glucosinolases, thioglucosidases or myrosinases. These enzymes are found in the plant and released upon mastication, or produced by rumen microorganisms. Hydrolysis of the glucosinolates yields glucose, hydrogen sulphate and some form of isothiocyanate, thiocyanate or nitrile, depending on the attached aglycone.

The major effect of glucosinolates in animal nutrition is that the metabolic products inhibit the function of the thyroid gland. Enlarged thyroids and growth depression are observed in poultry and pigs. Other effects include leg protrusion, reduced egg production and quality and liver damage in poultry. Pigs may have enlarged livers. (DRG)

Glucuronic acid A derivative of glucose, $C_6H_{10}O_7$, molecular weight 194, in which carbon 6 of glucose is oxidized to a carboxylic acid. In animal tissues, it is produced by dehydrogenation of uridine diphosphate (UDP) glucose. The acid group is ionized at pH 7 and so it usually exists *in vivo* as glucuronate. Glucuronic acid is a constituent of glycosaminoglycans such as hyaluronic acid and chondroitin sulphate, which form the extracellular matrix of connective tissues in many animal tissues. Dermatan sulphate, an important connective tissue proteoglycan, contains β-D-glucuronic acid and its carbon-five epimer α-L-iduronic acid. Glycosaminoglycans are covalently linked to extracellular proteins to form proteoglycans. Heparin has repeating units of D-glucuronic acid, usually sulphated at carbon two, and a sulphated glucosamine. Glucuronidation, conjugation of glucuronate, using UDP-glucuronate as the glucuronosyl donor, with foreign compounds, e.g. toxins or drugs, is a major detoxifying mechanism in animals; a more polar compound is produced that can be cleared more effectively by the kidney. Reduction of D-glucuronate by NADPH to L-glucuronic acid is the first step in ascorbic acid synthesis in plants and animals other than primates and guinea pigs. D-Glucuronic acid is produced by action of an oxygenase on inositol, the first step in the metabolism of inositol in animal tissues. Glucuronic acid is also a constituent of some bacterial and plant polysaccharides, though galacturonic acid is the predominant uronic acid in plants. (JAM)

See also: Carbohydrates; Dietary fibre; Pectic substances; Uronans; Uronic acids

Glutamate The anionic form of L-glutamic acid, $^{-}OOC{\cdot}(CH_2)_2{\cdot}CHNH_3^{+}{\cdot}COO^{-}$, which is a dispensable five-carbon dicarboxylic amino acid found in proteins. It is involved as an amino ($-NH_2$) donor in conversion of the keto-acid precursors of both dispensable and indispensable amino acids to their respective L-amino acids. When glutamate donates its nitrogen it becomes the citric acid cycle intermediate α-ketoglutarate $^{-}OOC{\cdot}(CH_2)_2{\cdot}CO{\cdot}COO^{-}$. Glutamate is the amino acid involved in nitrogen movement between amino acids and their keto-acid precursors. As α-ketoglutarate it takes up ammonium nitrogen to become glutamate, providing a means whereby non-amino acid N can be incorporated into amino acids. In this way animals can use non-amino acid nitrogen (urea-N, NH_4^+, NH_4Cl, ammonium citrate etc.) as a source of N for *de novo* amino acid biosynthesis. Glutamate plays a critical role in N excretion by the urea cycle. It is the critical intermediate for taking up ammonium-N (NH_4^+) and for releasing amino acid-N to NH_4^+, and for the transamination of the α-amino N (-NH_2) from amino acids to oxaloacetate ($^-OOC·CH_2·CO·COO^-$) to form aspartate ($^-OOC·CH_2·CHNH_4^+·COO^-$), which provides one of the two nitrogens in urea. It is also the indirect means whereby amino acid N, which is usually transaminated, can be converted to the ammonium-N required for the synthesis of carbamyl phosphate, a precursor of one of the nitrogens in urea.

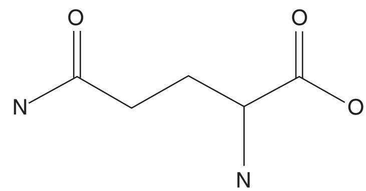


(NJB, DHB)

Glutamate dehydrogenase A liver enzyme involved in utilizing or producing ammonium N which can be utilized by incorporating it into α-ketoglutarate to form L-glutamate ($NH_4^+ + {}^-OOC·(CH_2)_2·CO·COO^- \rightarrow {}^-OOC·(CH_2)_2·CHNH_4^+·COO^-$). This N can then be transaminated to keto acid precursors of the various L-amino acids. Production of ammonium-N from L-glutamate is the reverse reaction. Glutamate dehydrogenase enzyme is found in many tissues. (NJB)

Glutamic acid: *see* Glutamate

Glutamine An amino acid found in protein ($H_2N·CO·(CH_2)_2·NH_2–COOH$, molecular weight 146.2). It is synthesized in the body from glutamic acid and ammonia via the enzyme glutamine synthetase. Glutamine contains both an amino and an amide nitrogen group. In the kidney, glutamine synthesis from glutamic acid, or its degradation to glutamic acid, involves uptake or release of free NH_4^+, and this process is under homeostatic control for regulation of acid–base balance. Glutamine is also synthesized in muscle tissue and much of the muscle glutamine is exported to the gut, where deamidation takes place. A considerable portion of the resulting glutamate is either transaminated to alanine and α-ketoglutarate or deaminated to α-ketoglutarate and NH_4^+. α-Ketoglutarate is thought to be an important energy source for the gut.



(DHB)

See also: Glutamate

Glutamyltransferase γ-Glutamyltransferase is an enzyme involved in transporting some amino acids across membranes in the kidney and liver. The amino acid is converted to the γ-glutamyl amino acid by reaction with glutathione (γ-glutamylcysteinylglycine). The reaction is AA + GSH → γ-glutamyl-AA + cysteinylglycine. The amino acid is released and the GSH resynthesized. (NJB)

Glutathione A tripeptide, γ-glutamylcysteinylglycine, found throughout the body. It is found as reduced glutathione (GSH) and oxidized glutathione (GSSG). It is the substrate for several enzymes. The enzyme glutathione reductase is involved in converting GSSG to GSH, i.e. GSSG + NADPH + H^+ → 2GSH + $NADP^+$. Under oxidizing conditions, cysteine in a polypeptide chain may be oxidized to form a cystine bridge. This may be required for the activity of the protein or render it inoperative. Reduced glutathione can react with one of the cysteines to make a GSH–cysteine mixed disulphide. Another GSH can react with this mixed disulphide to form oxidized glutathione (GSSG) and the cysteine in the polypeptide chain, thus restoring cysteine to its original form. Reduced glutathione also plays a role in protection against oxidative damage via its role as a substrate for the enzyme glutathione peroxidase. This same system is involved in reducing lipoperoxides produced by oxygen-dependent reactions catalysed by iron and copper. When involved in protection against oxygen damage, α-tocopherol becomes an α-tocopherol radical. GSH can react with the radical and regenerate α-tocopherol. Glutathione as a substrate for the glutathione *S*-transferase plays a role in detoxifiying various xenobiotics. In these systems glutathione reacts with the the xenobiotic (R) to form a product that can be excreted, i.e. R + GSH → R-SG. (NJB)

Glutathione peroxidase (GPX) A selenium-containing enzyme found in erythrocytes and many other tissues. It has selenocysteine at its active centre. The enzyme protects the cellular environment by destroying peroxides produced as a result of oxidative metabolism. The reaction for the destruction of hydrogen peroxide is 2GSH + HOOH → CSSG + $2H_2O$. In order for this system to function, the oxidized glutathione (GSSG) produced must be reconverted to reduced glutathione (GSH) by the following reaction: GSSG + NADPH + H^+ → 2GSH + $NADP^+$. The NADPH required for the this reaction is produced by glucose metabolism in the pentose cycle. (NJB)

Gluten The mixture of proteins in the endosperm of cereals. Cereal proteins are largely concentrated in the starch-rich endosperm, with the remainder in the bran and germ (e.g. 72%, 20% and 8% of total proteins, respectively). The most important grain proteins of the endosperm are prolamin (gliadin) and glutelin (glutenin) and are regarded as storage proteins. The amino acid composition of the proteins varies; for example, lysine concentration is about three times higher in glutelin than in prolamin. Wheat gluten contains high concentrations of the amino acids glutamic acid and proline (33% and 12% of total amino acids, respectively). The protein matrix is closely associated with the starch granules of the endosperm and is important in determining grain hardness. The concentration and type of gluten in wheat determine the baking qualities of wheat flours, giving dough that may be soft and extensible, or tough and elastic, or intermediate. Gluten has elastic properties that are important in bread making but that may limit cereals in the diets of ruminants. The properties of gluten may be the main reason why livestock find wheat unpalatable when finely ground. Wheat gluten, particularly if finely ground, forms a sticky dough and may lead to digestive upsets. (ED)

Further reading

Givens, D.I., Clarke, P., Jacklin, D., Moss, A.R. and Savery, C.R. (1993) *Nutritional Aspects of Cereals, Cereal Grain By-products and Cereal Straws for Ruminants*. HGCA Research Review No. 24. HGCA, London, 180 pp.

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D. and Morgan, C.A. (1995) *Animal Nutrition*, 5th edn. Longman, Harlow, UK, 607 pp.

Glutenin Also called glutelin, one of the main proteins in the endosperm of cereal grains. The collective term ‘gluten’, the mixture of proteins in the endosperm of wheat and other cereal grains, includes the four main proteins: glutenin, gliadins (prolamin), albumins and globulins. The glutenins and gliadins generally account for 75–80% of total gluten proteins. The amino acid composition of the proteins is variable: glutenin generally contains one-third less of the amino acid lysine than gliadin. Inter- and intramolecular disulphide linkages result in linear molecules of glutenins of either high or low molecular weight. While both molecular weight molecules are important, it is those of high molecular weight that have been directly related to the quality of wheat flour for bread making. Maize glutelin, occurring in the endosperm and germ, is the second main type of protein found in maize kernels. Although its concentration is lower than zein protein (main type), it does contain higher levels of the two essential amino acids lysine and tryptophan. (ED)

Further reading

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D. and Morgan, C.A. (1995) *Animal Nutrition*, 5th edn. Longman, Harlow, UK, 607 pp.

Glycerol The carbohydrate backbone ($CH_2OH{\cdot}CHOH{\cdot}CH_2OH$) of neutral fats (triacylglycerols) and of phospholipids (i.e. phosphatidylcholine, phosphatidylethanolamine etc.). Glycerol is derived from glucose catabolism via intermediate production of dihydroxyactone phosphate in the cytoplasm of the liver and other tissues. Dihydroxyactone phosphate can be reduced to glycerol-3-phosphate which can be used directly in triacylglycerol (neutral fat) and related syntheses. In neutral fat synthesis, two activated fatty acids (acyl-CoAs) react with *sn*-glycerol-3-phosphate to form a 1,2-diacylglycerol phosphate. After dephosphorylation, the diacylglycerol reacts with one acyl-CoA to form one triacylglycerol. In another important metabolic role, glycerol-3-phosphate is the starting material for synthesis of surfactant (*sn*1,2 dipalmitoyl lecithin) in which the two fatty acids of phosphatidylcholine (also called lecithin) are the 16-carbon saturated fatty acid palmitic acid. Glycerol, as glycerol-3-phosphate, is the starting material for the synthesis of a number of phospholipids, phosphatidylcholine, phosphatidylethanolamine, phosphatidylserine and phosphatidylinositol. These products are critical components of membranes and phosphatidylinositol is a precursor of the second messenger, inositol triphosphate.

Although the structure of glycerol shown above appears symmetrical, enzymes that react with it treat the 1 and 3 carbon atoms differently. This requires a specific nomenclature, such that the positions 1, 2, 3 are noted by stereochemical notation, *sn* 1, *sn* 2 and *sn* 3, respectively. The *sn* 3 position is the position which is phosphorylated, and in milk fat it is the position in which a medium-chain fatty acid is found. Lingual lipase and pregastric esterases release fatty acids from the *sn* 3 position of glycerol.

Free glycerol can be activated by glycerol kinase to form glycerol-3-phosphate in one or more tissues. Glycerol-3-phosphate can be a source of glucose carbon as well as the glycerol portion of neutral fat. Glycerol from neutral fat is the only portion of fat that is a net contributor of carbon to gluconeogenesis.

(NJB)

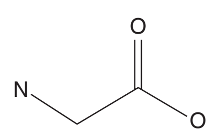
See also: Lipid metabolism; Gluconeogenesis

Key reference

Mayes, P.A. (2000) Oxidation of fatty acids: ketogenesis (pp. 238–249); Gluconeogenesis and control of blood glucose (pp. 208–218). In: Murray, R.K., Granner, D.K., Mayes, P.A. and Rodwell, V.W. (eds) *Harper's Biochemistry*, 25th edn. Appleton and Lange, Stamford, Connecticut.

Glycerolipids Lipids in which glycerol is connected to fatty acids by an ester bond. They differ from sphingolipids (which involve an ester bond between the hydroxyl of serine and palmitate) and cholesterol esters (with long-chain saturated or unsaturated fatty acids), both of which are classified as lipids but do not have glycerol as a component. (NJB)

Glycine An amino acid found in protein ($H_2N{\cdot}CH_2{\cdot}COOH$, molecular weight 75.1). It is synthesized in the body primarily from serine. In addition to its use in protein synthesis, glycine is used for synthesis of purines (including uric acid, the main nitrogenous excretory product in birds), creatine, haem, glutathione and various glycine conjugates. In collagen, the most abundant protein in the body, glycine makes up about one third of the amino acids. Serine, which is synthesized from glucose and an amino donor, can be converted to glycine by exchange of the hydroxy methyl group and glycine back to serine. This serine hydroxymethyltransferase-catalysed reaction (serine → glycine) is thought to be the most important source of *de novo* methyl group synthesis in the body.



(DHB)

See also: Serine

Glycocholic acid One of the bile acids which is a conjugate of cholic acid and glycine. It is formed from 7α-hydroxycholesterol via conversion to cholyl-CoA which reacts with glycine to form glycocholic acid.

(NJB)

Glycogen A glucose polymer with no fixed molecular weight $(C_6H_{10}O_5)_n$. It is a storage form of carbohydrate, found in measurable quantities in liver and muscle. Glycogen is a branched structure which has 10–15 α-D-glucopyranose units linked in α(1→4) glycosidic bonds after an 1→6 branch point where another series of 10–15 units are connected followed by another α(1→6) branch point. Because of the way glucose units are added to the glycogen structure, the last glucose molecule deposited is the first one to be released. Hence, glycogen does not act as a simple mixed pool.

Liver glycogen varies from as much as 4–6% of the wet weight of the liver soon after a meal (~ 2 h) to a trace 8–10 h after a meal. In muscle the variation in glycogen concentration is much less, being ~ 1% after a meal to traces by 8–10 h after a meal. The composition and size of the meal would be expected to have an effect on tissue glycogen concentration. If one takes the example of a 100 kg pig with a metabolic rate of 16,670 kJ day^{-1} (3980 kcal day^{-1}), the amount of glycogen in storage after a meal ($\frac{1}{4}$ in liver, $\frac{3}{4}$ in muscle), if totally used, could meet the animal's energy needs for about 13.4 h (~ 500 g at 17.4 kJ g^{-1} at 4.15 kcal g^{-1}).

Glycogen is synthesized in liver and muscle from glucose as glucose-6-phosphate. In the liver, glucose-6-phosphate can come from glucose taken up by the cell or from the metabolic production of glucose-6-phosphate in the process of gluconeogenesis. In muscle, glucose-6-phosphate is produced from glucose taken up by the cell. Glucose-6-phosphate, when converted to glucose-1-phosphate, is added to the glycogen molecule, making the glycogen molecule longer by one glucose molecule. Release of glucose from glycogen (glycogenolysis) involves the enzyme phosphorylase, which utilizes inorganic phosphate and releases glycogen-glucose as glucose-1-phosphate from the linear chain of α(1→4) linkages. Because glycogen is branched, hydrolysis of the α(1→6) branch must be broken by the debranching enzyme for the phosphorylase to complete the total hydrolysis of glycogen to glucose-1-phosphate. To be used for ATP production, glucose-1-phosphate must be converted to glucose-6-phosphate, so glucose from glycogen yields the 39 ATP equivalents while free glucose provides 38 ATP. (NJB)

See also: Gluconeogenesis; Glycogenolysis

Key reference

Mores, P.A. (2000) Metabolism of glycogen. In: Murray, R.K., Granner, D.K., Mayes, P.A. and Rodwell, V.W. (eds) *Harper's Biochemistry*, 25th edn. Appleton and Lange, Stamford, Connecticut, pp. 199–207.

Glycogenesis The process whereby glucose units can be stored in liver or muscle cells as the polymer glycogen. The glucose used in the process can come from the diet or can be derived by the process of gluconeogenesis in which non-glucose carbon can be converted into glucose in the liver and kidneys. (NJB)

Glycogenolysis The breakdown of glycogen in the liver, kidney or muscle to glucose-1-phosphate. Glucose-1-phosphate is converted to glucose-6-phosphate, which is a source of metabolic energy in the form of ATP. Glycogen in liver and kidney can be a source of energy for other organs after glucose-6-phosphatase hydrolyses glucose-6-phosphate to inorganic phosphate and free glucose. Muscle cannot release glucose from glycogen as free glucose for distribution to other tissues because it lacks the enzyme glucose-6-phosphatase. (NJB)

Glycolipids Modified sphingosines in which long-chain fatty acids are added to form ceramide. Ceramide can be altered by addition of one or more sugars (glucose or galactose). These glycosphingolipids are found in all tissues in the body but higher concentrations are found in nervous tissue. They are found in the outer leaflet of the cell membrane and contribute to the carbohydrates on the cell surface. (NJB)

Glycolysis The process whereby glucose in the form of glucose-6-phosphate is catabolized to pyruvate in the cytoplasm of cells. Glucose-6-phosphate is derived from glucose taken up by cells and converted to glucose-6-phosphate by glucokinase or by breakdown of glycogen with the conversion of the glucose-1-phosphate to glucose-6-phosphate. Under aerobic conditions, the pyruvate produced by glycolysis can be converted to acetyl-CoA and be further oxidized to CO_2 and H_2O in the mitochondrion. Under anaerobic conditions, the catabolism of glucose-6-phosphate in the cytoplasm produces NADH which is later converted to NAD when pyruvate is reduced to lactate. Regeneration of NAD is essential for the continued catabolism of glucose-6-phosphate. Anaerobic glycolysis results in the accumulation of glucose carbon in lactate. In this way ATP can still be produced from glucose when oxygen is not available. This process can only continue as long as glucose-6-phosphate is available and the cellular pH does not decrease (due to lactate accumulation) to a level that alters enzyme activity. Under normal aerobic conditions, glucose yields 38 ATPs in its conversion to CO_2 and H_2O. Under anaerobic glycolytic conditions where glucose-6-phosphate is converted to lactate, only eight ATPs can be produced. This ability to provide ATP under conditions of limited oxygen is a unique property of glucose catabolism. (NJB)

Glycosidases Enzymes involved in hydrolysing monosaccharides (or modifications of them) from glycoproteins. The enzymes cleave either terminal units (exoglycosidases) or specific linkages along the chains (endoglycosidases). For example, galactosidase is an exoglycosidase that removes the terminal galactose from an oligosaccharide chain. Endoglycosidases cleave at specific *N*-acetyl-glucosamine or *N*-acetyl-galactosamine sites in the oligosaccharide. They can also cleave sugars from non-carbohydrate substrates such as purines, pyrimidines, anthocyanins and flavolols. (NJB)

Glycosides Compounds formed by condensation of the hydroxyl group of the anomeric carbon of a monosaccharide with another compound that may or may not be another monosaccharide. If the unit attaching to the hydroxyl group is not a monosaccharide it is identified as an aglycone. These may be alcohols, glycerol, sterols, phenols or others such as the purine bases. (NJB)

Glycosylation The process by which sugar residues are attached to a protein to form a glycoprotein. Glycoproteins have many critical functions in the body. Proteins that end up in the plasma membrane or are secreted from the cell pass through the secretory pathway, which is composed of the endoplasmic reticulum and the Golgi apparatus, before reaching their final destination. Many such proteins become glycosylated during their movement through the secretory pathway. Glycosylation occurs only on certain residues in a protein, such as O-linked threonine and N-linked asparagines, and only some of these residues are glycosylated. Sugar residues are specifically added in highly complex structures containing many glucose, mannose or other sugar residues. All cell types display on their cell surface proteins that are imbedded in, or associated with, the cell's plasma membrane. Many of these proteins are glycoproteins which have crucial roles in cell–cell and cell–ligand (e.g. hormone) interactions. Blood type differences are due to the variation in cell surface glycoproteins on the red cell plasma membrane. The mucus secreted by epithelial cells in the mouth or intestine is largely composed of glycoproteins. The glycoproteins in mucus are essential for its properties as a lubricant. Some of the soluble proteins in the blood, such as antibodies (immunoglobulins) or some hormones, are glycosylated. Additional extracellular proteins that are glycosylated include collagen and other proteins that make up the scaffolding (extracellular matrix) that allows cells to form tissues. Glycoproteins can contain from as little as 4% of their weight as carbohydrate to as much as 60% or more. In diabetes, high levels of glucose can lead to glycation of haemoglobin but this does not occur through the normal process of glycosylation. (RSE)

Gnotobiotic animals Animals raised entirely free of microorganisms and subsequently infected with known organisms. The main uses of gnotobiotic animals are in disease research but they are also used in nutrition research when the influence of the **gastrointestinal microflora** is to be studied. (MFF)
See also: Germ-free animals

GnRH Gonadotrophin-releasing hormone, a decapeptide produced in the hypothalamus. GnRH acts upon the anterior pituitary to bring about the release of the gonadotrophins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH). (JRS)

Goat feeding Goats are ruminants and thus feed on plant material. They graze grass and other low-growing plants, as do cattle and sheep, but, given the opportunity, they will also readily browse the leaves and branches of accessible trees and shrubs not normally eaten by those species. They are generally more selective in their food preferences than other domesticated ruminants and will not eat, for example, mouldy hay or feed that has been contaminated with faeces. They are fastidious in their selection of plants and parts of plants, but also adapt readily to the available food sources. Given a wide choice of plant species, goats will tend to concentrate on those plants commonly regarded as weeds, such as willowherb (*Epilobium* spp.), rushes (*Juncus* spp.), thistles (*Carduus* spp.), blackberry (*Rubus* spp.) and gorse (*Ulex* spp.), in preference to sown grass and clover, though clover flowers are avidly consumed.

On sown pastures, which are frequently mixtures of ryegrass (*Lolium* spp.) and clover (*Trifolium* spp.), goats require a higher sward surface height (i.e. taller pasture) than do sheep if they are to achieve the levels of herbage intake required for good performance. While sheep will perform well on pastures with a sward surface height of 4–6 cm, goats require a sward height of around 8–9 cm. Sward management for goats is thus more akin to that needed for cattle than sheep. On unimproved indigenous pastures with a wide variety of plant species, goats select a diet markedly different from that grazed by sheep, and there is thus considerable scope for the complementary grazing of the two species; indeed, goats have been used in such situations to improve the quality of grazing for the benefit of sheep. Goats utilize medium to high quality foods (organic matter digestibilities of 0.6 or higher) with an efficiency similar to that of sheep, but with lower quality foods they are able to maintain higher digestibilities than sheep, possibly because of higher concentrations of rumen ammonia, slower rates of passage of digesta through the alimentary tract and greater rumen volumes. They are thus better adapted than most other ruminants to survive, and indeed thrive, in adverse nutritional environments.

The feeding of goats must take account not only of size (i.e. body weight) and physiological state (e.g. pregnancy or lactation), but also of the products for which the animals are farmed. Goats kept for commercial milk production require substantially higher levels of nutrition than Angora or cashmere goats farmed primarily for fibre production. The goat's diet must also be balanced in terms of energy, protein, vitamins and minerals.

Many of the larger dairy-goat farms house their animals all the year round to obviate the need to use anthelmintics to control stomach worms picked up from infected pasture. (Milk from animals treated with anthelmintics, antibiotics, etc., is not allowed to be sold for human consumption for some time following treatment.) On these farms the goats are generally fed forage *ad libitum* in the form of hay, freshly cut grass or, more commonly nowadays, grass or maize silage, supplemented with cereal-based concentrates. Maize silage is preferable to silage made from grass, as the feeding of the latter entails the risk of listeriosis, a disease carried by a soil-borne organism. The concentrate part of the diet is usually fed in the milking parlour to enable the quantity offered to be rationed in relation to the individual's level of milk production. In the case of high-yielding goats (producing more than, say, 1000 kg of milk per lactation) substantial quantities of concentrates may need to be fed to meet the animal's nutritional requirements, but is important to ensure that the total diet contains at least 40% roughage. Examples of suitable diets for dairy goats are: for a 70 kg doe producing 5 kg milk day^{-1}, 1.5 kg good quality hay, 2.0 kg kale, 0.5 kg dried sugarbeet pulp and 1.25 kg high energy concentrate; and for a 60 kg doe producing 3 kg milk day^{-1}, 1.2 kg good quality hay, 0.4 kg dried sugarbeet pulp and 1.4 kg medium energy concentrate (Mowlem, 1988).

Fibre goats kept primarily for fibre production have lower nutrient requirements than dairy goats. They generally acquire most of their nutrients from grazing and browsing, as there is no necessity to avoid the use of anthelmintics to control internal parasites. Some supplementary feeding is generally supplied during late pregnancy and early lactation.

Angora goats, which produce mohair and are shorn twice a year, may need to be housed for at least part of the year, depending on climatic conditions. In such situations the needs of non-pregnant, non-lactating animals can be met wholly from conserved forage, but in late pregnancy and during lactation some supplementary concentrates (about 0.5 kg day^{-1}, depending on the quality of the forage offered) will be required. The nutrient requirement for the growth of, say, 4–5 kg mohair year^{-1} is comparatively small and similar to that required for wool growth in sheep. Mohair production is affected by nutrition, and particularly by the level of dietary protein; high levels of feeding increase the weight of mohair produced but also increase the diameter of the fibre, i.e. there is an inverse relationship between fibre quantity and quality. The value of mohair produced per animal can therefore be regulated, at least to some extent, by feeding. The valuable fibre from cashmere goats is harvested only once a year, in the spring, by either combing or shearing. Where climatic conditions allow, cashmere goats are kept outdoors for at least the greater part of the year and obtain their nutrients from grazing, with some supplementary feeding being provided in late pregnancy and early lactation. The nutrient requirements for fibre production in cashmere goats are negligible and can be ignored in calculating dietary regimes. In contrast to mohair, the weight and diameter of the fine undercoat of cashmere goats is not influenced by dietary factors, though nutrition does affect the weight of the coarse outer coat or guard hair. There is thus no reason to restrict feeding in the expectation of improving fibre quality.

Angora and cashmere goat kids are reared naturally, suckling their dams until weaning at 3–4 months old. In dairy-goat herds, however, most kids, whether intended for herd replacements or for meat, are taken away from their dams at 1–2 days old, after receiving colostrum, and are artificially reared on a proprietary milk replacer. This may be offered *ad libitum* for the first 4–6 weeks or restricted to about 1 kg per kid per day, supplied twice daily. Thereafter the amount of milk replacer may be gradually reduced until the kids are weaned at 6–10 weeks old. A high-protein concentrate (16–18% crude protein) and good quality hay should be offered *ad libitum* from 2–3 weeks of age. By weaning, kids should be consuming 0.4–0.5 kg concentrate day^{-1}, at which level the concentrate input can be restricted but the hay or other suitable conserved forage should continue to be fed *ad libitum*. Comprehensive information on the energy, protein, vitamin and mineral requirements of goats for maintenance, growth, pregnancy and the production of milk and fibre is contained in the AFRC TCORN Report No. 10 (1997). (AJFR)

References

AFRC TCORN Report (1997) *Agricultural and Food Research Council, Technical Committee on Responses to Nutrients, Report no. 10.* CAB International, Wallingford, UK, 118 pp.

Mowlem, A. (1988) *Goat Farming.* Farming Press, Ipswich, UK, 183 pp.

Goats Goats are hollow-horned ruminant mammals of the family Bovidae. Evidence of the domestication of goats has been found in Neolithic sites at Jericho dating from 7000 BC; other sources claim domestication of goats dates from 9000 BC. The domestic goat, *Capra hircus*, is now found throughout the world and is absent from only the extreme polar regions. It is thought to derive from the so-called Persian wild goat or bezoar, *Capra aegagrus*, found in Turkey, Iran and western Afghanistan. The world population of goats is estimated at around 490 million (Russel and Mowlem, 1999).

Some breeds of goats and sheep look similar. Generally, but not infallibly, the two species can be differentiated by the fact the goats tend to carry their tails erect, whereas sheep's tails hang down. Male goats have a very distinctive odour, quite different from that of rams; and rams, but not goats, have a secretory gland on their hind feet. The definitive difference, though not visible, is that goats have 60 chromosomes and sheep have

54. Male goats are known as bucks or billies; female goats are generally termed either does or nannies. The young are kids, and juvenile females (generally between 1 and 2 years old) are referred to as goatlings. The term yearling is also applied to juveniles of either sex.

Goats are truly dual-purpose animals. Most of the world's goat population is kept for the production of meat and milk. Some breeds, such as the Sannen, the Anglo-Nubian and the alpine breeds, have been selected for high levels of milk production, and yields of more than 1000 kg year^{-1} are not uncommon. The world record milk yield of 3506 kg in one lactation is held by a British Sannen (Mowlem, 1988).

Other breeds are kept principally for fibre production, the best known being the Angora, which produces mohair (not to be confused with the fibre 'angora' that comes from a breed of rabbit). Mohair is a long, lustrous and generally white fibre that is harvested by shearing the goats every 6 months. Annual levels of production (from two shearings) are generally between 4 and 6 kg. The diameter of the fibre increases with age, from < 25 microns (μm) at the first shearing to 35 μm or greater at about 4 years of age. Angora goats are single-coated, i.e. they produce only one type of fibre, though many fleeces contain a small proportion of coarse chalky fibres, or kemps, which is regarded as a fault.

Cashmere goats are also farmed for their fibre. Unlike the Angora, which is a single breed, there are many distinct breeds of cashmere goats, the characteristics of which have been reviewed by Millar (1986). Cashmere goats are all double-coated, having an outer coat of coarse medullated guard hair and an undercoat, referred to variously as cashmere, down, pashm or pashmina, of fine unmedullated fibres. The mean diameter of cashmere fibres is typically around 15 μm, ranging from about 13 to 18 μm. Cashmere is harvested once a year, in the spring, either by combing the goats after they begin to moult, or by shearing. The combed fibre still contains a proportion of guard hair, although clearly much less than the fibre harvested by shearing. After harvesting, the two fibre types are separated by a specialized process known as dehairing. The weight of dehaired cashmere produced per goat ranges from about 150 g to < 400 g, those with the higher levels of production generally producing coarser fibre.

Whereas sheep prefer to graze plant material close to the ground, goats readily browse on leaves and small branches of trees and shrubs. Given a choice of plant species, goats tend to concentrate on those plants that are commonly regarded as undesirable (e.g. thistles (*Carduus* spp.), gorse (*Ulex* spp.), blackberry (*Rubus* spp.) and willowherb (*Epilobium* spp.) in preference to sown pasture species. There is thus considerable scope for the complementary grazing of goats and sheep on certain vegetation types, and particularly on the indigenous plant communities found on unimproved hill land. Concentrates are frequently fed to high-yielding dairy goats but it is recommended that their diet should contain a minimum of 40% roughage. In many of the larger dairy units the goats are housed all year round to minimize the risk of infection with internal parasites, as milk cannot be sold for human consumption for some time after the animals have been treated with anthelmintics. In these units the goats are generally fed forage *ad libitum,* supplemented in most cases with concentrates. Fibre-producing goats, particularly cashmere goats, are generally kept outdoors and receive supplementary feeding during late pregnancy and early lactation.

Goats are seasonally polyoestrus, with females coming into heat at regular intervals during the breeding season which, in the northern hemisphere, extends from about August to February. Female kids become sexually mature at about 6 months of age but are often not mated until they are approximately 18 months old, or until they have attained 75% of their mature weight. Male kids can attain sexual maturity between 3 and 6 months of age and are therefore frequently weaned when they are about 12 weeks old. The oestrous cycle is about 21 days and oestrus generally lasts for 1–2 days. Gestation length varies from about 146 to 156 days and averages some 150 days. Dairy goats have an extended lactation, milking continuously for more than 18 months, and in some cases are mated only once every 2 years. Fibre-producing goats, which suckle their kids, have shorter lactations of 12–16 weeks and are mated each year.

Goats are susceptible to similar ranges of bacterial and viral diseases, metabolic disorders and parasitic infections as in sheep. Where clostridial diseases are endemic these are generally controlled by vaccination. Goats tend to be more susceptible than sheep to helminth infections. These can be controlled by the same spectrum of anthelmintics as is commonly used in sheep. (AJFR)

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Goblet cells Specialized cells in the epithelial layer of villi. These cells produce mucus consisting of mucopolysaccharides (**mucin**), which protect the epithelium against degradation by the luminal digestive enzymes. In birds, numerous goblet cells substitute for **Brunner's glands**, which are lacking in their duodenum. (SB)

Goitre A condition characterized by enlargement of the thyroid gland as the body attempts to increase production of thyroid hormone. Generally this condition occurs because of iodine deficiency, or the presence of goitrogens in the diet, which interfere with iodine utilization. (JPG)

See also: Hypothyroidism; Iodine

Goitrogen A compound that interferes with the synthesis or secretion of thyroid hormones and causes hypothyroidism. Goitrogens fall into two main categories. (i) Cyanogenic goitrogens impair iodide uptake by the thyroid gland. Cyanogenic glucosides can be found in many feeds, including cassava, linseed, raw soybeans, beet pulp, maize, sweet potato, white clover and millet. Once ingested, they are metabolized to thiocyanate and isothiocyanate. These compounds alter iodide transport across the thyroid follicular cell membrane, reducing iodide uptake and retention by the thyroid gland. This effect is easily overcome by increasing dietary iodine. (ii) Progoitrins and goitrins (thiuracils) found in cruciferous plants (rape, kale, cabbage, turnips, mustard) and aliphatic disulphides (onions) inhibit thyroperoxidase, preventing formation of mono- and diiodotyrosine and the condensation reactions necessary to synthesize thyroid hormone. With goitrins, especially those of the thiouracil type, hormone synthesis may not be readily restored to normal by dietary iodine supplementation and the offending feedstuff needs to be reduced or removed from the diet. (JPG, CJCP)

See also: Goitre; Hypothyroidism; Iodine

Gonadotrophins A group of glycoprotein hormones involved in the control of reproduction. Follicle-stimulating hormone (FSH) and luteinizing hormone (LH) are produced by the anterior pituitary. Chorionic gonadotrophins are produced by the chorion, the outer membrane surrounding the developing embryo. (JRS)

Goose Geese were domesticated over 5500 years ago, probably by the Egyptians. Commercial breeds belong to the genus *Anser* and are descended from the wild swan goose, *Anser cygnoides* and/or *Anser anser*, the greylag goose (Romanov, 1999). In some European countries geese are traditional Christmas fare. They grow rapidly and some breeds reach a mature body weight of over 15 kg, with the gander (male) much heavier than the goose (female). They are farmed for their meat, liver fat, down and feathers. Geese make excellent watchdogs and are also used to control weeds in a variety of crops; they have been particularly effective in controlling the rapidly spreading water hyacinth. Geese are hardy, have a long life span, and are resistant to many avian diseases. Their disadvantage is their generally low reproductive rate and low hatchability. Currently, China is the largest producer of goose meat with over 200 million birds producing 1.8 million metric tonnes (t) out of a world production of 2.1 Mt. In 2001, Ukraine produced 97,200 t, Egypt 42,200 t, Hungary 34,500 t and Taiwan 30,000 t.

Of the 59 breeds of geese, the majority are found in the Eastern European countries. The European and Asian domesticated breeds probably originated from two species of the greylag goose: the western (*Anser anser anser*) and the eastern (*Anser anser rubriostris*). The most common breeds are the giant White Emden (10–15 kg), the Grey Toulouse, the African, and the small White and Brown Chinese, characterized by a large prominent knob on the head and weighing only 4.5–5.5 kg. Geese are seasonal breeders and do not come into lay until around 40–50 weeks of age. Some strains of Toulouse geese produce 150 eggs per year; most breeds lay only 40–60 eggs. Egg weight (120–170 g) varies according to breed but gradually increases during the laying season. For breeding, the ratio of ganders to geese is 1:4 to 1:6. They should be run together for about 6 weeks before they will breed. Fertility (< 70%) is low compared with other poultry species, while hatchability in incubators is normally about 80%. Consequently only about 60 goslings hatch from 100 eggs. A goose can incubate 9–12 eggs, taking 31 days to hatch. Geese make excellent mothers. The Large Grey goose is popular in Europe, because it grows rapidly and can be made to produce large fatty livers.

The growth of geese is the most rapid of the poultry species. At 4 weeks of age they are 40% of their adult weight, compared with 15% for meat chickens and 5% for turkeys. Shown in Table 1 are body weights and feed conversion ratios of three genotypes – medium (M), heavy (H) and crossbred of M (maternal) and H – and of two sexes, raised under intensive conditions, given a high quality diet (230 kg crude protein and 12.3 MJ apparent metabolizable energy kg^{-1}) and grown to 105 days.

The most rapid growth in males and females occurs at 30–35 days of age; these genotypes have mature weights of 6.9 kg for ganders and 5.7 kg for geese.

The meat of geese is fatter than that of other poultry species. The fat is mainly in the skin (> 500 g kg^{-1}) and only 110 g kg^{-1} in the carcass. Breast meat, relative to body weight, is about 9.5% of body weight at 7 weeks, increasing to 18% (1.3 kg) at 16 weeks in geese weighing 6.9 kg. Only about 75% of the carcass is meat, the rest being skin and bone. Breast meat yield and carcass characteristics of the geese in the previous table at 105 days are shown in Table 2.

Table 1. Liveweight (g) of geese of three different genotypes and the two sexes at different ages (Wittman, 1997).

Age (days)	Medium	Crossbred	Heavy	Males	Females
0	111	95	124		
21	1657	1646	1959	1808	1688
49	4579	4843	5693	5318	4495
63	5012	5267	6197	6224	4952
77	6112	6179	7952	6954	6154
105	6800	6944	8739	7710	6879
Feed conversion ratio:					
Day 1–21	1.38	1.41	1.43		
Day 22–105	5.45	5.42	4.9		

Table 2. Carcass composition of three breeds of geese and two sexes at 105 days.

	Medium	Crossbred	Heavy	Male	Female
Carcass weight (g)	4479	4613	5799	5067	4668
Dressing (%)	65.7	66.7	66.4	65.4	68.0
Breast (%)	28.8	28	28.1	28.3	28.3
Thigh (%)	21.8	21.1	20.8	20.6	22.1
Abdominal fat (%)	7.6	6.4	6.8	6.9	6.9

Dressing percentage is lower than found in chickens (72%) and breast meat yield considerably higher, although these comparisons are made at different physiological ages. Carcass analysis of ganders and geese weighing 6.53 and 5.68 kg, respectively, gave identical fat (281–299 g kg^{-1}) and crude protein (CP) contents (145–150 g kg^{-1}) (Stevenson, 1985).

Force-feeding of both ducks and geese, practised in Ancient Egypt 4500 years ago, is now banned in several countries. The aim is to produce a liver of about 600 g from which *pâté de fois gras* is manufactured. This delicacy has unique organoleptic properties. Goose liver is said to be of superior quality for making *foie gras* compared with **ducks**. The livers of force-fed geese can weigh over 1 kg. France is the largest consumer of liver fat at 15,000 t per year: most of this is from ducks but about 800,000 geese are killed for their fatty livers each year. Hungary and Israel are large producers, the latter using around 700,000 geese annually. China is poised to be a very big producer of liver fat in a joint venture arrangement with France. Goslings are force-fed several times a day for 14–35 days when 9–12 weeks of age. Diets range from only moist maize to a more balanced diet with protein sources and oil. An example of a liver production trial in Israel in which goslings were force-fed a wet mash for 23–24 days from 9 weeks old is given in Table 3.

The lipid content of liver from force-fed geese varies greatly but increases, as liver weight increases, to well over 50%. In contrast, the liver of a normal young gosling weighs about 100 g, with only 5% lipid.

Geese are also kept for their down and feathers. A goose weighing 5 kg will produce about 400 g, but factors such as genotype, age, diet and frequency of plucking will determine yield. After China, which has the largest geese and duck populations, Hungary is the biggest producer of feathers and down with 7% of the global market share estimated to be over 60,000 t per year. There may be three or more pluckings and yield increases as the geese get older.

Geese are excellent survivors and can be farmed out-of-doors with a minimum of shelter and care. There are many small gaggles free-ranged on smallholdings throughout the world, and often with ponds which also provide a refuge from foxes. Geese in China are managed in small and large numbers with freedom to go out-of-doors. If eggs are artificially incubated, the goslings need artificial heat for the first 2 weeks. Indoor lighting should be low to stop feather stripping. Geese utilize grass and weeds very effectively and can survive with a minimum of supplementary feeding or sometimes none, though productivity under these circumstances is low.

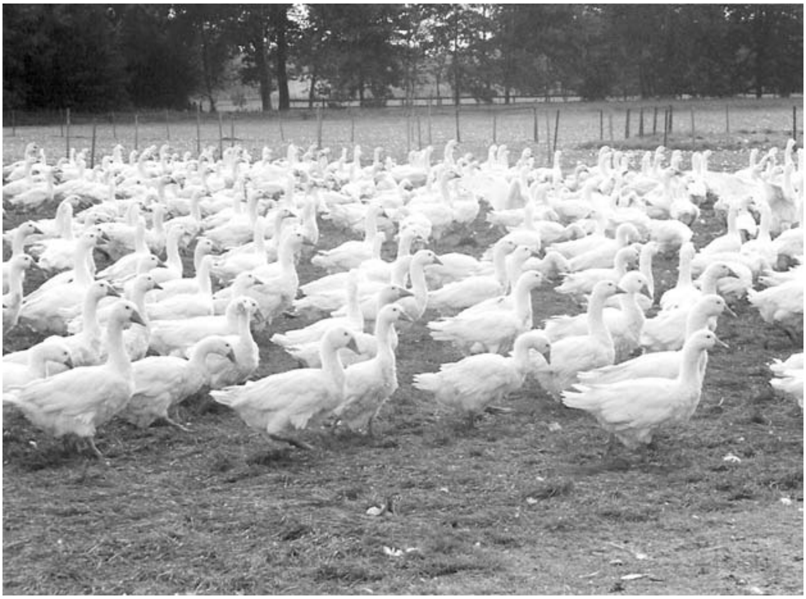
There is some debate as to how well geese can utilize forage. Their ability to digest fibre is limited and it follows that, if they are going to grow and lay on pasture, it must be of high quality. The determined apparent metabolizable energy (AME) and digestible components of rye grass with 157 g CP kg^{-1} when offered to geese, Pekin ducks and their cross (Mulards) are shown in Table 4.

They also utilize grass seeds, and scavenge for insects, snails, larvae etc. Semi-intensive systems, in which good quality pasture is supplemented with grain or concentrates, allow excellent growth of goslings. In Europe, particularly in Hungary and Poland, geese are produced in intensive systems on deep litter (straw). Houses may be fully enclosed or have an outside fenced yard.

Little is known about the nutrient requirements of geese for meat and egg production. Growth rate and protein deposition of goslings is very rapid, especially during the first 4 weeks (reaching almost 3 kg) and their

Table 3. Liver and body weight of goslings force-fed a wet mash at 9 weeks for 23–24 days.

	Body weight (g)			Liver weight (g)	Fattening time (days)	Feed intake (kg)
	Initial	Final	Gain			
Males	3763	7582	3818	862	24	19.44
Females	3270	6760	3490	808	23	17.96



Good quality pasture, supplemented with grain or concentrates, allows excellent growth of goslings.

Table 4. Apparent digestibility (%) and metabolizable energy (AME) of components of rye grass given to geese and ducks.

Species	Digestibility of organic matter	Digestibility of crude protein	Digestibility of crude fibre	Digestibility of NDF	AME (MJ kg^{-1} DM)
Geese	39.5	54.1	16.3	16.3	6.1
Pekin ducks	39.6	28.1	21.1	21.1	7.2
Mulards	45.7	19.1	22.1	26.1	6.7

diets have similar or lower specification to those of broiler chickens in the starter period (1–21 days): 230 g CP kg^{-1} and 12.5 MJ AME kg^{-1}. At 7 weeks, protein retained in feathers (80–90 g kg^{-1}) is 33% of the total, and 50% of that in the carcass (Nitsan *et al.*, 1981), considerably higher than in chickens or turkeys. From research in the USA, recommendations for CP were 200, 160 and 140g kg^{-1} for 0–4, 5–6 and 7–9 weeks, respectively. Goslings given diets with different energy concentrations (11, 12 and 13 MJ AME kg^{-1}) with CP concentrations of 200 g kg^{-1} in starter diets (0–4 weeks) and 160 g kg^{-1} in finisher diets (5–9 weeks) had similar body weights at 4 and 9 weeks. With increasing dietary energy concentration, food intake declined but energy intake increased and efficiency of energy utilization also increased. The starter diet did not influence performance in the grower period (Stevenson, 1985). Goslings were therefore able to cope with a wide range of dietary energy concentrations. Eviscerated carcass yield was similar between the sexes at 630g kg^{-1}, as was breast meat yield (140–150 g kg^{-1}). Requirements have been published for a few essential nutrients. They are generally lower than for broilers, reflecting differences in body composition. Geese breeder diets are also of lower nutrient specification than those of high-producing laying hens and there are recommended specifications in the literature. When duck breeder diets fed to geese were supplemented with additional vitamins, including A, D and E, fertility in young and old geese improved from 72 to 81%, and 40 to 55%, respectively; hatchability also increased considerably. (DF)

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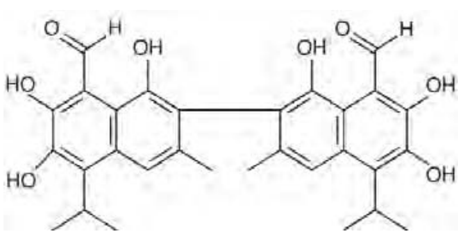
Gossypol $C_{30}H_{30}O_8$, molecular weight 518. A yellow polyphenolic compound found naturally in the pigment glands of cotton (*Gossypium* spp.). Gossypol is the predominant polyphenolic pigment but at least 15 other compounds of similar structure are present, which may be yellow, purple, blue or green. Gossypol can be found in cottonseed meal used as a protein supplement after oil extraction.

Gossypol may bind to proteins, reducing their nutritional availability. General effects of gossypol toxicity include depressed appetite and loss of body weight, cardiac irregularity and laboured breathing. Reproduction in both males and females may be impaired. In poultry, gossypol toxicity causes olive-green yolks in eggs and decreased egg hatchability. Toxicity of gossypol may be either acute or chronic, as the biological effects of gossypol are cumulative. Gossypol also binds minerals, especially iron. Iron salts can be added to help to bind gossypol and limit the depletion of minerals. Use of whole cottonseed or cottonseed meal should be restricted, to limit the possibility of gossypol toxicity. (DRG)



Gossypose: *see* Raffinose

Grain Also called a caryopsis, grain is the edible seed of a grass, especially a cereal plant. Cereal grains comprise the embryo ('germ') and endosperm, surrounded by three protective layers (aleurone, testa and pericarp), together known as bran. Starch, as amylose and amylopectin, is the main carbohydrate present in cereal grains and occurs in the form of granules. The endosperm also contains proteins, which increase in concentration from the centre outwards. (ED)
See also: Barley; Maize; Oats; Rye; Triticale; Wheat

Grain legumes Plants that utilize atmospheric nitrogen through root nodules in symbiosis with bacteria (*Rhizobium* spp.). They yield seeds in pods. Examples include soybeans, peas, field beans, lupins, groundnuts, leucaena, acacia and others. The seeds tend to have higher protein contents than cereal grains but the proteins are often relatively low in sulphur amino acids. (TA)

Grain sprouting: *see* Germination; Malting

Gramineae The grasses, including pasture grasses and cereals. (JMW)

Grape (*Vitis vinifera* L.) The majority of grapes are grown for wine. After juice has been pressed from the berries, the residue (pomace) accounts for about 10% of the initial weight. If stalks have been removed before pressing the pomace consists of 40% seeds and 60% skin and pulp. Seeds can be removed from dried pomace to leave skin and pulp (marc). Dried marc has value as a ruminant feed (see Table 1). The seeds can be pressed for oil (8–22%), leaving oil seed cake, which has little feeding value due to its high fibre and tannin levels (Table 2).

Pomace from stalked grapes can be fed to dairy cattle up to 6.5 kg day^{-1}, supplemented with concentrates and legume hay. Inflammation of the digestive musosa has been reported at higher levels of inclusion. Well-balanced broiler diets with up to 20% pomace allow excellent growth. Up to 10% of the ration for horses can comprise grape marc,

Table 1. Grape nutrient composition (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Pomace – stalk, skin, pulp and seed	40.6	11.1–13.5	27.0–40.0		4.5– 7.4	35.5–48.7		
Pomace – skin, pulp and seed	46.5	13.7	23.6	12.8	7.0	42.9	0.82	0.20
Marc	88.9	18.3	32.0	8.0	6.4	35.3	1.63	0.33

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Grape digestibility (%) and ME content.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Pomace – stalk, skin, pulp and seed	18.4	8.5	77.8	40.9	6.04
Pomace – skin, pulp and seed	9.2	34.5	45.3	41.9	5.15
Pomace – stalk, skin and pulp	14.0	27.0	55.0	36.0	4.65
Marc	5.5	5.0	58.9	42.2	5.03

which has a lower fibre content than pomace. The digestibility of marc is improved by soaking in hot water. (LR)

Further reading

Gohl, B. (1981) *Tropical Feeds.* FAO Animal Production and Health Series, No. 12. FAO, Rome.

Grass Grasses belong to the family *Gramineae*, which also includes cereals. They have long narrow leaves, jointed stems and spikes of small wind-pollinated flowers. Temperate (C_3) and tropical (C_4) grasses follow different photosynthetic pathways and the C_4 grasses generally contain less protein than C_3 grasses.

Grass is the major feed resource for herbivores and, therefore, for most ruminant livestock production systems. It occurs naturally, as in most of the world's natural grasslands (including rangelands) and permanent pasture (both of which may be improved by the introduction of beneficial species, often members of the legume family), or is planted, using selected species, to meet a defined production objective. Whereas many sown pastures are on land that could be used for either grass or arable crop production, permanent pasture and natural grasslands often occupy land unsuitable for arable use.

Grasses are annual, biennial or perennial. Propagation is either by seeds or vegetative reproduction, or both. To obtain a dense sward, tillering above ground (stolons) and below ground (rhizomes) is of major importance.

Natural grassland usually contains several species of grasses, legumes and herbs, often interspersed with larger species such as bushes and trees, making it a suitable habitat for both grazers and browsers. Natural grasslands in temperate areas often consist of unfenced uplands or common lands. Extensive management is practised, with grazing- and fire-resistant species such as purple moor grass and heather often being dominant (Frame, 1992). In tropical semi-arid regions, natural rangeland consists of a mixture of annual and perennial grasses, of which perennials are often more highly valued nutritionally. However, after drought, if the soil seed bank is adequate, annuals recover first.

Permanent pasture is unlikely to be ploughed for arable cropping. It may evolve from natural pasture or be sown and is usually based on perennials, often with some soil-nitrogen enriching legumes (e.g. clover), thus reducing the need for nitrogenous fertilizers. Management should concentrate on maintaining a dense sward of nutritious species, not open to invasion by poor quality and low-yielding grasses such as Yorkshire fog (*Holcus lanatus*), meadow grasses (*Poa* spp.) and bent (*Agrostis* spp.).

Grass is the major feed resource for most ruminant livestock.

Leys are normally sown on arable land and have a lifespan of 2–5 years. They need to contain easily established and rapidly growing species, such as the ryegrasses (*Lolium pratense* or *L. multiflorum*), with or without a legume.

When establishing grass, the choice of species is governed by ease of establishment, persistence, yield and nutritive value. Soil type, rainfall and temperature preference are also important. In the growing stage grasses are high in crude protein, ranging from > 300 g kg^{-1} dry matter (DM) in young, heavily fertilized grass down to 30 g kg^{-1} DM or even less in mature tropical grasses, and relatively low in indigestible fibre. Fibre content tends to be inversely related to protein content, ranging from 200 g kg^{-1} DM in young grasses to > 400 g kg^{-1} DM in mature grasses. The DM content of young growing grass is lower (150–250 g kg^{-1}) than in the mature crop (350 g kg^{-1}) but the DM of standing tropical grasses in the dry season can be even higher. Green grass usually contains many of the B-group vitamins and vitamin E. It is also rich in carotene, a precursor of vitamin A. At any stage of growth the DM is influenced by the climate. At and after flowering the stem increases in fibre (cellulose, hemicelluloses and lignin); carbohydrates and protein move into the seeds. Leafiness is a major determinant of nutritive value, and management (particularly of sown pastures) is aimed at encouraging leaf growth and use of the plant (grazing or conservation) at a young stage (see table).

Between the vegetative and milk stages, the digestibility of crude protein and crude fibre of

Dry matter (g kg^{-1}) and composition (g kg^{-1} DM) of *Hyparrenia rufa* at four stages during growth in Brazil (from Speedy and Waltham, 1998).

		Composition		
Stage of growth	Dry matter	Crude protein	Crude fibre	Ash
Vegetative	297	92	289	149
Full bloom	343	35	314	136
Milk stage	352	28	337	115

Hyparrenia rufa in sheep fell from 604 and 619 g kg^{-1} DM to 165 and 473 g kg^{-1} DM, respectively (Speedy and Waltham, 1998).

Utilization of grass is by grazing, cutting for feeding green or conservation as hay, dried grass or silage for winter feeding. In tropical rangelands the grass is often left as 'standing hay', the nutritive value of which will deteriorate rapidly as the dry season progresses. It is usually taken as a bulk crop after the grass has reached the full-flower stage. Grass may also be cut at a younger stage and dried artificially in a high-temperature drier. Silage is made at an earlier stage than hay, ensiling being carried out at, or shortly after, cutting. Many grassland systems are based on a mixture of grazing and conservation, rather than a single use. (TS)

See also: Grazing

Further reading

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Grass carp (*Ctenopharyngodon idella*) One of the major Chinese carp of the family Cyprinidae. It has been introduced into the fresh waters of many regions in the world such as central Asia, Japan, America, Europe and the Arabian Peninsula, for both aquaculture and aquatic weed control. As the name implies, grass carp are herbivorous and feed on aquatic plants. A very popular fish in culture, often in polyculture with other freshwater fish. The grass carp, like other Cyprinids, has a toothless mouth but has specialized pharyngeal teeth for rasping aquatic vegetation. (RMG)

Grass tetany Hypomagnesaemic tetany, usually associated with the consumption by ruminants of lush, high quality pasture that is low in magnesium or contains high concentrations of potassium, nitrogen or tricarbaryllic acids (which interfere with the absorption of magnesium across the rumen). Magnesium concentrations in plasma, and especially cerebral spinal fluid, decrease from a normal value of 1–1.1 mM to < 0.5 mM, at which point normal nerve function can no longer be supported. This leads to uncontrollable muscle spasms (tetany) and tonic convulsions, as a result of the result of excessive release of acetyl choline at the neuromuscular junctions, hyperexcitability and rapid death. The syndrome is often accompanied by hypocalcaemia secondary to the low blood magnesium concentration.

Magnesium ions are absorbed mainly from the reticulorumen. The chief factor that affects this absorption is the potential difference across the ruminal epithelium. Active absorption of magnesium ions is reduced when this potential difference is increased by an increased concentration of potassium ions within the rumen. This can be the result of a high intake of potassium ions because of the ingestion of heavily fertilized grass, coupled with an increased potassium concentration in saliva in an attempt to correct a dietary sodium deficiency. A low dietary intake of phosphorus also reduces the absorption of magnesium ions. The condition is seen in older animals in which the skeletal reserves of magnesium are less available. Pregnant and heavily lactating cows are more susceptible to grass tetany because of their increased requirement for magnesium.

In the case of convulsing animals, treatment is by intravenous administration of magnesium and calcium salt solutions, though the results are often disappointing. In mild cases the animals can be treated with oral drenches containing magnesium salts. In housed animals, prevention is easily achieved by feeding higher amounts of magnesium (adding 20–30 g magnesium in a mineral form each day to the diet) but it can be difficult to ensure that grazing animals get sufficient supplemental magnesium. Prevention by oral supplementation of the concentrates with magnesium oxide to provide at least 60 g per day is recommended during periods of grazing rapidly growing grass, especially that treated with potassium and nitrogenous fertilizers.

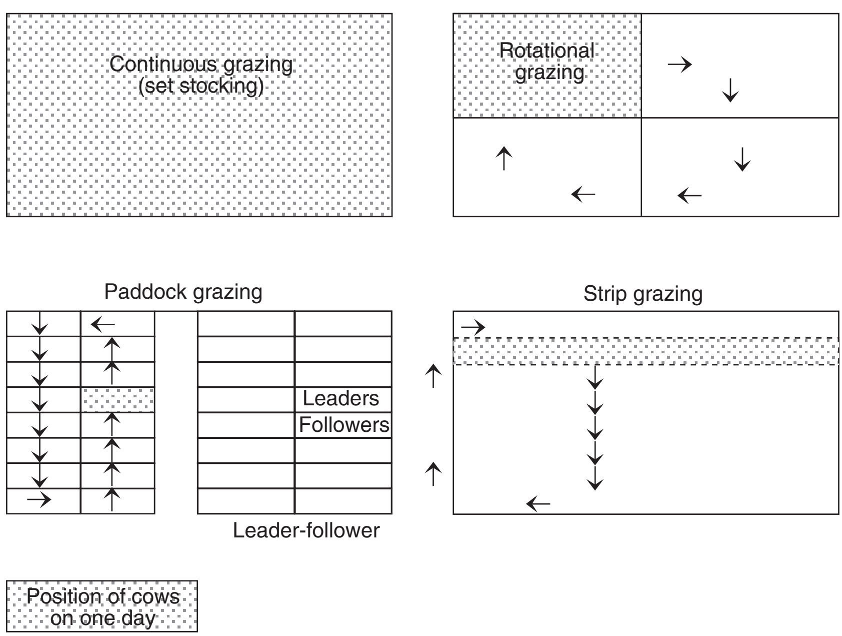
(ADC, JPG)

Grazing The consumption of grass in the field by livestock. In temperate climates this will normally be growing grass consumed during the summer months. In the tropics it refers to the consumption of standing hay in the dry season, as well as of green material during the wet season.

The stage of growth of a sward is a major determinant of its nutritive value. Cell wall contents increase markedly with age and protein concentration falls. This implies that regular defoliation, preventing flowering and seeding, ensures the highest quality herbage, accepting a possible reduction in total yield of dry matter. The digestibility of young grass can be in excess of 0.8, falling below 0.5 in winter grazing or 'foggage' (in temperate regions) and well below this value in dry-season standing grazing in tropical natural grassland.

The amount of herbage available and the grazing behaviour of the animal dictate the amount of material the animal eats. These factors include bite mass, bite rate, length of time of the meal and the number of meals per day. Sheep graze the sward to a lower level than cattle and are more selective. Cattle digest fibre to a greater extent than either sheep or goats. Most grazing activity occurs during the hours of daylight, the other major activities in a 24 h period being ruminating, drinking, walking, grooming, lying and standing. Maximum use of the herbage available is often achieved by mixed-species grazing, as preferences and grazing behaviour vary between livestock species.

There are several systems of grazing. *Set stocking* involves a fixed number of livestock grazing a given area of land over a considerable time. It is often employed where factors such as the cost of fencing and provision of water preclude the use of small paddocks. It is suitable for areas of natural grazing but, if animal numbers are high, the continuous grazing pressure and destruction of the natural habitat can lead to land degradation and erosion. This can be offset by feeding supplements at grass. If numbers are low, insufficient grazing pressure in the growing season will lead to uneaten grass becoming rank. *Continuous grazing* differs from set stocking in that animal numbers and the land area available can be adjusted as the season advances. Frame (1992) uses the term 'continuous stocking' and also describes the 1.2.3 system, by which, in the early grazing season, one-third



Diagrammatic representations of the continuous, rotational, paddock and strip-grazing systems.

of the area is grazed and two-thirds cut for silage; the whole area is thereafter grazed. Systems based on removal of livestock at regular intervals have the advantages of allowing the application of fertilizer during the season and interspersing grazing with conservation, when regrowth is sufficient. However, they require more fencing and water points than in set stocking systems. *Rotational grazing* is when stock is moved to a fresh paddock at predetermined intervals and the recently grazed area is allowed a recovery period; the length of the periods can be from days to months. A simple example is the division of a large grazing area into four paddocks (e.g. 7 days grazing, 21 days rest). *Paddock grazing* is a form of rotational grazing in which the duration of grazing (often as brief as 1 day) depends on the number and size of the paddocks (normally a large number of small areas), the number of animals and the amount of herbage available; the period of rest will be calculated to match the expected recovery time of the sward. Again, grazing can be replaced by conservation when the amount of regrowth allows. Both rotational and paddock grazing should aim to avoid undergrazing when herbage is plentiful and overgrazing when it is short. *Strip grazing*, or allocation of fresh material by moving an electric fence, is often used for intensively managed dairy cows, the intention being to keep a supply of fresh, untrodden grass in front of the animals at all times. *Creep grazing* (including leader/follower systems) describe systems in which young stock are allowed access to fresh herbage in front of their dams. This allows them maximum opportunity for selection, leading to improvement in intake of nutrients and growth rate.

With all these grazing systems the land benefits from hoof action and the direct application of manure. However, there are instances, especially with dairy cows, where it is beneficial to move the grass to the livestock: this is called *cut and carry* or *zero-grazing*. This gives the farmer closer control of grassland and conserves energy expenditure in the stock, but it is labour and machinery intensive. For most farmers the disadvantages outweigh the advantages. *Tethering*, an extreme form of controlling grazing livestock, is used where grazing pressure is high. In many tropical areas it is most common in the wet season where arable crops cannot be adequately fenced. It also allows safe grazing of roadside verges. Animals often have access to limited grazing and cut feed. (TS)

See also: Grass

Reference and further reading

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Green-crop fractionation: *see* Fractionation, green-crop

Green feed Plant material harvested for immediate use as animal feed, without preservation. (JMW)

Grinders Machines used in feed processing to reduce particle size and especially to rupture cereal grains. Two main types of grinder are used in the animal feed industry. The most common is the hammer mill, in which feed material is fed into a grinding chamber where it is shattered by the impact of 'hammers'; these are rectangular pieces of hardened steel attached to a shaft which rotates at high speed. Perforated metal screens round the periphery of the chamber retain coarse particles for further grinding and allow properly sized material to pass. Hammer mills are easy to operate and maintain, and the cost of wearing parts is low.

The other main type of grinder used for animal feed is the roller mill, in which feed material is passed between two or more counter-rotating, fluted rollers. Coarser material can be sifted after rolling and re-circulated for further reduction. Compared with hammer mills, roller mills are less noisy and dusty, more energy efficient and produce few finer and fewer oversize particles. (AM)

Gross energy The heat released when the carbon and hydrogen present in a substance are completely oxidized to carbon dioxide and water. Gross energy is synonymous with heat of combustion and is determined by burning a sample of the substance in a **bomb calorimeter**. (JAMcL)

Gross protein value (GPV) A measure of the effectiveness of a 'protein' (usually a mixture of proteins) added to a diet containing a cereal base. The response to the test protein is compared with the response obtained when casein, as a standard, is used in place of the test protein. The response is in units of grams of body weight gain per unit of protein consumed when incorporated into the diet containing the cereal. GPV has no units; it is simply a ratio. It is not equally applicable to all species or ages of animal, because of differences in the pattern of their amino acid requirements. (NJB)

Groundnut Groundnuts or peanuts (*Arachis hypogaea*) are leguminous plants that are commonly grown in the tropics, primarily for their oil (about 500 g kg^{-1}). The seeds are produced in pods beneath the ground and the oil is extracted by pressing either the shelled seeds or the whole pods. The residual meal, either decorticated or undecorticated, is used as a high-protein feedstuff for both ruminant and non-ruminant animals. It is susceptible to fungal contamination by *Aspergillus* spp. which produces aflatoxins, potentially causing aflatoxicosis in animals. The protein content of decorticated groundnut meal is about 500 g kg^{-1}; for undecorticated meal it is about 300 g kg^{-1}.

The crude fibre content of undecorticated meal is about 300 g kg^{-1}, while the decorticated meal has about 100 g kg^{-1} (with neutral detergent fibre about 130 g kg^{-1}). The decorticated meal, which has an apparent metabolizable energy (AME) for poultry of 13–14 MJ kg^{-1}, is the more suitable for non-ruminants and the undecorticated for ruminants (AME about 10 MJ kg^{-1}). The ME depends on the content of residual oil. The lysine and sulphur amino acid contents of the protein are relatively low. The forage material can be fed to ruminants: it has a protein content of about 100 g kg^{-1} dry matter. (TA)

Grouper Marine finfish belonging to the subfamily Epinephelinae, commonly known as groupers or rock cod. There are approximately 159 grouper species in 15 genera worldwide. The more popular cultured species belong to the genus *Epinephelus*. Groupers are coastal warm-water fishes widely distributed in tropical and subtropical waters. Most are found in coral reefs and off rocky coasts but some species inhabit estuarine areas. By nature, groupers are predatory and are exclusively carnivorous – a major problem in aquaculture of this species. The bulk of groupers for human use comes mainly from the capture fisheries. Due to increasing consumer demand and depletion of wild fish stocks, the culture of groupers is expanding in South-east Asian countries. (RMG)

Growth The dynamic process by which animals change from a single newly fertilized cell into an adult. At its simplest, it means getting bigger and heavier. Growth of the whole animal or of one its complex parts can be neatly divided into two aspects: increase in size and change in form.

Rates of liveweight gain are agriculturally important but, for genetic and nutritional studies, investigations may be made of the growth of particular components of the body. There are several approaches for measuring growth. Dissection allows measurements to be made of individual tissues (bone, muscle and fat), specific organs or parts of the body, individual cells or even an organelle. Numerical growth refers to changes in the number of units, ranging from population growth (whole animals) down to micro-populations such as the number of cells, the number of glands or the number of follicles. Growth may also be considered in terms of changes in linear dimensions such as height, width, length, girth and circumference. For certain studies, growth of areas of the body may of interest, such as surface area of the whole animal, respiratory surface or absorptive surface of the gut. Chemical growth refers to changes in the mass of a chemically defined entity of the body, e.g. protein, lysine, lipid, ash or calcium.

At the cellular level, growth is usually considered as having two components: increase in number, described as *hyperplasia*; and an increase in the actual size or mass of the cell, called *hypertrophy*. As a general rule hyperplasia is a feature of early growth and hypertrophy of later growth. During normal metabolic activity, complex molecules are continually assembled and dismantled in a process known as turnover. Growth itself can be considered as the balance between anabolism and catabolism or synthesis and degradation. This is also called net accretion.

Temporal growth

Growth rate is a measured unit of change over a given time interval. The mass of an animal, or that of one of its parts, when plotted in relation to time produces a characteristic sigmoid growth curve. Its appearance is that of a rather flattened italicized capital S. Over the life of the animal, the first part of the curve is often described as 'self-accelerating' and the second part as 'self-decelerating' until an asymptotic value is reached that is mature weight. Blaxter (1989) pointed out that the growth curve is closely related to feed intake and derived an equation to show the relationship. It is a matter of debate whether growth requirements drive feed intake or intake drives growth.

The condensation of animal growth curves into algebraic formulae has exercised mathematicians for many years. Such efforts vary from the merely empirical to those that attempt to model and integrate the intrinsic complex biological interactions that are involved. A relatively simple curve that models all phases of the growth curve is the so-called Gompertz equation. This produces a sigmoid curve with an inflection at about one-third of the mature size. Discussions and descriptions of **growth equations** are given by Lawrence and Fowler (2002) and Bakker and Koops (1978). Though growth equations have their place in biology, they are not always applicable. Seasonal shortages of feed and stresses imposed by disease and varying stocking density and pregnancy can cause major perturbations to the curve.

Relative or allometric growth

Some animals grow without any obvious change in shape. Many aquatic or marine creatures, such as fish, tend to fall into this category. Such growth is called *isometric* because each component increases by the same percentage increment over a period of time. However, most animals can be seen to be either 'mature' or 'immature' by changes in their conformation. For example, calves are not miniatures of adult cattle. Changes in proportion are a response to the changing physical and physiological needs of the animal as it increases in mass. As Brody (1945) pointed out, the strength of muscles is closely related to their cross-sectional area or the square of linear size. However, in land animals, weight, which has to be supported and moved, increases as the cube of linear size. The effect is that farm animals become more muscular with a more compact appearance as they grow larger. Baby animals tend to have large heads relative to the rest of their bodies and large eyes relative to the size of their heads. Limbs tend to be poorly muscled and spindly in the young but well muscled and sturdy in the adult. These changes occur because the components are growing at different percentage growth rates. This is called *allometric* or *differential* growth.

Huxley (1932) was one of the first to show that most tissues and parts tend to grow in logarithmic relationship to each other and to the whole animal. He proposed the relationship

$$\log Y = \log a + b \log X$$

where Y = weight of part, a = the value of Y when log X = 0, and X = weight of whole minus weight of part. Such a relationship implies a constant ratio between the percentage growth rates of X and Y. When the slope b is 1, the relationship is isometric; if $b < 1$ then growth of the part is slowing down relative to the whole (early maturing); and if $b > 1$ then the part is growing more quickly than the whole in percentage terms.

The tendency of animals to grow more rapidly in their distal regions when young and then broaden and thicken at the top of the legs and in the pelvic region is sometimes called *centripetal* growth (Hammond, 1932). Hammond and his school described those tissues or parts that went through their growth programme early in life as *early maturing* and those growing as the animal approached adulthood as *late maturing*. For tissues, the sequence in order of completion of the growth cycle from early to late maturing was: (1) nervous tissue, (2) bone, (3) muscle and (4) fatty tissue; and for regions the sequence was (1) extremities or distal parts (e.g. metatarsals and metacarpals), (2) medial (tibia fibula, radius and ulna), (3) proximal (femur and power muscles at the top of the legs) and (4) axial (lumbar vertebrae and loin muscles and adipose tissues).

Fluctuations in nutrition may disrupt some of these elegant patterns. Growth rates can be deflected and so can some of the inter-structural relationships. The most obvious example is the extreme flexibility of the adipose tissue depots. Comparing the proportions of tissues and organs on a fat-free basis (either chemical or dissectable fat) often reveals underlying relationships that are obscured if fat is included.

The changing relationship between parts and tissues during growth is of considerable interest, especially for agricultural purposes. Not all components of liveweight or carcass weight gain have equal economic value and a knowledge of growth patterns can greatly assist in optimizing strategies for economic production of meat. (VRF)

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Growth disorders Growth disorders are usually assumed to mean reductions in growth, in particular dwarfism, which is detected in all the major species of farm animals. Often specific breeds have been developed with dwarf characteristics; for example, several breeds of cattle have been developed, including the Dexter, Japanese Brown and dwarf zebu. The proportion of cattle within a breed that have dwarf characteristics is variable. The selection of dwarf animals has always been a feature of the domestication process, because they are easier to handle and have lower maintenance requirements than larger breeds of the species. However, in recent years the greater mechanization of livestock production has favoured the selection of larger farm animals, which are little handled by humans and are fed *ad libitum*. Thus the small cattle breeds that were developed in Britain over the last 200 years, for example, are not popular for intensive production systems.

In many breeds a proportion of the animals are particularly small. Affected cattle usually have limbs that are disproportionately short, compared with their trunk size, with wide epiphyses of the femurs and humeri. This may be due to incomplete maturation of carpal and tarsal bones and incomplete maturation and abnormal flaring of epiphyses of the short humeri and femurs. A short vertebral column is a feature of Dexter cattle.

The reasons for dwarfism are not only genetic. They include abnormal feeding of dams during pregnancy, twinning, mineral deficiencies (especially iodine, zinc and manganese) and infectious diseases (e.g. Akabane virus infection in pregnant ewes). One inherited characteristic that can produce dwarfism is inadequate IGF-1 production. Another possible cause is heat stress, which will prematurely terminate pregnancy, particularly in housed sheep. This leads to inadequate growth of brown fat reserves in the final stages of pregnancy.

Sometimes a congenital chondrodysplasia is lethal, causing abortion or neonatal mortality, but this may also occur with infectious agents. A number of severe, simply inherited growth disturbances have been identified in farm animals. These disorders are controlled by defective alleles at major loci referring to hormones or hormone receptors, e.g. growth hormone receptor for the recessive sex-linked dwarfism in chickens.

Mineral deficiency may be a factor. In ruminants, the critical time for the most severe effects of mineral deficiency is the mid trimester, when the neurons of the cerebral cortex and basal ganglia are formed. At this time, an iodine deficiency could affect maternal thyroid function. There is now evidence indicating transfer of maternal thyroxine, with impaired fetal thyroid function following in the third trimester to augment the effect of reduced maternal thyroid function.

When caused by disease, dwarfism is often accompanied by skeletal deformation, e.g. the endemic osteoarthropathy Kashin-Beck disease in Chinese poultry.

Some growth disorders are potentially beneficial, such as double muscling in cattle and sheep, which increases the ratio of muscle to the inedible parts of the carcass. In the last 25 years a genetic mutation that increases the rate of muscle growth has appeared in the Belgian Blue breed of cattle and it is suspected to exist in other breeds. Double-muscled cattle have a considerably increased ratio of muscle to fat, particularly in the male, and they have smaller organ weights. The increase in size of the muscles is accompanied by an increase in tenderness, which enhances the commercial value of the fore- and hindquarter cuts. The trait is controlled by a major gene, which was recognized in some sheep breeds long before its recent appearance in the cattle. However, in Belgian Blue cattle the trait is associated with difficult calvings in pure-bred animals, which require specialist management to keep the number of Caesarean births to a minimum. The increased cost of care during calving may be financially justified by increased growth rate potential but the growth disorder arouses concerns for the welfare of the cows. (CJCP)

Growth equations A growth equation, or growth function, is a mathematical function describing the **growth** of an animal over time. The general form is

$$W^{o} = f_{\theta}(t)$$

where W is liveweight, t is time, and f is the growth function. The function f depends on parameters θ. Growth functions may also be used to model measures of growth other than liveweight, such as height, or weight of some body component of the animal.

General functional forms, such as polynomial or spline functions, may provide adequate fits to a single set of growth data over time. These functions tend to require many parameters, with no biological significance. A number of growth functions have been proposed that are derived from equations describing biological processes such as autocatalysis or senescence, and which require fewer, more meaningful parameters. We will describe the most well-known and important of those here: the exponential, logistic, Gompertz and Richards equations.

It is unrealistic, however, to expect to describe growth, the result of complex genetic and environmental interactions, with any analytical function of a small number of parameters. These functions are most successful at describing growth in completely controlled environments, for example an 'unlimiting' environment in which an animal may meet its growth potential. More complex environments require more complex simulation models.

The *exponential* growth equation is derived from the assumption that, since the animal itself is the mechanism of growth, the rate of its growth is at any time proportional to its weight. This autocatalysis assumption implies the differential equation

$$\frac{dW}{dt} = \mu W \qquad (1)$$

where $\mu > 0$ is the growth rate parameter. The resulting growth function is

$$W = W_0 \, e^{\mu t}$$

Here W_0 is the inital, non-zero, weight. This function predicts an unlimited increase in weight over time, so it is only a realistic description of the initial phase of growth of an animal.

The *logistic* growth equation provides a correction to the exponential by restricting growth based on availability of a substrate, which is assumed to decrease as the animal grows. Assuming that growth is proportional both to W and to $W_m - W$, the amount of substrate left out of a fixed quantity W_m, we have

$$\frac{dW}{dt} = \mu W (W_m - W), \qquad (2)$$

and

$$W = \frac{W_0 W_m}{W_0 + (W_m - W_0 e^{-\mu t}}$$

The weight reaches a maximum W_m once the substrate is exhausted.

Farm animals stop growing because they reach maturity, not usually because they run out of food. The *Gompertz* equation assumes exponential growth as in (1), but assumes that the rate of growth μ itself decreases exponentially over time,

$$\mu = \mu_0 e^{-Dt},$$

where $D > 0$ is a second parameter describing rate of senescence. Explicitly,

$$W = W_0 e^{\mu 0(1-e^{-Dt})/D}.$$

The mature weight, approached as t gets large, is

$$W_m = W_0 e^{\mu 0/D}.$$

The family of Richards growth equations have the form

$$W = \frac{W_0 W_m}{(W_0^n + (W_m^n - W_0^n)e^{-kt})\frac{1}{n}}$$

Here W_0 and W_m are as before, and $n \geqslant 1$ and $k > 0$ are new parameters with no simple biological interpretation. The Richards equation specializes to the logistic when $n = 1$ and the Gompertz when $n = 0$. Richards equations are therefore a mixture of mechanistic models such as these, and empirical, non-biologically based models. (RG)

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Growth factors Polypeptide hormones that promote cell growth, proliferation and anabolic processes. Some well-recognized members of this group include the insulin-like growth factors (IGFs), epidermal growth factor (EGF), transforming growth factors (TGFs), nerve growth factor (NGF) and fibroblast growth factor (FGF). Of particular importance are the IGFs (I and II). These hormones comprise a family structurally related to insulin with multifunctional metabolic and anabolic properties and may influence differentiation and be mitogenic in developing muscle. They exert their actions by occupation of membrane-bound receptors as well as interactions with soluble binding proteins. The IGFs are synthesized by various tissues and act by paracrine and autocrine mechanisms. Blood-borne IGFs, synthesized mainly in the liver, exhibit endocrine activity. Manipulation of muscle growth and mass by increasing expression or insertion of IGF genes is a possible future strategy. (MMit)

See also: Growth; Muscle

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Growth models All animals and plants have the potential to grow at a rate determined by their genotype. This potential growth rate is often constrained by one or more of many environmental factors, such as disease, inadequate food supply, or too high an environmental temperature. In modelling **growth**, different approaches may be used, depending on whether the model is to predict the potential or the constrained growth rate of the animal. Modelling, or predicting, potential growth is simple, but predicting the effects of the various constraining factors on potential growth, and the consequences on subsequent growth once the constraints are removed, is far more complex.

A number of **growth equations** may be used successfully to represent unconstrained growth. Such equations result in a smooth, sigmoidal curve of body weight (w) over time (t). Differentiating such equations results in a representation of weight gain over time (dw/dt), which reaches a maximum, and then declines to zero, when the animal reaches its mature body weight. In place of body weight, other characteristics of the animal may be used to represent growth, such as the degree of maturity (u) ($u = P/P_m$, where P and P_m are the protein weight and mature protein weight of the animal, respectively). In unconstrained conditions the chemical composition of the body may be predicted with the use of the allometric relationships that exist between different components of the body. Body protein weight may be used as the predictor (independent variable) and body water, body ash and body lipid as dependent variables. Whereas body lipid content varies between individuals and between species, the three remaining chemical components exhibit a fixed relationship with one another at maturity, even between most species. Nevertheless, the body lipid weight of a given animal is also allometrically related to the body protein weight under unconstrained conditions. As a result, once the growth of body protein has been modelled by means of a growth equation, the growth of the other chemical components of the body may be predicted by allometry, and the sum of the four components would then result in a prediction of the body weight of an animal over time. The growth of any integuments, such as feathers or hair, may be modelled in the same manner.

Modelling constrained growth

Modelling the effects of constraining factors on the growth of an animal is more complex than modelling unconstrained growth. These constraints may influence the growth process in different ways, and theories should be developed to account for each of these effects before they can be modelled successfully. For example, the constraint might act at the level of food intake, which, if reduced either in quantity or through a change in quality, would result in a reduced growth rate. A reduction in food intake may have little to do with the feed composition, or the daily amount allocated, but may be due entirely to unfavourable environmental conditions, such as high temperatures. Conversely, a disease may influence the growth process, possibly through a reduction in the rate of metabolic processes in the body or by reducing the uptake of nutrients from the small intestine. The resultant growth constraint may or may not be the same as that due to a reduction in food intake. Of importance in modelling the effect of a given constraint on the growth of an animal is having a plausible understanding of how the limited supply of dietary nutrients would be partitioned between functions.

In order to describe growth, whether constrained or not, in terms of the supply of dietary nutrients, it is necessary to describe the feed in terms that are relevant to the animal. In the successful growth models that have been developed, some of the dietary nutrients, such as digestible amino acids, are considered to be resources, whereas others, such as metabolizable energy (ME), must be transformed into resources, using a set of rules, given that the ME scale does not take account of the contributions of the different chemical components of the feed to its energy content, nor does it effectively predict the heat increment associated with the digestion and metabolism of the given feed. Predicting the amount of heat produced by the animal in a given state, and consuming a given amount of a given feed, is critical in determining whether the animal will be successful in consuming the amount of food that is required for potential growth, or whether the **environmental temperature** is too hot to allow it to do so. The animal must retain its thermal balance, and if the animal is unable to dissipate the heat produced during digestion, metabolism, maintenance and growth it has no alternative but to reduce food intake. In modelling constrained growth through the prediction of voluntary food intake, therefore, the model must integrate information about the animal, the feed that it is being offered, and the environment in which it is kept.

Modelling compensatory growth

There are many reports in the literature claiming that animals are capable of catching up with their counterparts in weight after a period during which they did not grow to their potential, i.e. they were able to compensate for the growth lost by growing faster during the rehabilitation period. This would imply that, in addition to growing faster, animals utilize their feed more efficiently during rehabilitation. In modelling such **compensatory growth**, care must be taken to identify which, if any, of the chemical and/or physical components of the body exhibit such growth during the period of rehabilitation.

Depending on the extent to which growth and body composition have been affected, the animal may, at the end of the period of abnormal growth, have a protein deficit (with an associated water deficit) and either a deficit or an excess of lipid relative to its ash weight in the empty body. In addition, it may have abnormally high or low weights of the food-processing organs and gut-fill compared with normal animals at the same ash weight. In other words, the chemical and physical composition of the animal at the end of the period of constraint is likely to be very different from that of an animal having grown normally. It may be assumed that the animal would attempt to rectify any insult to its growth, thereby regaining its genetically determined physical and chemical composition at a given ash weight. But the response in the growth of the different body components once the animal has been returned to a non-limiting environment will depend not only on its composition before the restriction was lifted but also on factors to do with the feed offered and the environment in which it is placed.

Growth models that are useful in real-world situations are those that attempt to predict both chemical and physical growth, under both unconstrained and constrained conditions. Because of the complex interactions between the animal, the feed that it is being offered, and the environment in which it is kept, such models of growth must take account of all of these factors. (RG)

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Growth promoters The most potent growth promoters are the gonadal steroids, since rapid growth and sexual development coincide at puberty. Most powerful are the androgens, principally testosterone, produced predominantly in the testes and important in increasing the efficiency of growth by increasing the nitrogen incorporation into muscles. Androgens also cause epiphyseal plate fusion in bones, and exogenously administered androgens can reduce skeletal size. Exogenous androgens such as trenbalone acetate, if permitted, have their greatest effect in heifers or cull cows, due to the low level of natural male steroids in the female. In the European Union both synthetic and naturally occurring growth promoting hormones were banned in 1986.

Oestrogens are also potent growth stimulators in young steers. They increase growth hormone, leading to increased muscle production, decreased fat production and reduced losses of urinary nitrogen. In the older animal, oestrogens cause epiphyseal plate fusion in bones in the same way as androgens. Both synthetic oestrogen-mimicking agents, such as diethyl stilboestrol and zeranol, and naturally occurring female steroids, principally oestradiol, are most effective on steers, though combined-action trenbalone acetate and oestradiol implants are effective in stimulating growth in bulls, steers and calves. The efficacy of synthetic steroid use is greatest in cattle, intermediate in sheep and of limited value in pigs. Because of the stimulation of muscle growth by both oestrogenic and androgenic hormones or hormone-mimicking agents, it is often necessary to supply extra rumen-undegradable protein to implanted animals.

Other hormone mediators of growth include the β-agonists, which are synthetic analogues of adrenaline and noradrenaline, such as clenbuterol and cimaterol. These reduce intramuscular fat considerably, by up to 30%, with a corresponding increase in protein deposition of 10–15%. As a result the food conversion efficiency is often increased by a similar proportion (10–15%). The effects on weight gain and feed intake are variable, depending on the relative impact on fat and protein deposition. There is evidence that cattle treated with β-agonists are more susceptible to dark cutting, and the low level of muscle glycogen and carcass fat can give rise to cold shortening (cross-bonding between actin and myosin fibres) if the carcass is rapidly chilled post mortem to 10–15°C. The increase in carcass yield may be accompanied by smaller non-carcass components. The action of β-agonists is not sex specific but all animals are susceptible to tachycardia (elevated heart rate) and increased basal metabolism rate, which may be perceived as reducing their welfare. The risk of residues is low as the β-agonists are rapidly metabolized, and after withdrawal of the substance from the feed the animal's nitrogen metabolism rapidly reverts to normal.

Surprisingly the administration of growth hormone to growing cattle does not result in large increases in muscle growth, perhaps because of the lack of additional receptors. However, immunization against somatostatin, which is the agonist of bovine somatotrophin (bST), can increase growth but it also tends to increase carcass fatness. Somatostatin inhibits other hormones, such as insulin and the thyroid hormones, which may explain its action.

Antimicrobial compounds are routinely used in some cattle production systems to modify the gut microflora. The most commonly used is monensin sodium, which was originally developed as a coccidiostat for poultry. In the rumen of cattle it is active in reducing the population of acetate- and hydrogen-producing bacteria, such as *Ruminococcus* spp. and *Bacteroides fibrisolvens*, allowing propionate producers such as *Selenemonas ruminatum* to flourish. This increases the efficiency of growth by about 5%, partly because acetate production is accompanied by methane loss via eructation. As a result of its mode of action, there are no effects of such growth promoters on carcass composition. The widespread use of monensin sodium was not possible until it could be incorporated into feed blocks that could be offered to the cattle when they were out at pasture. If cattle are offered feeds with added monensin sodium indoors and then turned out to pasture with no supplement, there is a considerable check to growth as the rumen microflora adapt.

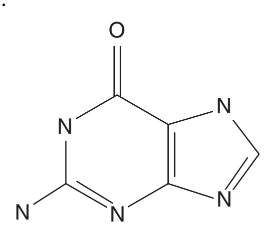
There is increasing concern over the routine use of antimicrobial compounds in cattle production systems, principally because of the risk of transfer of resistant bacteria from animals to humans via the food chain and the possible transfer of resistant genes from animal bacteria to human pathogens. Currently within the EU, animal feed additives are only allowed if there is no known adverse effect on human or animal health, or the environment. Although there were originally ten licensed antimicrobial growth promoters, four of these (bacitracin zinc, spiramycin, tylosin phosphate and virginiamycin) were withdrawn in 1999 because of fears that human health would ultimately be compromised by their use. A human antibiotic similar to virginiamycin is currently being developed, which it is suspected could be rendered ineffective with continued use of virginiamycin in animal food. A further two antibiotics (olaquindox and carbadox) have been banned due to possible risks to human health during the manufacturing process, leaving only four that can legally be used (monensin sodium, salinomycin sodium, avilamycin and flavophospholipol).

Probiotics are an alternative to antibiotics when they are used therapeutically, but are not very effective as growth promoters. They promote colonization of the gut by benign bacteria, such as *Lactobacillus* spp., thereby excluding pathogenic bacteria by reducing nutrient availability or, in the case of lactobacilli, acidifying the gut contents with lactic acid. Their use in cattle is restricted to the pre-ruminant calf, where they may prevent *Escherichia coli* from colonizing the gut and causing scours.

Photoperiodic manipulation of cattle growth can achieve desirable changes in composition but it is doubtful whether weight gain is increased. In autumn, ruminants in natural photoperiod naturally begin to divert nutrients from muscle to fat deposition, to give them a store of nutrients that can sustain them through the winter. This would have been of particular benefit to wild ruminants, although nowadays adequate conserved food is usually made available to prevent cattle losing weight in winter. Many wild herbivores naturally lose weight in winter; for example, the bison catabolizes considerable amounts of fat tissue through the winter on the American plains. In intensive rearing of cattle, food is available in similar quantity and quality throughout the year but the animals still use the cue of declining photoperiod to start diverting more nutrients to fat deposition in autumn. By extending the photoperiod in autumn to 16 h of light daily, they will deposit lean tissue as if it were still summer. This could be useful if the animals are to be slaughtered in midwinter, as they will put on more muscle and less fat tissue. If they are being kept until the spring, photoperiodic manipulation will have no benefit, as cattle in natural photoperiod start to divert nutrients away from fat deposition to muscle growth in spring. (CJCP)

Guanidine Iminourea, $(NH_2)_2 \cdot C{=}NH$. It is related to urea. The guanidinium ion is a strong organic base at physiological pH. Naturally found in turnips, mushrooms and other plant materials, it has also been identified in urine. (NJB)

Guanine A purine, $C_5H_5N_5O$, one of the purine nucleic acid bases. It is the base in the nucleoside guanosine and the nucleotide guanosine monophosphate. In DNA it pairs with cytosine, a pyrimidine base, to stabilize the helical structure of DNA. This same base pairing is found in the tertiary structure of some RNA. (NJB)



Guar Also known as the clusterbean, guar (*Cyamopsis tetragonoloba*) is a drought-resistant, tall-growing annual legume. Within its comparatively large endosperm is a large proportion (19–43%) of galactomannan gum, which is the primary product of this crop. The refined gum is used for a variety of human nutritional products. The remaining guar meal, which contains approximately 35% protein, provides a palatable protein supplement feed for livestock when pelleted and toasted. (DA)

See also: Galactomannans; Gums

Guinea fowl The guinea fowl originated in semi-arid areas in western and northern Africa. In certain developing countries, such as Nigeria (Nwagu and Alawa, 1995) and India, guinea fowl production is still largely based on a tradition of extensive, small-scale farming. In Nigeria and South Africa, guinea fowl are also hunted. Guinea fowl breeding is highly developed in France (48 million day-old keets in 1999), Italy (15 million) and Belgium (365,000). With 76% of European guinea fowl production, France is the largest producer in the world (57,000 t in 1999, representing 2.5% of the total French poultry production). France is also the largest consumer in the world (53,300 t in 1999; 0.9 kg per person per year) and the only country in which there are commercial breeding programmes.

Selection of guinea fowl is similar to that of light meat-type strains of **chickens** and is mainly aimed at increasing body weight and **feed efficiency** without decreasing reproductive ability. Between 1975 and 1985, body weight at slaughter and feed efficiency were increased annually by 40 g and 0.04, respectively. The yield of eviscerated **carcass** increased from 66 to 70% and the proportion of breast muscle to body weight from 17 to 19% (Sauveur and Plouzeau, 1992). Since 1988, French breeding programmes have focused on three different products: a standard bird weighing 1.6 kg at 11 weeks of age, a heavy bird (1.8 kg at 12 weeks for males and 1.5 kg at 10.5 weeks for females) intended for jointing and a slow-growing bird (1.9 kg at 14 weeks) for the '*label rouge*' market (27% of the total production in 2000).

For growing guinea fowls reared on litter in closed buildings, a temperature programme is used which decreases from 28°C on day 1 to 20°C on day 56. It then remains constant at 20°C. **Light** intensity decreases at a constant rate from 20 lux on day 1 to 5 lux on day 20 and then remains constant at 5 lux. The following lighting programme is applied: days 1–3, 24 h of light; days 4–11, 22.5 h; days 22–36, 21 h; days 37–62, 19.5 h; day 63 until the end, 18 h. The stocking density is 13 birds m^{-2} for *label rouge* and 17 birds m^{-2} for standard conditions. After 6 or 8 weeks of age (summer or winter periods), the guinea fowls reared under *label rouge* conditions have free access to open space (2 m^2 per bird).

The stocking density for future breeding birds is 8 birds m^{-2}. Between 1 and 14 days of age their day length decreases from 24 h to 7 h and then remains constant. The highest testis weight is obtained with photostimulation begining at 20 weeks of age and increasing day length regularly (1 h per week) from 7 to 15 h. For females, photostimulation occurs directly at 27 weeks of age. Light intensity is also increased from 5 to 15 lux for both sexes (Le Coz-Douin, 1992).

The feed recommendations for growing guinea fowls are presented in Table 1 (Larbier and Leclercq, 1992). Birds are slaughtered when the growth rate slows down. The feed conversion ratio is then high: 2.7 and 3.5 for standard and *label rouge* birds, respectively.

For future breeders the feed must be restricted during the growing period. Three diets can be used: starting (0–4 weeks), 12.5 MJ metabolizable energy (ME) kg^{-1}, 20% crude protein and 1.2% lysine; growing (5–12 weeks), 12.1 MJ ME kg^{-1}, 15% crude protein and 1.2% lysine; and rearing (13–22 weeks), 12.1 MJ ME kg^{-1}, 12% crude protein and 1.0% lysine. During the laying period, the daily feed consumption must provide 1.25 MJ, 14.5 g protein, 580 mg lysine, 530 mg sulphur amino acids, 3.8 g calcium and 0.45 g available phosphorus (Larbier and Leclercq, 1992).

Table 1. Feed recommendations (g kg^{-1}) for growing guinea fowl (Larbier and Leclercq, 1992).

Period (weeks)	0–4	4–8	8–12
ME (MJ kg^{-1})	13	13	13
Crude protein	230	180	140
Lysine	11.8	9.6	6.0
Sulphur amino acids	8.85	7.20	4.5
Tryptophan	2.12	1.74	1.08
Threonine	8.14	6.62	4.14
Calcium	10.0	9.0	8.0
Available phosphorus	4.0	3.5	2.5

Under natural conditions guinea fowl are seasonal breeders. Egg laying and sperm production peak between April and September, with the highest levels from late May to July. Wild birds are monogamous. Under intensive production, the reproduction period is between 25 and 66 weeks of age, with animals in individual cages (one male per seven to eight females) and using artificial insemination (once a week, 70–80 $\times$ 10^6 spermatozoa until 45 weeks of age, then 100–120 $\times$ 10^6 spermatozoa). The volume of ejaculate collected from males twice a week is about 90 μl, with 7 $\times$ 10^6 spermatozoa. It is possible to obtain 184 eggs per female during the whole laying period, with 95% fertility and 73% hatchability. Egg weight is about 45–52 g, with a higher eggshell mass than pullet eggs (15% vs. 10%). The optimum incubation conditions are 37.4°C and 56–58% relative humidity (RH) for 24 days, then 36.9°C and 72–74% RH on day 25, 36.5°C and 85–88% RH on day 26 and 36.5°C and 90–95% RH on day 27 (Le Coz-Douin, 1992).

The main diseases in guinea fowl are caused by parasites (*Eimeria*, *Trichomonas*, *Capillaria*, *Candida* and *Aspergillus*). Among the infectious diseases, salmonella, coryza, Newcastle disease, influenza, swollen head syndrome, transmissible enteritis and X disease can be found.

Cut yields are presented in Table 2. At 84 days of age, the protein, lipid and mineral contents of guinea fowl carcasses (without feathers) are 18.3 and 17.9%, 13.5 and 20.0% and 3.5 and 3.3% for males and females, respectively (Larbier and Leclercq, 1992). Guinea fowl meat is characterized by a high protein content and a low lipid content, with a high ratio of saturated/unsaturated fatty acids (Table 3). (EB)

References

Cerioli, C., Fiorentini, L. and Piva, G. (1992) Nutritive value of guinea fowl meat. *Rivista della Societa Italiana di Scienza Dell'Alimentazione* 21(4), 373–382.

Larbier, M. and Leclercq, B. (1992) Alimentation des oiseaux en croissance et des reproducteurs. In: *Nutrition et alimentation des volailles*. INRA Editions, Paris, pp. 171–194 and 227–254.

Table 2. Cut yields (% of body weight) of standard and *label rouge* guinea fowl.

	Slaughter age (days)	Body weight (kg)	Ready to cook yield	Abdominal fat	Thigh with shank	Breast
Standard	77	1.7–1.8	70.3–71.5	2.0–2.3	25.2–25.3	15.8–17.2
Label rouge	98	2.0	69.6–69.8	1.5–2.4	24.6–25.3	16.0–17.8

Table 3. Composition (g 100 g^{-1}) of breast and thigh meat without skin (Cerioli *et al.*, 1992).

	Water	Protein	Lipids	Ash	ME (kJ 100 g^{-1})	SFA	MUFA	PUFA	S/US
Breast	74.16	25.76	1.90	1.28	475	34.26	38.46	27.74	0.52
Thigh	72.40	24.02	3.29	1.27	492	33.92	38.22	27.84	0.51

SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids (% total fatty acids); S/US, saturated/unsaturated

Le Coz-Douin, J. (1992) *L'élevage de la pintade*. Editions du Point Vétérinaire, Maisons-Alfort France, 252 pp.

Nwagu, B.I. and Alawa, C.B.I. (1995) Guinea fowl production in Nigeria. *World's Poultry Science Journal* 51, 261–270.

Sauveur, B. and Plouzeau, M. (1992) Technical and economic aspects of guinea fowl production in the world. In: *Proceedings of 19th World Poultry Congress*, Amsterdam, The Netherlands, 20–24/9/92, vol. 3, pp. 319–324.

Gums Homo- and heteropolysaccharides, typically stem exudates or seed extractives, that are water soluble and usually viscous in aqueous solutions. Also known as mucilages, they are widely used as thickeners in industry. Common plant-derived gums are arabinogalactans, pectins and glycanoxylans; common examples include guar, locust bean and larch wood gums, and gums arabic, ghatti, karaya and tragacanth. Microbially derived gums include xanthan gum, dextran and pullulan. Molecular weights are highly variable but generally the lower the molecular weight, the lower is the viscosity. (JAM)

See also: Carbohydrates; Dietary fibre; Galactomannans; Hemicelluloses; Storage polysaccharides

Gut: *see* Gastrointestinal tract

H

Haemagglutinins Agents that cause the agglutination, or clumping together, of red blood cells. They may be antibodies, viruses or plant lectins. Antibodies to erythrocytes of a different blood group can cause haemagglutination after a second blood transfusion. Viruses that can act as haemagglutinins include adenoviruses, parvovirus, togavirus, some coronaviruses, picornavirus and myxoviruses (e.g. influenza viruses).

Plant haemagglutinins (also called plant lectins or phytohaemagglutinins) are heat-labile toxic factors that are found principally in some legume seeds or beans. Some are found in the tuber or sap. They are proteins with a specific affinity for sugar molecules and are found on cell surfaces. Though lectins can affect a range of cells, some show special affinity to red blood cells of different animal species. As well as causing agglutination of red blood cells, lectins may bind to intestinal epithelial cells, reducing the action of some digestive enzymes and thus decreasing the absorption of nutrients and reducing growth rates. They can cause death (consumption of as few as five castor oil beans have been recorded as fatal to humans). Legume seeds/beans containing haemagglutinins are normally cooked and sometimes pre-soaked before human consumption. Heat treatment during pelleting may reduce haemagglutinin activity in animal feed, but usually the amount of leguminous seed protein that can be fed is limited. (EM)

Haematocrit The proportion of blood volume that is made up by red cells. It is measured using centrifuged blood treated with an anticoagulant. Haematocrit values will depend on the number and size of red blood cells. Haematocrit varies between species, e.g. sheep 32, cattle 40, pig and horse 42, dog 45. (EM)

See also: Blood

Haemochromatosis An excessive absorption of iron, relative to requirements, usually due to impaired regulation of the absorption mechanism. Excretion of iron is limited, since excess iron is stored. Although hereditary haemochromatosis is quite common in humans, it is rarely detected in other animals. It has been observed in cattle and sheep exposed to high levels of iron in feed or water. High molybdenum concentrations in the diet may enhance iron absorption. Large amounts of iron are found in the liver, lymph nodes and connective tissue, where the excess iron is stored as haemosiderin, principally in lysosomes. These tissues are darkened and brown. An excess of stored iron can cause cell death. Late in the course of the disease the liver becomes cirrhotic and there may be myocardial disease. This is a chronic condition and should not be confused with acute iron toxicity, when excess iron is given, for example as an injectable or oral supplement. (EM)

Haemoglobin The major functional component of the erythrocyte, transporting oxygen from the air in the lungs to body tissues. Haemoglobin is a coiled, folded and soluble combination of a porphyrin molecule, haem, which has an iron atom in the centre, and a protein, globin. It is found in two major forms: oxyhaemoglobin in arterial blood and carboxyhaemoglobin in venous blood. Haemoglobin is measured as total haemoglobin in g dl^{-1} blood, or as the mean content of haemoglobin (MCH) per red blood cell or as the mean cell haemoglobin concentration (MCHC). Normal values range from 8 to14 g dl^{-1} in cattle and sheep and from 10 to 14 g dl^{-1} in pigs. (EM)

See also: Blood

Haemosiderin Haemosiderin is believed to be a degradation product of ferritin containing fragments of the ferritin protein associated with its mineral core. The assembled ferritin macromolecule forms a hollow sphere-like structure in which the walls are made of 24 copies of ferritin subunits. Iron is deposited in ferritin in a form that has similarities to the mineral ferrihydrite. Degradation of the protein shell may be required for iron release from ferritin. Haemosiderin accumulates in some tissues during iron overload. (RSE)

Hair Hair follicles are generally present over almost the whole body, but follicle density varies to reflect the different needs for insulation. Thermal balance is influenced by the quantity and quality of hair and can be partly controlled by pilo-erection. Although hair serves an invaluable thermoregulatory function, its physical presence and its moderation of the thermal environment facilitate colonization by a number of obligate parasites, such as fleas and ticks.

Hair growth is affected by the seasons, determined mainly by photoperiod but also by nutrition. Photoperiod is used as a cue for weather and food availability, and the hair growth is greatest in spring and summer to prepare animals for harsh conditions later in the year. Many animals lose hair at the start of spring in preparation for new growth.

The lustre of the hair of farm animals indicates whether the quality of nutrition is adequate. It can, for example, be used to distinguish calves that have been well fed on their mother's milk from undernourished, bucket-fed calves. High quality protein is required for good hair growth, particularly in ruminants such as sheep or cashmere goats that are used primarily for wool or hair production. Specific amino acids, in particular methionine and cysteine, may be deficient and need to be provided in rumen-protected supplements. Hair mineral analysis can provide a useful index of exposure to some toxic heavy metals, such as arsenic, cadmium and lead, but not zinc or copper. External contamination must be carefully avoided. The adequacy of copper intake can be assessed by hair colour in farm animals, since low copper intakes reduce pigmentation because of the involvement of copper in the enzyme tyrosinase, the amino acid tyrosine being a precursor of the pigment melanin. Adequate zinc and selenium are also important for hair growth and quality. Residues of growth promoters can be detected in hair and may be used for detection of illegal use. (CJCP)

Halibut The genus *Hippoglossus* is composed of two large, right-eyed flatfish species: the Atlantic (*Hippoglossus hippoglossus*) and Pacific (*H. stenolepis*) hal-

Halibut may reach 200 kg, but the usual market weight is 10–25 kg. Photo courtesy of Ms D.J. Martin-Robichaud.

ibuts. The adults are long-lived, attaining weights of 200 kg, though 10–25 kg is the usual size of market fish. Both species principally inhabit cold, boreal and subarctic oceans. Research into culture of both species began in the early 1980s, much of it focused on the difficult larval stages of hatchery production. Norway first marketed cultured halibut in 1993. (RHP)

Harvesting The first process in the conservation of forage crops. Weather conditions and stage of maturity of crops at time of harvest determine feed value and field losses. Grass crops needs to be harvested at optimum quality and quantity. Field losses due to poor weather conditions at harvest can exceed 5% of the total dry matter yield of the conserved crop. (RJ)

Hatchery waste Hatchery waste consists of infertile eggs, dead embryos, shells of hatched eggs and unsaleable chickens. This can be made into protein-rich hatchery waste meal (HWM) by cooking (100°C for 15 min), drying and grinding. The high calcium content limits its use as feed but up to 4% has been included with excellent results in broiler diets. Higher weight gain, feed efficiency, protein efficiency ratio, protein digestibility, net protein utilization and biological value were observed in poultry rations containing 12% HWM compared with those containing similar amounts of fish meal. Hatchery wastes can be preserved by fermentation, or by dry extrusion, which eliminates microbial pathogens, including salmonella and *Escherichia coli*. The boiling of hatchery waste coagulates the protein, and this can be pressed and dried to produce a coagulated hatchery waste (CHW), which contains little calcium but has 1.86% lysine and 0.66% methionine. Dried raw eggs can be fed to animals but biotin deficiency may be induced by avidin contained in raw egg whites, leading to cracked hoofs, dry rough skin and loss of hair in pigs fed > 30% in the diet. Heating the eggs before drying can prevent this, as this destroys the avidin. About 10% of the egg is shell, containing 94% calcium carbonate, which can be sterilized, ground and used in pig and poultry diets. (JKM)

Key reference

Rasool, S., Rehan, M., Haq, A. and Alam, M.Z. (1999) Preparation and nutritional evaluation of hatchery waste meal for broilers. *Asian-Australasian Journal of Animal Sciences* 12, 554–557.

Hay Field-dried grass or other forage. Haymaking produces a stable forage product of adequate nutritive value with minimum loss at a reasonable capital and labour cost. The method of conservation is to dry the mown forage to remove 70–95% of the water present, using wind and solar energy whilst the crop lies in a swath or windrow in the field. The final dry matter (DM) content of the hay needs to be 85–88%. Thus 3.5 t water ha^{-1} have to be evaporated from an immature crop at 80% moisture to produce 1 t of ‘dry’ hay at 12% moisture content, compared with < 2.5 t of water when a more mature crop, containing only 75% of moisture, is dried down to the 15% at which it can be safely stored.

Immature crops are generally more difficult

Nutrient composition (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE	Calcium	Phosphorus
Hatchery byproducts[a]	937	372	0	360	217	51	220	5.2
Coagulated hatchery waste[a]	988	510	0	25	403	62	–	–
Hatchery waste meal[b]	–	442	19	140	300	98	72.6	8.4

[a] FAO (2002).
[b] Rasool *et al.* (1999).
NFE, nitrogen-free extract.

to dry because they contain more leafy material which packs together and reduces the movement of drying air through the crop. However, while a mature crop is easier to make into hay than an immature crop, the hay produced will be of lower feeding value. Thus, in deciding when each crop should be cut and which haymaking system should be adopted, a balance has to be struck between the ease and certainty of the making process and the likely feeding value of the hay that will be produced.

When forage crops are cut for hay, the plants continue to respire until the moisture content falls below 40%. Dry matter is lost during this process. The loss may be as high as 15% but is more usually about 5–6% of the total dry matter. When the moisture content of hay drying in the field reaches about 40%, further dry matter losses may occur during tedding, raking and baling. Losses from these operations may average 15%. Dry matter losses from these mechanical sources are especially severe because most of these losses come from the most valuable leafy part of the plant. Using hay crimpers and conditioners can reduce dry matter loss. Their use reduces drying time in the swath, exposure to the weather, leaf shattering and respiration losses.

The keys to keeping dry matter losses of hay to a minimum are to bale at a moisture level low enough to prevent excessive heating and to prevent infiltration of moisture into the hay after it has been baled. When hay is baled, its moisture content should not be higher than 18–22%. At higher levels of moisture, excessive heating and moulding will result in further dry matter losses. Moisture levels for safe storage of hay vary with size and density of the bale and type of hay. In general, hay in small rectangular bales should be baled at less than 22% moisture to keep moulding and heating to a minimum. Large round bales retain internal heat much longer than conventional bales; therefore, hay in large bales should have less than 18% moisture.

The stage of maturity at time of harvest is one of the most important factors affecting forage quality. Most forages will have a 20% loss in total digestible nutrients (TDN) and a 40% loss in protein from a delay of only 10 days past the optimum stage of harvest. For instance, perennial ryegrass harvested at its optimum 66% digestibility will contain *c.* 15% protein and 16% soluble sugar. In contrast, 2 weeks later most of the crop will reach the seed-head stage with a protein content of 11%, which represents a 25% loss in the value of hay. Legume–grass mixtures should be harvested when the legume reaches the desired stage of maturity regardless of the growth stage of the grass. Overall losses due to late haymaking can reach staggering proportions. Shattering and wilting losses are always proportionately higher with late-cut than with early-cut forages. If hay is baled with a moisture content of 20–22% and covered during storage, it should not lose more than 5% of its original dry matter during the first year of storage. It will lose very little of its digestible nutrients during that time or in succeeding years. Hay may suffer some loss of carotene, the precursor of vitamin A, following prolonged storage.

Large bales stored outside will suffer variable losses, depending upon the moisture of the hay at baling time, the amount of rain during the storage period, the space between the bales, the type of hay (grass or grass–legume), and the skill of the operator making the bales.

The weight loss in hay stored outdoors is quite variable but is usually in the range of 6–15% of the total hay stored. The second type of loss in outside storage is the loss in digestibility of the hay during feed-out. Some general guidelines can help to reduce outside storage losses:

- Always store bales in a well-drained area.
- Use a minimum of 1 m between bale rows for air circulation (the more space, the better).
- If bales are stored side by side, leave at least 0.6 m between bales.
- Avoid storing bales under trees and in the shade of buildings.
- If space is available, store some of the bales inside, especially the higher quality hays that should be used near the end of the feeding period.

Treatments designed to accelerate drying rates of forages reduce the potential for rain damage during field curing. Mechanical conditioning has long been used to accomplish this. Chemical drying agents have been proposed as an additional means of reducing the duration of field curing.

Potassium carbonate solutions are effective in increasing drying rates of lucerne (alfalfa) and combinations of potassium carbonate and emulsions of fatty acid esters are even more effective. Under favourable conditions drying agents are effective in reducing the time needed to cure hay by one-third to one-half. They are least effective under cool, humid conditions. However, drying agents are of limited effectiveness with grass hay.

Several carbonate-based commercial formulations are available and have generally produced similar results when used on lucerne. The carbonate-based drying agents function by modifying the waxy cutin layer of the plant so that it is more permeable to water. The formulations are most effective when applied to stems at cutting. Commercially available applicator kits include a holding tank and pump, hoses, nozzles and deflector bar mounted in front of the header about 200–250 mm above the cutting level. This device pushes plant tops over so that the spray can be directed primarily at the stems. The use of solutions containing potassium carbonate alone is cost effective for lucerne except under cool, humid conditions. Because sodium carbonate is cheaper, solutions of one-half potassium carbonate and one-half sodium carbonate may further improve the cost effectiveness of this treatment.

The use of hay preservatives permits greater flexibility in haymaking operations. Hay can be baled at moisture levels of up to 35%, thereby reducing the time required for curing. This reduces the severe leaf-shattering losses associated with handling dry forage. Because moisture content is difficult to determine accurately in curing windrows, preservatives can ensure proper preservation when hay is baled at moisture levels of 20–35%.

Anhydrous ammonia has fungicidal properties and has been used successfully in the preservation of high-moisture hays. Use of 1% anhydrous ammonia has been shown to reduce storage dry matter losses and prevent heating and mould development in hays containing up to 32% moisture. Increased crude protein content is an additional benefit of ammonia preservation. However, this method of chemical preservation has not received wide acceptance because of problems in applying the ammonia to large amounts of hay.

Recent work suggests that dry urea could be used as an alternative to anhydrous ammonia in preserving high-moisture hays and increasing the crude protein content of poor-quality hays. Application equipment has not yet been developed for this material, although some urea products and an enzyme product produced as pellets are available in the UK. Organic acids have been the most widely accepted hay preservatives. Materials such as propionic acid and ammonium isobutyrate act as fungicides to reduce mould development, heating and deterioration in hays baled at high moisture content. The most common commercial formulations consist of propionic acid and mixtures containing propionic acid and ammonium isobutyrate, acetic acid or formaldehyde. Flavouring ingredients have also been added to some of the commercial products. Organic acid preservatives must be applied at an appropriate rate as the hay is fed into the baler. Applicators consisting of a corrosion-resistant tank, a pump powered by the tractor's electrical system, spray nozzles and plastic tubing, which are commercially available, can be attached directly to most con-

The chemical composition of hay crops.

Crop	DM (%)	ME (MJ kg^{-1} DM)	Crude protein (% DM)	Fibre (% DM)
Grass hay				
high digestible	85.0	9.0	10.1	32.0
low digestible	85.0	7.5	9.2	36.6
Lucerne hay				
early flower	85.0	8.3	19.3	32.1
full flower	85.0	7.7	17.1	35.3
Red clover hay	85.0	9.6	18.4	26.6
Vetch and oats	85.0	8.1	13.8	28.8

ventional balers. Recommended application rates are based on the moisture content of the hay. These rates are appropriate for propionic acid alone, mixtures of propionic acid and acetic acid (80:20) or formaldehyde (70:30) and ammonium isobutyrate. Although hays containing moisture levels > 35% can be effectively preserved with these materials, the practice is not recommended because of preservative costs and difficulty in handling wet bales.

The chemical compositions of a range of hay crops are shown in the table.

There is a highly significant relationship between feed intake and digestibility with crops conserved as hay or dehydrated forages. For example, young steers ate 3.95 kg DM of well-made perennial ryegrass hay of 70% digestibility but only 3.4 kg of hay made from the same grass species cut 4 weeks later and at 60% digestibility. In the first trial the liveweight gain per day was 0.9 kg while there was only 0.7 kg gain from the more mature hay. (RJ)

Key references

McDonald, P., Henderson, A.R. and Heron, S.J.E. (1991) *The Biochemistry of Silage*, 2nd edn. Chalcombe Publications, Cambridge, UK.

Nash, M.J. (1985) *Crop Conservation and Storage in Cool Temperate Climates*, 2nd edn. Pergamon Press, Oxford, UK.

Raymond, F. and Waltham, R. (1996) *Forage Conservation and Feeding*, 5th edn. Farming Press, Ipswich, UK.

Haylage High dry matter (DM) silage. The point at which silage can be classified as haylage is arbitrary but a DM content of 50% or greater is often used as a guide. Haylage is made almost exclusively in big bales for use in feeding horses and sometimes sheep. The high DM content results in a restricted fermentation, thus the pH is often 5.5. Typical ranges for haylage composition are: crude protein 90–120 g kg^{-1} DM; crude fibre 300 g kg^{-1} DM; digestible energy 6 MJ kg^{-1} DM. (DD)

Heat balance It is axiomatic that the rate of metabolic **heat production** (M) must be matched by the rate of heat loss (H) or else heat storage in the body (S) occurs and the mean body temperature alters.

$$M = H + S \qquad (1)$$

Most farm animals are homeothermic or warm-blooded, but their deep-body temperature does alter by approximately 1°C between cold and hot environmental conditions; deep-body temperature can also rise by a similar amount during exercise. Variations in the temperatures of the limbs and peripheral regions of the trunk are considerably greater. Poikilotherms, which include fish, are animals whose whole body temperatures fluctuate, remaining close to that of their environment.

The rate of heat storage may theoretically be measured either by **calorimetry** (from M – H in equation 1) or by thermometry (change in mean body temperature % weight % specific heat). Neither of these methods is practical for everyday use; the first because extremely precise calorimetry is needed, and the second because the different body regions are neither defined nor accessible for temperature measurement. Instead, an empirical formula has been developed with the form:

$$S = 3.47 \times W \times (aT_b + (1 - a)T_s) \qquad (2)$$

where W is body mass, T_b and T_s are rates of change of deep-body and mean skin temperatures and 3.47 J g^{-1} represents the mean specific heat of body tissues. This formula has been validated for humans and cattle using prolonged simultaneous measurements by direct and indirect calorimetry and thermometry. In humans, values of the weighting factor, a, have been found ranging from 0.65 to 0.8. For cattle the value is higher, i.e. 0.86, which is probably because cattle have a higher proportion of their total body weight in the trunk than do humans. It is likely that still higher values of a would be appropriate for sheep and poultry. T_S is itself an average of skin temperatures of different skin regions weighted according to their areas.

For most homeotherms the maximum change in heat stored in the body between night and day or due to muscular work is small; it seldom exceeds the amount of heat normally produced in an hour. An exception is the camel, which has the facility to allow its deep-body temperature to alter by up to 6°C between night and day. This unique adaptation to desert conditions gives the camel a heat storage capacity equivalent to 3 h of heat production and thus economizes on the use of water for evaporative cooling. (JAMcL)

See also: Energy balance

Further reading

McLean, J.A. and Tobin, G. (1987) *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, pp. 181–183.

Heat increment of feeding When an animal consumes food, its heat production is increased. The increase is known as the heat increment of feeding, which has been described as the energy wasted incident to the utilization of food. The underlying causes of the heat increment are numerous and still imperfectly understood. Contributing sources include the physical or muscular work associated with eating, chewing and swallowing food, propelling it through the digestive tract and excreting the waste, chemical energy for driving digestive reactions, secretions and absorption and for intracellular synthesis of **adenosine triphosphate (ATP)** and other temporary energy reserves. Another contribution is the increased heat of fermentation, especially in ruminants, though this is not strictly part of the metabolizable energy (ME = gross energy of food minus energy of excreta). Expressed as a proportion of ME, the heat increment of feeding is $(1 - k)$, where k is the efficiency of utilization of the feed.

Heat increment can be measured as either (1) the extra heat produced in response to a single meal, or (2) the difference between the mean levels of heat production resulting from two different feeding levels. Method (1) is difficult to perform in practice, because the rate of heat production rises immediately when food is eaten and subsides only slowly; the response to one meal is seldom complete before the time for the next one. Method (2) involves establishing the animal for several days at a fixed level of feeding before measuring the average heat production over 24 h in a calorimeter; the whole procedure must then be repeated at another feeding level.

The heat increment $(1 - k)$ is the complement of the efficiency of energy utilization (k; *see* **Energy utilization**). The values found by these methods depend not only on the type of food, but also on the level of feeding and the form in which energy is retained or expended. The heat increment, or wasted energy, per unit of ME intake is greater at the high levels of food intake needed to promote growth, lactation, pregnancy, egg-laying, etc., than that at the lower level needed for maintenance. It is also greater with roughage diets than with concentrates. The heat increment of feeding is thus a limiting factor in attaining adequate nutrient intakes in highly productive animals, especially in warm climates. On the other hand, the heat increment is useful to animals that must survive in extreme cold and on poor-quality forage. (JAMcL)

Further reading

Blaxter, K.L. (1989) *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge, UK.

Heat processing: *see* Heat treatment

Heat production The heat generated by metabolic processes in the body. The rate of heat production is also known as the metabolic rate or the rate of energy expenditure. Heat production represents a large part of the total food energy and it derives from a complex chain of chemical reactions. Despite this, it can be estimated with remarkable accuracy by calculation from the rates of **oxygen consumption** and **carbon dioxide** production. This is possible because of a natural law first discovered by Germain Hess in 1838. Hess's law states that the heat produced in a chemical reaction is always the same regardless of whether it proceeds directly or via a number of intermediate steps. It means effectively that the heat of metabolizing a nutrient through the complex web of metabolic reactions that occur in the body may be estimated from measurement of the heat produced in burning the same nutrient in a **bomb calorimeter**.

The quantity of heat produced by an animal depends on many factors, including its size, the quantity and quality of food it consumes and its productive processes (maintenance, growth, lactation, etc.). It can only be estimated with any accuracy if all of these factors are known. The table gives a very crude guide to the rates of heat production of growing farm animals, expressed in kJ day^{-1} and in watts. The values given should be multiplied by approximately 1.5 for pregnant animals, by 1.75 for laying hens and by 2 for lactating animals, or even by as much as 3 for a high-yielding cow. For maintenance conditions they should be reduced to about two-thirds. (JAMcL)

See also: Indirect calorimetry

Rates of heat production.

	Chickens		Sheep		Pigs		Cattle	
Body weight	kJ day^{-1}	W	MJ day^{-1}	W	MJ day^{-1}	W	MJ day^{-1}	W
50 g	45	0.5						
70 g	65	0.7						
100 g	95	1.1						
150 g	140	1.6						
200 g	175	2.0						
300 g	215	2.5						
500 g	250	2.9						
700 g	335	3.9						
1 kg	410	4.7						
1.5 kg	560	6.5						
2 kg	670	7.7	1.2	14				
3 kg			1.5	17				
5 kg			1.8	21	1.6	20		
7 kg			2.1	24	2.1	25		
10 kg			2.6	30	3.0	35		
15 kg			3.5	40	4.2	50		
20 kg			4.5	50	6.0	65	5.0	60
30 kg			5.9	70	8.2	95	6.3	75
50 kg			7.2	85	12.2	140	10.3	120
70 kg			10.0	120	13.5	160	13.0	150
100 kg					15.0	175	16.5	190
150 kg					17.5	200	21.0	245
200 kg					20.0	235	25.0	290
300 kg							31.5	360
500 kg							40.0	470

Heat stress A condition in which environmental conditions make it difficult for the animal to lose the heat it produces, so that body temperature tends to rise (hyperthermia). Heat stress may be caused by high environmental temperature alone or in conjunction with high humidity, which limits evaporative heat loss. Heat stress can be alleviated by shade, by increased air movement and, in non-sweating species, by the provision of sprinklers, wallows, etc. (MFF)

Heat treatment Raw materials may be heated to dry them, to improve their nutritional value or to alter their structure. Heat may be applied directly, e.g. by the sun, by an oven or as steam, or indirectly, by passing material under pressure through an orifice. Under the correct conditions heat may improve the nutritional value of the material but if the conditions are incorrect heat can reduce the nutritional value or even make the material worthless. Heat is frequently used to dry raw materials (e.g. grass, blood, skimmed milk). It may also be applied with pressure to break down complex protein or carbohydrate structures and make the nutrients, which would otherwise pass straight through the animal, available for digestion. Heat is used to gelatinize starch, making it more available to many non-ruminants. It also decreases the product's density: this is useful for fish food. Heat can break down some antinutritional factors such as trypsin inhibitors, making an otherwise unacceptable material usable. Extrusion is a process by which materials are forced under pressure through a small orifice, which increases their temperature. Steam may be added to increase the temperature further but overheating can denature heat-sensitive ingredients such as amino acids and vitamins, reducing their nutritional value. (MG)
See also: Extrusion; Pressing; Toasting

Heavy metals A group of 66 elements usually defined as those with a specific gravity

Main symptoms of trace element deficiencies and excesses.

Element	Deficiency symptoms	Toxicity symptoms
Arsenic	Reduced growth rate and milk yield, reproductive disorders, sudden death	Acute: restlessness, rapid breathing, muscular and visual disorders, inflammation of digestive tract, death Chronic: reduced growth rate, weakness, haemorrhages, muscular disorders, tissue inflammation
Cadmium	–	Kidney malfunction, gastric disorders, reproductive disorders, osteomalacia, reduced growth rate and feed conversion efficiency
Chromium	Impaired growth, decreased life expectancy, eye disorders	Depressed growth, liver and kidney damage, scouring, nervous degeneration
Cobalt	Ruminants: anaemia, muscular atrophy, listlessness, loss of appetite, depressed growth, reduced viability of young	Blood disorders, anaemia, loss of appetite, impaired growth
Copper	Anaemia, impaired reproduction, depressed appetite and growth rate, ataxia, bone disorder, cardiovascular disorders, depigmentation, defective keratinization, scouring (cattle), swayback (sheep)	Retarded growth, weight loss, anorexia. Other symptoms vary with species. Terminal stage is haemolytic crisis
Iron	Anaemia, depressed growth, lethargy, lowered resistance to infection	Reduced feed intake and growth rate, weight loss, scouring, reduced milk yield Acute: diphasic shock, vascular congestion, anorexia, diarrhoea
Lead	–	Vary according to species, e.g. stiff gait, fractures, osteoporosis, kidney disorders, impaired vision, reproductive disorders, neurological disorders Acute: blindness, excessive salivation, hyper-irritability, convulsions, death
Manganese	Impaired reproduction, depressed growth, skeletal disorders, ataxia	Anaemia, depressed growth rate, leg stiffness
Molybdenum	Not reported for grazing livestock	Secondary copper deficiency
Nickel	Not reported for grazing livestock. Laboratory animals show non-specific symptoms including retarded growth and anaemia	Kidney damage, hyperglycaemia, respiratory disorders, reduced growth rate, increased mortality
Selenium	Impaired reproduction, muscular dystrophy, ill-thrift	Chronic: anaemia, dullness, rough coat, hair and hoof loss, stiffness, lameness
Silicon	Stunted growth and bone formation	Depressed digestibility, growth rate and reproductive performance, kidney stones
Tin	–	Ataxia, muscle weakness, anorexia
Vanadium	Impaired growth and reproduction, disturbed lipid metabolism, reduced milk yield and milk fat content	Chronic: depressed growth rate Acute: diarrhoea, dehydration, haemorrhage, emaciation, prostration
Zinc	Impaired reproduction, severe inappetence, depressed growth, skin abnormalities	Anaemia, depressed intake, reduced liveweight gain and feed conversion efficiency

Adapted from Smith, S.R. (1996) *Agricultural Recycling of Sewage Sludge and the Environment*. CAB International, Wallingford, UK, pp. 101–103.

< 4.5 or 5 g cm^{-3}. This definition does not include some lighter elements, such as cadmium, that are nevertheless usually considered heavy metals by virtue of their position in the periodic table. Many heavy metals can be used in animal metabolism but essentiality has only been demonstrated for a few (iron, zinc, copper, manganese, cobalt, molybdenum, selenium, chromium, tin, vanadium, nickel and arsenic) and for two in specific circumstances (lead and rubidium). Some of these are required in such small quantities that deficiencies are very rare or even unknown (see table).

The heavy metals are principally used by the body for catalytic and regulatory purposes. The capacity of some heavy metals (particularly the transition elements Zn, Cu, Ni, Co, Fe, Mn, Cr and V) for multiple valencies and their affinity for oxygen, nitrogen and sulphur ligands has rendered them invaluable as catalysts in enzyme and catalytic processes. Many of the heavy metals have been identified as essential components of metalloenzymes, though competition between metals for binding sites indicates that the sites are not specific to one element. Toxicity may arise when metals that are present in only low concentrations in nature, such as cadmium and lead, are concentrated in plant material, soil or industrial waste that is consumed by farm animals. Typically, the toxic metal will replace an essential element in the animal's metabolism; for example, cadmium and lead have a strong affinity for zinc- and calcium-binding sites, respectively, leading to a failure in the processes controlled by these elements (see table).

Deficiency problems mainly occur when livestock that are not native to an area, and are not adapted to the local mineral concentrations, are introduced and often required to grow or reproduce rapidly as part of an intensive agricultural production system. Such deficiencies may not be due to a primary deficiency of an element but a secondary effect of high concentrations of an element with which it interacts. An example is the induction of copper deficiency in cattle by high concentrations of molybdenum in pasture.

Some heavy metals, therefore, play a vital role in animal metabolism and, even though they are only required in trace quantities, they can be deficient as a result of human manipulation of animal production on a global scale. Others are less likely to be deficient but may be toxic when human activity creates concentrations that would not normally be encountered. (CJCP)

Further reading

Underwood, E.J. and Suttle, N.F. (eds) (1999) *The Mineral Nutrition of Livestock*, 3rd edn. CAB International, Wallingford, UK.

Hemicelluloses Mixtures of xylans, glucomannoglycans, arabinogalactans, arabinans and arabinoxylans. They are primarily structural polysaccharides in plant secondary cell walls and may be associated with lignin. Common in grasses, annuals, hardwoods, cereal grains, fruits and vegetables. Also present as the principal food reserve in several algae. (JAM)

See also: Carbohydrates; Dietary fibre; Gums; Storage polysaccharides; Structural polysaccharides

Hen feeding All the nutrients the modern commercial layer, layer breeder or broiler breeder hen requires, for both maintenance and production, must come from the compound feed, in the daily feed allowance. The feed is normally provided in the physical form of a coarsely ground mash containing some whole grains. This ensures that birds develop a normal gizzard to aid digestion and lower the pH at an early stage of digestion, thereby reducing the chance of infection from feed-borne sources. Feed may also be presented as a pellet or crumble but this normally leads to increased feed intake.

Commercial laying hens are normally kept in one of three different types of production systems: cages, barn or free-range. The vast majority of birds, worldwide, are kept in wire mesh cages. These are constructed in banks three to six cages high and of unspecified length. Each cage normally accommodates about five birds; however, the limiting criterion is to provide each bird with a minimum of 550 cm^2. Water is supplied via a nipple drinking system with two nipples per cage to ensure provision of normal water intake of about 200 ml per bird per day. If water intake is affected, feed intake will decline and so will egg production. A feed trough at the front of the cage provides at least 10 cm of feeding space per bird from which to consume the normal daily allocation of between 110 and 120 g of feed. **Feed intake** increases with age as body size increases and hence egg size also increases. **Nutrient requirements** only change marginally during the adult life of the bird but different diets must be fed at different stages of life, because of changes in appetite. When the bird first starts to lay she is in a net energy deficit, because her appetite is low and her nutrient intake cannot meet her egg output. As a consequence she uses body reserves to lay. As appetite increases, she comes into surplus and can replenish her fat reserves. In later life the nutrient concentrations have to be reduced as appetite increases further, to avoid the hen laying too large an egg and compromising the shell quality. Throughout the 76 weeks of the bird's life she will be in lay for up to about 385 days, during which time she may lay 330 eggs. This equates to 85% production or six eggs every 7 days, with an average egg size of 63 g. This means that the hen has a total egg mass capacity in excess of 20 kg with a feed conversion ratio (FCR) of 2.15.

It is essential that the bird receives all her daily nutrient requirements within this feed allowance. In particular she must receive sufficient calcium carbonate to enable her to create approximately 3 g of eggshell each day. She also deposits about 6 g of fat in the yolk. All the materials used for egg production have to be digested, absorbed and then synthesized on a continuous basis by the hen. The hen needs to receive the daily nutrients shown in the table. Failure to do so will result in a rapid decline in egg production. However, hens are very adaptable and can recover quickly when the nutrient supply is restored.

Daily nutrient intake requirement of laying hens.

Crude protein (g)	19.6
Crude fat	3.5
Lysine (g)	0.85
Methionine (g)	0.43
M+C (g)	0.8
Threonine (g)	0.62
Tryptophan (g)	0.22
Calcium (g)	4.2
Available phosphorus (g)	0.42
Sodium (g)	0.16
Chloride (g)	0.17
Linoleic acid (g)	2.0
Energy (MJ kg^{-1})	11.5

Altering the proportion of methionine in the diet can directly affect egg size. However, as egg size increases shell thickness decreases, because the hen produces the same amount of shell on a daily basis. An increase in the essential fatty acid content of the feed can also increase egg size but body weight remains the single largest determinant of egg size.

Feed intake is increased in alternative laying systems, such as deep litter (also known as barn and free-range). This is due partly to increased maintenance requirement due to greater activity, as well as lower environmental temperatures depending on the climate, combined with large diurnal changes, requiring a higher expenditure for thermoregulation. As a consequence of the higher intake, nutrient density can be decreased but the total energy intake usually increases. In many cases the amino acid content is maintained on these systems to maximize egg size to meet market demand.

Feeding systems used for these production systems can be track feeders, using chain drag distribution, pan feeders or tube feeders. The birds have free access to feed and water and, as a consequence, tend to eat an average of 125–135 g a day, which can increase to 150 g in cold weather.

Both broiler breeder and layer breeder hens are kept in barns, with the birds roaming freely within the confines of the house. This is to allow natural mating to occur for the production of hatching eggs. Males form < 10% of the population. Although the male does not require the same high calcium level in the feed, it is usual, for practical reasons, to provide only one feed.

Layer breeder diets are similar to commercial laying hen diets but with additional vitamins and without yolk pigmenters. Broiler breeders are a case apart as their feed is restricted throughout life. Their average daily feed intake is > 150 g but they can have an appetite of > 200 g. It is important that not all the energy is from carbohydrate, such as cereal starch: a minimum oil concentration of 40 g kg^{-1} is recommended. These hens have a high requirement for vitamins. Vitamin E is often added above the requirement as it is known to improve the immunocompetence of the bird and thus help to fight disease. (KF)

Hens: *see* Domestic fowl

Hepatoma A carcinoma derived from the parenchymal cells of the liver. It is a form of primary hepatic carcinoma whose cells organize into associations that resemble cells of the hepatic cords of the liver lobule. (NJB)

Herbicide residues Herbicides are chemicals used to control or kill unwanted vegetation. Many are quite selective for specific plants and have low mammalian toxicity. Most problems with herbicide toxicity involve human error or accident, due to accidental ingestion of concentrates or sprays. Very rarely are herbicide-treated forages toxic to livestock. Most signs of herbicide toxicity are neurological, with incoordination and convulsions. Most ingested herbicides are rapidly cleared in animals, with clearance times of a few hours. Glyphosphate ('Roundup'), one of the most common herbicides, has very low mammalian toxicity. Despite popular belief to the contrary, herbicide residues on feeds and foods are of very little toxicological concern. (PC)

Herbivore Any animal obtaining its nutrient requirements from plant material by grazing or browsing. Herbivores have various adaptations of the alimentary tract, facilitating the prehension (e.g. specialized lips and teeth) and digestion (e.g. stomachs of several compartments, or a caecum) of fibrous plant material. Domestic herbivores include cattle, sheep, goats, deer, horses and camelids. (AJFR)

Herbivorous fish A fish (usually warm-water species) that feeds on plant material, whether it be macrophytes, phytoplankton or detritus. Cultured herbivorous fishes include various Chinese and Indian carps, some tilapia species, mullets and milkfish. Chinese and Indian carps are usually reared as species mixes that occupy different herbivorous niches in culture ponds. Herbivorous fish are characterized by the presence of the enzyme maltase throughout the digestive tract, to utilize maltose generated by the digestion of starch. Digestion of cellulose depends on the presence of gut microflora. (RHP)

Further reading

Pillay, T.V.R. (1993) *Aquaculture: Principles and Practises*. Blackwell Scientific Publications, London.

Herring: *see* Fish products

Hexose A monosaccharide with the elemental composition $C_6H_{12}O_6$. Aldohexoses have six-carbon pyranose rings whereas the ketohexose fructose has a five-carbon furanose ring. As single units they are referred to as monosaccharides; as polymers they are called polysaccharides. In the open-chain form hexoses have four asymmetric carbon atoms; thus there are 16 possible **isomers**. Carbon 6 of the pyranose ring has two possible orientations, designated D and L. Within the D series there are eight isomers. Of these eight isomers, three (glucose, mannose and galactose) are important in animal metabolism. (NJB)

Key reference

Mayes, P.A. (2000) The pentose phosphate pathway and other pathways of hexose metabolism. In: Murray, R.K., Granner, D.K., Mayes, P.A. and Rodwell, V.W. (eds) *Harper's Biochemistry*, 25th edn. Appleton and Lange, Stamford, Connecticut, pp. 219–229.

Hexuronic acids Hexose sugars with the general formula $C_6H_{10}O_7$, in which carbon 6 is oxidized to an acid. D-Glucuronic, D-mannuronic and D-galacturonic acids are found in natural products. D-Glucuronic acid is a constituent of plant materials and a constituent of chondroitin and mucoitin sulphates of glycoproteins. Some xenobiotics are glucoronidated and excreted as a means of detoxification. Ascorbic acid (vitamin C) was initially classified as hexuronic acid. Galacturonic acid is a component of pectins, plant gums and mucilages. D-Mannuronic acid as a polymer is alginic acid and is used as a thickener in the food industry. (NJB)

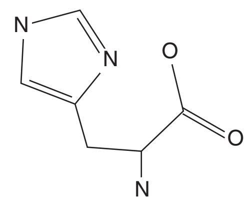
High-density lipoprotein (HDL) One of the four major classes of plasma lipoproteins: chylomicrons, very low-density, low-density and high-density lipoproteins. As the ratio of lipid to protein increases in these particles, their density decreases and they can be separated by use of an ultracentrifuge. Their density varies from 0.95 to 1.281. HDLs are synthesized and secreted from both the liver and small intestine. Specific apolipoproteins are associated with HDL particles and participate in the selected receptor-mediated endocytosis of the particle. Apolipoproteins most commonly associated with HDL are apo C, apo E and apo A. (NJB)

Hind-gut: *see* Large intestine

Hippuric acid Benzoylglycine, $C_6H_5{\cdot}CO{\cdot}NH{\cdot}CH_2{\cdot}COOH$, containing a peptide bond between benzoate and glycine. Liver enzymes activate benzoate in a manner similar to fatty acids, i.e. benzoate, $C_6H_5{\cdot}CO^-$ + ATP → benzoyl-AMP + P~P. Benzoyl-AMP reacts with glycine $H_2N{\cdot}CH_2{\cdot}COOH$ to become hippurate $C_6H_5{\cdot}CO{\cdot}NH{\cdot}CH_2{\cdot}COO^-$. Benzoic acid is not apparently catabolized but is conjugated with glycine and excreted in urine as hippuric acid. Detoxification of benzoate is one of the liver function tests. In grazing animals hippuric acid makes up a greater fraction of urinary nitrogen than that usually observed in non-ruminants. It was first identified in the urine of the horse. (NJB)

Histamine Histamine ($C_3N_2H_3{\cdot}CH_2CH_2{\cdot}NH_2$, molecular weight 111.15) is formed by the decarboxylation of histidine in mast cells, enterochromaffin-like (ECL) cells and certain hypothalamic neurons. Outside the nervous system, histamine is released in response to physiological and inflammatory stimuli. It acts as a paracrine substance by diffusing to surrounding cells to exert its effects on target tissues. In the stomach, histamine is released from ECL cells in the lamina propria following hormonal and neural stimulation. It acts on specific H2 receptors of parietal cells in the gastric mucosa to induce acid secretion. A number of pharmacological inhibitors to the H2 receptor have been developed, including cimetidine, ranitidine and famotidine. These agents antagonize histamine's effects on acid secretion in the stomach. Histamine is also released from mast cells and acts on H1 receptors in a variety of tissues. In general, it is a potent vasodilator but also stimulates smooth muscle contraction in various tissues. (GG)

Histidine An amino acid ($C_3N_2H_3{\cdot}CH_2CH{\cdot}NH_2{\cdot}COOH$, molecular weight 155.2) found in protein. This essential amino acid can be decarboxylated to form histamine, a vasoactive amine. Also, free histidine can react in the body with β-alanine to form the dipeptide, carnosine, which is found free in muscle tissue. After being incorporated via peptide linkage into protein, some of the histidine may be methylated at the 1 or the 3 position of the imidazole ring. The resulting 3-methylhistidine is found primarily in muscle actin: after its release during muscle protein turnover, it cannot be utilized or metabolized. Its excretion in the urine is therefore used as an index of muscle protein catabolism. Some animals can methylate carnosine at the 1 position of the imadazole ring, and this forms the dipeptide, anserine. Other animals may methylate carnosine at the 3 position, resulting in the dipeptide balenine. Carnosine in feeds of animal origin is fully active as a source of histidine, but neither anserine nor balenine can be metabolized to histidine. Homocarnosine is another dipeptide that is synthesized (in brain tissue) from carnosine. The functions of carnosine, anserine, balenine and homocarnosine are not known. (DHB)



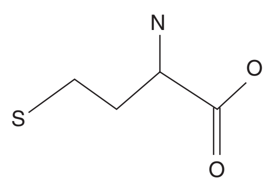
See also: Essential amino acids

Hog In the USA, a synonym for pig; but elsewhere in the English-speaking world the term refers only to a castrated male pig. Also refers to a yearling sheep (but more usually hogg or hogget). (MFF)

Hogget A yearling sheep not yet shorn (sometimes hog or hogg). (MFF)

Homeostasis The maintenance of a steady state in the cellular environment of an organism. It may require a coordinated physiological response involving the brain, nerves, heart, lungs, kidneys and spleen. Take the example of the buffering capacity of the body fluids: this requires coordination of changes in urinary excretion by the kidney and altered respiratory rates by the lungs to adjust excess acid or alkali. At a cellular level homeostasis requires control of individual steps in uptake, transport and enzyme activities such that components are altered to maintain cellular concentration gradients and substrate fluxes so that a physiological steady state can be maintained. (NJB)

Homocysteine A sulphur-containing amino acid ($HS{\cdot}CH_2{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 135.2) not found in protein. It is synthesized as an intermediate in the trans-sulphuration pathway of methionine catabolism. The compound can exist in either reduced (homocysteine) or oxidized (homocystine) form, and some tissue homocysteine may be bound and some free. About half of the homocysteine formed in metabolism is methylated back to methionine, using either betaine or 5-methyltetrahydrofolate as a methyl donor. The remaining homocysteine reacts with serine to form cystathionine, and this compound is subsequently degraded to α-ketobutyrate and cysteine. This is the trans-sulphuration pathway of cysteine synthesis. High levels of plasma homocysteine are thought to be a risk factor in cardiovascular disease in humans. (DHB)



See also: Cysteine; Methionine; Non-protein amino acids

Homocystine: *see* Homocysteine

Hooves Hoof disorders with a nutritional aetiology include laminitis in horses, and laminitis, sole ulcer and white line disease in cattle (penetration of the junction of the wall and the sole by dirt or other small particles). Laminitis in horses is most common in overweight ponies on grass, but also occurs after systemic illnesses including severe metritis, colic, cereal overeating, and overwork on hard ground. The horse shows lameness in several feet and is reluctant to move, standing with the legs placed forward. There is heat and pulsation in the feet and the horse may sweat. Treatment is contentious, but non-steroidal anti-inflammatory drugs (NSAIDs) are widely used, with removal of the original cause. Corticosteroids are regarded as harmful. Acute laminitis is rare in cattle, but can follow excess feeding of starchy feeds, with limited intake of fibre. Treatment is usually administration of NSAIDs. Sub-acute laminitis in cattle is said to be common in dairy cows fed large amounts of concentrates and living in uncomfortable cubicles so that lying times are reduced. It is thought to be a predisposing factor in the aetiology of sole ulcers and white line disease. Sole ulcers are the most common foot lesion in dairy cows in some surveys, followed by white line disease. Causative factors may include excessive starchy or high-protein concentrates and feeding grass silage with low dry-matter concentration. The strength of hooves in pigs and horses is improved by a high concentration of biotin in the diet: evidence for a similar effect in ruminants is less clear. (WRW)
See also: Biotin; Foot diseases; Laminitis

Hormone A compound produced by one tissue that is released from the organ into the blood and travels to another organ where, after binding to a specific receptor (binding protein), it initiates a chain of events that alters some aspect of cell function. An example is the action of insulin in stimulating glucose uptake by skeletal muscle. Hormones fall into two general classes: lipid-soluble, such as steroid hormones (e.g. glucocorticoids); and water soluble, such as proteins, peptides and amino acid derivatives. In general, steroid hormones regulate sexual development and function (oestrogen, testosterone), electrolyte balance (aldosterone), and stress responses (glucocorticoids). Polypeptide hormones regulate a multitude of cellular functions including gastrointestinal function, metabolism and cell growth. Hormones may act on the same cell that secretes the hormone (autocrine), on nearby cells (paracrine) or on cells in a distant organ (endocrine). (RSE, GG)
See also: Epinephrine; Gastrin; Gastrointestinal hormones; Gonadotrophin; Gonadotrophin releasing hormone; Glucagon; Glucocorticoids; Insulin; Insulin-like growth factor; Motilin; Norepinephrine; Oestrogen; Pancreatic hormones; Plant oestrogens; Parathyroid; Progesterone; Prolactin; Thyroid; Vasoactive intestinal polypeptide; and individual hormones.

Horse feeding Horses have widely varying individual needs, particularly in respect of specific feeds that are accepted and eaten. Needs are also affected by such characteristics as age and dental health. Thus, horses should be fed as individuals, making allowance for apparent differences in energy needs, irrespective of body weight, and differences in performance capability, muscular strength and activity. The nutrient and feed requirements given in the tables overleaf are satisfactory for perhaps 95% of the population of healthy animals of each type and age in an equable environment.

The horse is a selective grazing and browsing non-ruminant herbivore that uses soluble and insoluble dietary carbohydrates as its primary energy source. Pastures grazed exclusively by horses decline in value owing to the spread of ungrazed weed species and the build-up of intestinal parasitic worms. Mixed grazing with ruminants aids the maintenance of satisfactory plant species and the containment of a worm burden in the grazing sward. Forage preserved as hay, silage or haylage should be free from contamination by mould and by soil, as soil increases, particularly, the risk of botulism transmission. Haylage should have a dry matter content of at least 50%.

Horses use their lips, tongue and teeth in the prehension and ingestion of feed. The adult horse has 40–42 teeth. Forage is sheared off by the 12 incisors and taken in with use of the lips. Grinding by 24–26 molars and premolars reduces feed to a particle size suitable for swallowing, when it is mixed with saliva. Thus, for horses with sound teeth, large cereal grains such as barley and oats need not be crushed or ground but small grains, such as millet and grain sorghum, should be rolled, cracked or coarsely ground before feeding. Rough rice (i.e. the grain before removal of the hull) and dehulled rice are reasonably satisfactory but rice bran is unsuitable for feeding on its own. Maize grain is frequently very hard and should be cracked before feeding, especially for older horses or those with poor teeth.

Many by-products are suitable for horse feeding, including wheat bran, oil-extracted rice bran, dried sugarbeet pulp, citrus pulp, dried grass, dried lucerne (alfalfa), good quality fats and mould-free chopped carrots. Other cut root vegetables can be used with care. Potato tubers must not be green. Satisfactory proteinaceous by-products include meals of soybean, sunflower seed, cotton seed (low in gossypol), groundnut (aflatoxin-free), rapeseed (low in goitrogenic glucosinolates), cooked linseed, peas and field beans. All concentrate feeds should be free from mould and pathogenic bacterial contamination.

The adult horse's stomach holds only 8–9 l (550 kg Thoroughbred mare). A probable consequence of this is that the grazing horse takes many small feeds distributed throughout a 24 h period. Horses given a large daily allowance of cereal grain should receive this in several small meals, otherwise the stomach contents achieve too high a proportion and amount of dry matter. The small intestine of a 450 kg horse is approximately 20–25 m in length. Most of the digestion occurs in this organ. The large intestine is made up of a blind dilated pouch, the caecum, having a volume of 25–35 l in a 500 kg horse, the ventral and dorsal colon, with a capacity of approximately 70 l, and the rectum. In the large intestine, undigested forage and other feed residues are held for many hours. During this time microbial fermentation occurs, with the production and absorption principally of **volatile fatty acids**, water and gas.

Whereas the wild horse subsists on leafy browsed and grazed forage, the higher energy requirement and restricted feeding time of the domesticated working horse requires that forage is supplemented with more energy-dense feed, such as cereal grain. This may introduce a risk to health, if starch in excess of 0.4% of body weight is given at each meal. A large daily allowance of cereals requires that this is divided into three to five meals and that any increase in daily intake is no more than 200 g daily for a 500 kg horse. An excessive starch intake may lead to gastric ailments and result in sufficient starch reaching the large intestine to cause an explosive fermentation, a rise in L-(+)-lactic acid content of the lumen of the caecum and ventral colon, with the risk of metabolic acidosis.

Water that does not come from piped mains should be demonstrably free from pathogenic microbial and chemical pollution before being supplied to horses. It is good husbandry to provide a source of safe drinking water for all horses. Nevertheless, horses that are maintained entirely on high-quality pastures in temperate latitudes can subsist without a supply of free water, unless they are lactating or heavily worked, or the ambient daylight temperature persists above 25–30°C. For the maintenance of an adult horse in an equable environment, the total water requirement is approximately 2 l kg^{-1} dry matter intake. Horses that are managed on air-dry concentrates, or are lactating or are worked in tropical and subtropical regions should preferably have *ad libitum* access to water. (Asses can survive without a source of free water for long periods.) Heavily worked horses should be offered water frequently during hours of work to avoid excessive intakes at any one time.

Horses have a metabolic requirement for all the recognized vitamins and minerals. If adult horses receive a diet of cereal grain and high-quality forage, adequate quantities of ascorbic acid are synthesized in the tissues and adequate amounts of the other water-soluble vitamins (apart from biotin and possibly thiamine), as well as vitamin K, are synthesized by the gut microflora and are absorbed. Thus, the dietary requirements are for vitamins A, D and E, biotin and possibly thiamine.

Cereals and forage for horses should be produced under conditions of good husbandry, harvested without microbial and other damage, stored soundly and be no more than 2–3 years old. If horses are to subsist on root vegetables and poor-quality forage, other vitamins will be needed in the diet for optimum performance.

Young foals need a dietary source of cyanocobalamin (B_{12}), normally obtained from the milk of their dam, and early-weaned foals should be given a supplementary source of all the B vitamins. Vitamin A supplementation is necessary for all horses if the forage contains insufficient amounts of β-carotene. The horse converts the mixed carotenes of grass and clover to vitamin A relatively inefficiently (approximately 40 μg carotene μg^{-1} vitamin A produced). Vitamin D_2 or D_3 supplementation will be needed if the forage has been artificially dried, or if horses are housed for long periods. Outside the temperate latitudes, or in high temperate latitudes, vitamin D supplementation is necessary. The minerals calcium (Ca), phosphorus (P), magnesium (Mg), sodium (Na), potassium (K), chloride (Cl), sulphur (S), copper (Cu), cobalt (Co), fluorine (F), iodine (I), iron (Fe), manganese (Mn), selenium (Se), zinc (Zn) and probably silicon (Si) and chromium (Cr) are required in the diet. Horses given tropical forage that contains significant amounts of oxalates (more than 5 g total oxalates kg^{-1} with a Ca:oxalate ratio of less than 0.5:1) will require further supplements of Ca in their diet. If mineral problems are suspected, the dietary amounts of digestible Ca and P are the minerals most likely to be in error. Horses that receive at least half the dry matter of their diet as good quality leafy forage grown in temperate latitudes, with cereal grain, may need no mineral supplementation. An exception to this is where horses are heavily worked, especially in hot weather, when they will require additional sodium chloride. In some places soils, forages and other crops contain inadequate copper, selenium or iodine and supplements of these will be required. The soil in a few regions contains toxic amounts of selenium and crops grown on such soils should not be used for horses. Some pasture species absorb certain heavy metals (e.g. cadmium) through their roots. Such grazing areas and herbage can become harmful.

The daily digestible energy (DE, in MJ day^{-1}) requirement for maintenance can be estimated from equations 1 and 2. This requirement is directly proportional to body weight and for horses ranging in size from 125 kg to 600 kg the requirement is in accordance with the relationship (where w is the weight of the horse, kg):

$$DE = 5.9 + 0.13 \quad (1)$$

For horses exceeding 600 kg body weight, physical activity is generally less and the relationship is:

$$DE = 7.61 + 0.1602w - 0.000063w^2$$
(NRC, 1989) (2)

The energy needs for growth, work, etc., are given in Table 1. Dietary protein, Ca and P requirements are given in Table 2 and the dietary requirements for other minerals and the vitamins are given in Table 3. The dietary requirement for protein assumes that the protein is derived from forage of adequate digestibility, cereal grain and protein concentrate meals of reasonably high biological value (BV). With this assumption the BV of the mix should be adequate. If root vegetables are used, with protein concentrates of poorer indispensable amino acid balance, the lysine and possibly the threonine content of the diet

Table 1. Digestible energy (DE) (MJ day^{-1}) requirements of horses and ponies for various functions[a].

	Mature weight			
	200 kg	400 kg	500 kg	600 kg
Mature horse				
maintenance	31.0	56.1	68.6	81.2
Mares				
Last 90 days				
gestation	35.6	64.9	79.5	94.5
Lactating mare				
1st 3 months	64.0	101.2	122.3	141.0
3 months to				
weaning	51.0	82.4	102.0	120.9
Stallion				
Breeding	38.9	70.3	85.8	101.7
Non-breeding	35.0	62.0	75.0	89.0
Weanling				
6 months old	35.0	57.3	67.4	75.7
Yearling				
12 months old	39.7	68.2	84.1	100.0
Long yearling				
18 months old	37.5	69.0	87.9	104.6
Two-year-old				
Excluding work	33.0	64.0	78.7	98.3
Maintenance plus				
1 h moderate work	47.7	90.0	110.1	135.1

[a] The required daily intake (kg) of air-dry feed may be estimated by dividing the DE day^{-1} values in this table by the air-dry DE kg^{-1} content of feed stuffs. Typical values are 7–8 MJ kg^{-1} for a grass and clover hay mixture, 11.5 MJ kg^{-1} for oat grain and 12.8 MJ kg^{-1} for barley grain.

Table 2. Recommended nutrient concentrations in diets with 90% dry matter and 9 MJ DE kg^{-1} for horses and ponies.

	Crude protein (g kg^{-1})	Ca (g kg^{-1})	P (g kg^{-1})
Mature horses and ponies at maintenance[a]	72	3.2	2.0
Mares, last 90 days of gestation	94	5.5	3.0
Lactating mare, first 3 months	120	5.5	3.0
Lactating mare, 3 months to weaning	100	4.0	2.5
Creep feed	160	8.0	5.5
Foal, 3 months old	160	8.0	5.5
Weanling, 6 months old	135	6.0	4.5
Yearling, 12 months old	115	5.0	3.5
Long yearling, 18 months old	105	4.0	3.0
Two-year-old, light training	95	4.0	3.0
Mature horse, light to intense work	95	3.2	2.0

[a] Also for non-breeding stallions. In the breeding season stallions should receive a diet providing 94 g crude protein kg^{-1} feed.

Table 3. Mineral and vitamin requirements of horses and ponies kg^{-1} diet (90% dry matter and 9 MJ DE kg^{-1}).

	Mature horse maintenance[a]	Last 90 days gestation, lactation and growing horse[b]
Sodium (g)	3.5	3.5
Potassium (g)	4.0	5.0
Magnesium (g)	0.9	1.0
Iron (mg)	40	50
Zinc (mg)	60	80
Manganese (mg)	40	40
Copper (mg)	15	30
Iodine (mg)	0.1	0.2
Selenium (mg)	0.2	0.2
Cholecalciferol, vitamin D_3 (mg)	10 (400 IU)	10 (400 IU)
Retinol, vitamin A (mg)	1.5 (500 IU)	2.0 (666 IU)
D-α-Tocopherol, vitamin E (mg)	30	30
Thiamine (mg)	3.0	3.0
Available biotin (mg)	0.2	0.2

[a] Also for the stallion out of the breeding season.
[b] Also for the stallion in the breeding season.

will limit performance. In this situation higher concentrations of dietary protein, or synthetic supplements of lysine-HCl, will be needed for optimum performance. (DLF)

Hydrochloric acid An inorganic acid, HCl, which is secreted into the stomach from the parietal cells in the gastric glands. The secretion varies with the diet but the HCl concentration in gastric juice is normally about 0.1 M, sufficient to lower the pH of the digesta to less than 3.0. HCl is bactericidal, it denatures proteins and it is essential for the activation of pepsinogen, the secreted inactive precursor of pepsin. (SB)
See also: Stomach

Hydrogen Gaseous hydrogen, H_2, is formed during anaerobic fermentation in the rumen of ruminants and, to a lesser extent, in the large intestine of most animals. Some or most of the hydrogen released by fermentation may be converted to **methane** by methanogenic bacteria. (SB)
See also: Fermentation

Hydrogen cyanide: *see* Cyanide

Hydrogen sulphide An extremely toxic gas (H_2S). It is produced by anaerobic fermentation in animal wastes and in intestinal contents from sulphate, SO_4^{2-}. It can be produced in the metabolism of methanethiol CH_3SH (methyl mercaptan), which is derived from the metabolism of the amino acids methionine and *S*-methylcysteine. (NJB)

Key reference

Benevenga, N.J. and Steele, R.D. (1984) Adverse effects of excessive consumption of amino acids. *Annual Review of Nutrition* 4, 157–181.

Hydrogenated fats Triacylglycerols, mainly of vegetable origin and rich in polyunsaturated fatty acids, that have undergone chemical hydrogenation to reduce their iodine value and increase their melting point. This process is used to produce margarines and can result in the production of *trans* unsaturated fatty acids. Unsaturated fats are also hydrogenated by the microflora of the rumen. (JRS)

Hydrogenation: *see* Hydrogenated fats

Hydrolases Enzymes that catalyse hydrolytic cleavage by adding water across C–O, C–N, C–C and other bonds. An example of a C–O hydrolase is cholesteryl ester hydrolase, which produces free cholesterol and a free fatty acid. Another example is lipase, which produces free fatty acids and glycerol from triacylglycerols. Peptidases hydrolyse C–N bonds, separating the carboxyl carbon of one amino acid from the amino-nitrogen of another. A C–C cleavage occurs in L-tyrosine catabolism when fumarylacto-acetate is converted to acetoacetate and fumarate. (NJB)

Hydrolysis The process whereby water is added across C–O, C–N, C–C and other bonds to create two compounds with their original functional groups. Hydrolysis of the C–O linkage converts the functional group from an ester to an alcohol and an acid. Hydrolysis of the C–N linkage in a peptide functional group produces an acid and an amine. The converse process is called condensation. (NJB)

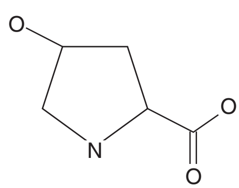
Hydroxybutyrate In metabolism, 3-hydroxybutyrate ($CH_3 \cdot CHOH \cdot CH_2 \cdot COO^-$) is one of the ketone bodies and is usually produced from acetoacetate ($CH_3 \cdot CO \cdot CH_2 \cdot COO^-$) followed by reduction of the keto group by NADH to form 3-hydroxybutyrate (*see* **Ketones**). (NJB)

Hydroxycholecalciferols: *see* Calciferol

Hydroxylysine An amino acid ($H_2N \cdot CH_2 \cdot CHOH \cdot (CH_2)_2 \cdot CHNH_2COOH$, molecular weight 163.2) found in protein (mainly collagen). It is synthesized in the body by hydroxylation of protein-bound lysine. (DHB)

See also: Lysine

Hydroxyproline An amino acid ($C_4OH_8N \cdot COOH$, molecular weight 131.1) found in protein (mainly in collagen). It is synthesized in the body by hydroxylation of protein-bound proline. (DHB)



See also: Proline

Hypercalcaemia A condition of excessively high blood calcium concentration which, if prolonged, can lead to metastatic calcification of soft tissues. The major nutritional cause of hypercalcaemia is vitamin D intoxication. (JPG)

See also: Hyperparathyroidism

Hypercarotenosis Excessive accumulation of carotenoids in the plasma and tissues following ingestion of large amounts of β-carotene and other carotenoids. It can give a yellow-orange tint to skin and internal organs but does not result in vitamin A intoxication. (JPG)

See also: Vitamin A

Hyperglycaemia An elevation of blood glucose. A brief hyperglycaemia is to be expected after a meal; a prolonged elevation of plasma glucose concentration can be detrimental to health. In non-ruminant animals the expected plasma glucose concentration is 4.4–5.5 mmol l^{-1} (80–100 mg dl^{-1}). Prolonged elevated plasma glucose concentrations of 16–28 mmol l^{-1} (300–500 mg dl^{-1}) such as those observed in diabetes are detrimental. An increased glucose loss in the urine (glycosuria), increased urine volume (polyuria) and a decreased body protein content (because of a decrease in protein synthesis and increased use of protein for gluconeogenesis) are all expected consequences of prolonged uncontrolled glucose concentrations. (NJB)

Hyperinsulinaemia An elevation in the concentration of plasma insulin. A brief hyperinsulinaemia may be expected after a meal but a prolonged elevation of plasma insulin may be deleterious. Clinical reference values for serum insulin vary from 29 to 181 pmol l^{-1} (4–25 μU ml^{-1}). The consequences of excessive levels of insulin are low plasma glucose concentrations (< 3 mmol l^{-1}), resulting in a limitation of glucose to support the nervous system. This can lead to progressive deterioration of normal behaviour, i.e. disorientation, lethargy, coma, convulsions and death. (NJB)

Hyperkeratosis Hypertrophy of the stratum corneum of the skin. This may be caused by poisoning with chlorinated naphthalenes (insecticides such as BHC and DDT, generally no longer used because organochlorine compounds enter the food chain) and is seen as thickening and roughness of the skin. (WRW)

See also: Parakeratosis; Skin diseases

Hyperlipidaemia Elevated levels of lipids and cholesterol in the blood, also called hyperlipaemia. It is associated with decreased feed intake and mobilization of adipose tissue at times of high nutritional demand, particularly in obese animals. This can alter the lipid content of platelets and the endothelial cells that line blood vessels, and the risk of thrombosis (blockage of blood vessels) increases. Hyperlipidaemia is seen in cattle and horses with fatty liver disease and in dogs with pancreatitis. (EM)

See also: Liver diseases

Hypermagnesaemia A condition of abnormally high blood magnesium concentration. Small (20–50%) increases in blood magnesium concentration are harmless and often occur secondary to disorders that elicit an increase in parathyroid hormone secretion, which increases renal conservation of magnesium. (JPG)

Hyperparathyroidism Abnormally increased activity of the parathyroid glands which may be primary or secondary. The primary condition is associated with either a tumour or hyperplasia of the parathyroid cells. Secondary hyperparathyroidism is usually of nutritional origin, often as a result of an excessive intake of phosphate relative to calcium, leading to the formation of insoluble calcium phosphate in the more alkaline regions of the small intestine. This in turn leads to incipient hypocalcaemia. A deficiency of vitamin D may also be responsible for a decrease in plasma calcium ion concentration, as may an excessive intake of oxalate. Chronic renal failure with consequent impaired excretion of phosphate also leads to secondary hyperparathyroidism. (ADC)

Hyperphagia Overeating, when spontaneous food intake is more than required for meeting nutrient requirements. Temporary hyperphagia can be induced by selective damage to the ventromedial hypothalamus, or provision of highly palatable food; but it is difficult to identify with certainty in birds (*see* **Overfeeding**). Compare with hypophagia (undereating) and aphagia (no eating). (JSav)

Hypertension High arterial blood pressure. Measurement of arterial blood pressure is more difficult in animals than in humans but, even so, hypertension appears to be less common and most likely to be a result of disease in a variety of organs. Arteriosclerosis, which is similar to the vascular changes seen in humans, can be found in pigs with organomercurial poisoning and oedema disease, and in the vessels of the heart in mulberry heart disease and hepatosis dietetica. (EM)

Hyperthermia A condition in which the core body temperature is elevated above the normal range for more than a brief period of time. It can result from heat stress, when the animal is unable to dissipate heat as fast as it is produced and gained from the environment. It can also be symptomatic of disease, especially certain infectious diseases. The susceptibility to hyperthermia is increased by the heat increment of feeding. (MFF)

Hypervitaminosis Excessive intake of one or more vitamins, especially A and D which, being fat-soluble, accumulate in the liver. Adverse symptoms, which occur at several hundred thousand IU vitamin A or D kg^{-1} ration, are typically growth depression and renal tubular mineralization for vitamin D and lameness for vitamin A. There is some antagonism between these two vitamins, and hypervitaminosis A may also be alleviated by large doses of vitamin E. (CJCP)

Hypocalcaemia A condition of abnormally low calcium concentration in the blood which disrupts nerve and muscle function. The onset of lactation in ruminants can cause acute hypocalcaemia (*see* **Milk fever**), requiring intravenous calcium administration to prevent death. Prolonged inadequate dietary calcium can also cause a moderate chronic hypocalcaemia. Renal failure causes hypocalcaemia in many species. (JPG)

Hypoglycaemia A deficiency of glucose in the blood. It can quickly affect the nervous system and result in disorientation and collapse, so glucose levels are maintained at normal levels by a range of homeostatic mechanisms, even in the early stages of starvation. When there is a high requirement for glucose, e.g. in the heavily pregnant ewe or lactating animal, low energy intake may lead to hypoglycaemia and then to acetonaemia (ketosis). Hypoglycaemia is common in newborn, weak lambs and piglets. (EM)
See also: Ketosis; Liver diseases

Hypomagnesaemia A condition of abnormally low blood magnesium concentration which can interfere with cell function, especially nerve cell function, leading to tetany and convulsions. It is caused by inadequate dietary magnesium or, as commonly occurs in ruminants, interference with magnesium absorption by potassium or ammonia. (JPG)

Hyponatraemia Inadequate intake of sodium. It mainly affects grazing herbivores. Salt is an inexpensive ingredient of herbivore feed supplements and so it is usually added in sufficient quantities to prevent hyponatraemia. It is mainly unsupplemented grazing animals that are susceptible. The appetite for sodium is acute in most herbivores but very high concentrations are unpalatable, so that salt can be added at comparatively high levels to feed blocks to regulate the intake of energy-rich ingredients.

Sodium is readily taken up by plants and the concentration varies considerably with the soil type and the plant's translocation ability. Although sodium is an essential trace element for farm animals and its concentration in animal food is very variable, the homeostatic mechanisms for maintaining a constant sodium concentration in blood are extensive. It is therefore effectively conserved, principally by recovery in the kidney, but is not stored as effectively as other minerals. The losses of sodium in milk are not homeostatically controlled and high-yielding lactating dairy cows grazing pasture without supplements are particularly at risk of inadequate sodium intake. In addition, the use of potassium fertilizer restricts sodium uptake by the grass plant, with concentrations sometimes declining to below 1 g Na kg^{-1} dry matter. Cattle grazing tropical grasses are especially at risk, as the sodium concentrations of such grasses are very low and sodium losses in sweat can be high.

The effects of hyponatraemia on herbivores are non-specific and relate principally to attempts by the animal to restore the sodium balance. Milk production is reduced in dairy cows and a pica develops that causes the cattle to lick objects. There is a general loss of appetite and the animal loses condition and acquires a haggard appearance, with lustreless eyes and a dry, harsh coat. The best diagnostic method is to assess the ratio of sodium to potassium in saliva, which is used to recycle surplus sodium. The ratio should be between 17:1 and 25:1; anything less than 15:1 indicates possible sodium deficiency. The correct diagnosis can often only be confirmed by observing the impact of supplementation, with a rapid increase in appetite and milk production. (CJCP)

Hypophosphataemia A condition of abnormally low phosphorus (inorganic phosphate) concentration in the blood. Dietary phosphorus inadequacy is the common cause and, if chronic, leads to rickets and osteomalacia. Severe acute hypophosphataemia can occur at the onset of lactation in dairy cows, contributing to the 'downer cow' syndrome. (JPG)
See also: Parathyroid; Rickets

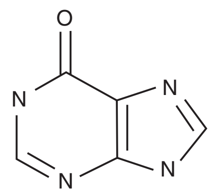
Hypothalamus An area of the brain beneath the thalamus at the base of the cerebrum. It controls many peripheral autonomic mechanisms, somatic functions and endocrine activity. In particular the hypothalamus regulates water balance, body temperature, sleep, hunger and thirst. It also influences the release and inhibition of hormones from the anterior pituitary gland (hormones affecting reproduction) and the thyroid (hormones affecting metabolism). (EM)

Hypothermia A condition in which the temperature of the body is below the normal range for more than a brief period of time. It can result from exposure to a cold environment, when the animal is unable to generate heat as fast as it is lost, and can also occur in certain disease conditions. The susceptibility to hypothermia is increased in animals that have a low rate of heat production, e.g. newborn mammals that have not suckled. (MFF)

Hypothyroidism A syndrome involving inadequate secretion of thyroid hormones by the thyroid gland, causing retarded growth, impaired reproduction, reduced milk production and an inability to increase metabolic rate in response to cold weather. Nutritional causes include dietary iodine deficiency or the presence of goitrogenic substances in the diet. (JPG)

See also: Goitre; Goitrogen; Iodine

Hypoxanthine An organic compound with the elemental composition $C_5H_4N_4O$, normally found in solution in cells. It is one of the intermediates in the catabolism of the purine adenosine to uric acid. Uric acid is the end-product of purine (adenosine and guanosine) catabolism and is excreted in the urine. (NJB)



Hypoxia Inadequate oxygen supply. This can be caused by vasoconstriction during parturition. The resulting lethargy may result in mammals failing to suckle in the crucial hours after parturition. (JMF)

I

Ideal protein The pattern of amino acids (mg g^{-1} N) in the diet that can meet the needs of an animal with the lowest dietary intake of nitrogen. Because the amino acids absorbed by non-ruminants are derived directly from the diet (which is not true of ruminants), the concept of 'ideal protein' is usually applied only to non-ruminants. To develop the amino acid pattern of 'ideal protein', the first step has been to define an appropriate ratio of available lysine to energy for the animal in question, taking into account its maintenance requirements for amino acids, its expected level of production, composition of gain, genetics, sex and environment. The requirements for the other indispensable amino acids are then related to lysine, using data from experiments identifying maximum responses to incremental additions of amino acids, with growth, nitrogen retention or amino acid accretion as criteria. Factors to be taken into account are the variation in digestibility, amino acid availability and amino acid interactions in digestion, transport and uptake, as well as their use for protein synthesis and catabolism. An additional concern is that the pattern of amino acids required changes with body weight and rate of growth: at higher body weights and at lower rates of growth a larger proportion of the daily requirement is for maintenance and a smaller proportion for protein accretion. Because the pattern of amino acids required for maintenance has been shown to be different than that needed for growth, the overall pattern changes. Some concern must also be focused on the amount and pattern of dispensable amino acids that need to accompany the ideal pattern of the indispensable amino acids, because 'ideal protein' is a concept that addresses more than an ideal indispensable amino acid pattern. In summary, 'ideal protein' is a working model, not a fixed value, because in all probability, in food animal production, 'ideal protein' changes over the production period. (NJB)

Ileal digestibility: *see* Digestibility

Ileum The distal section of the small intestine located between the jejunum and the large intestine. At the end of the ileum is the ileocaecal junction where digesta enter the caecum (as in the horse) or the ileocaecocolic junction where digesta enter both the caecum and colon (as in pigs, ruminants and poultry).

The absorptive surface of the ileum is relatively smaller than in the upper intestine because the villi are shorter and the crypts not as deep. Because the **absorption** of those degradation products that are absorbable in the small intestine is completed at the terminal ileum, digesta collected from this site are often used to determine the **digestibility** of nutrients in the upper digestive tract.

In birds, the proximal ileum is the most important site for absorption of the end-products of digested lipids, carbohydrates, and proteins.

In the ileum there is nearly complete reabsorption of **bile** acids via a specific transport system, which operates by sodium co-transport, directly back to the liver (enterohepatic recirculation). There are also mechanisms for electrolyte absorption, including chloride-coupled sodium absorption, chloride–bicarbonate exchange, bicarbonate absorption and potassium absorption, though generally these systems are more important in the colon.

In newborn animals the ileum is the main site for the absorption of immunoglobulins by pinocytosis. The same mechanism is probably also involved in the absorption of the complex between B_{12} and intrinsic factor, a glycoprotein with a molecular weight of 60,000 from the gastric mucosa.

The ileum plays an important role in controlling the transit of digesta through the small intestine so as to ensure efficient absorption of nutrients. This control is achieved by isolated segmental contractions that are also more effective in mixing than propelling. (SB)
See also: Gastrointestinal tract

Imino acids Amino acids that have an imine R·HC=NH group. Most of the α-amino acids released upon hydrolysis of protein can be described by the general formula $R{\cdot}HCNH_2{\cdot}COOH$, where the amino group $-NH_2$ is on the α carbon. Two amino acids that do not have this general structure are proline ($C_5H_9NO_2$) and hydroxyproline ($C_5H_9NO_3$), which are correctly designated as α-imino acids. (NJB)

Immune tolerance A lack of response by the immune system to an antigen to which it has been previously exposed. Tolerance can be acquired during early gestation before the fetus becomes immunocompetent, e.g. to an early viral infection leading to persistent infection or to an antigen from a non-identical twin sharing placental circulation. The blockade theory describes immune tolerance in the neonate caused by the continued presence of an antigen in the thymus 'deleting' the immune response. It is believed that immune tolerance in old age is caused by either a lack of immune cells, the action of T suppressor cells or possibly the absence of interleukin-2, a cytokine released by T cells that stimulates the immune response. (EM)

Immunity The ability of animals to resist disease, usually resistance to an infection or infectious disease. There are two major types: innate and acquired (Fig. 1). Innate immunity acts as a first line of defence by presenting chemical and physical barriers to infectious organisms and other noxious substances gaining entry to the body. Antimicrobial proteins and enzymes are present in mucous secretions, which cover many of the non-keratinized surfaces of the body, e.g. respiratory and gastrointestinal tracts. Acids and lipids present on the skin deter bacterial establishment. The presence of body hair acts as a physical barrier to damage or infection. The presence of cilia on epithelial cells prevents pathogens reaching the cells. Natural immunity is influenced by genetic and age factors and some pathogens are completely or partially host-species specific. The presence of certain genes may confer resistance or susceptibility to a particular pathogen. Irrespective of previous exposure, animals may be resistant to specific pathogens at a certain age; for example, rotavirus only causes disease in the very young animal.

Internal innate mechanisms involve body cells and fluids. These can act independently to protect the animal from invasion but also act in combination with specific immune defences. Phagocytosis is the recognition, adherence and engulfing of foreign material by granulocytic leukocytes (neutrophils), monocytes and macrophages. Once within a phagosome inside the phagocytic cell, the foreign invader, e.g. bacterium, is killed by a variety of chemicals, including acids, proteolytic enzymes and lysosyme peroxidase. However, some bacteria can survive phagocytosis, e.g. some staphylococci, listeria and mycobacteria.

Interferons are cellular proteins produced early in response to microbial infection, par-

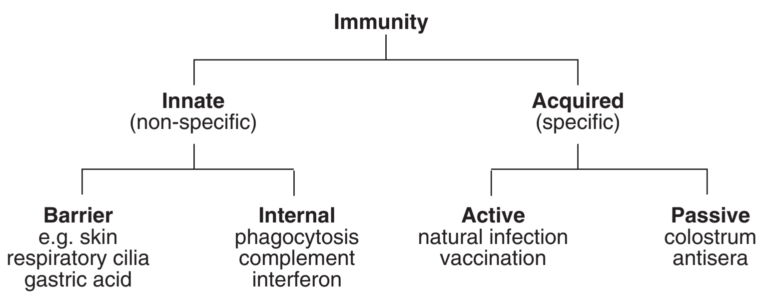


Fig. 1. Different types of immunity.

ticularly by viruses. They spread by the blood (and saliva) and diffuse through extracellular fluids to cells that have an interferon receptor. Interferon prevents viral replication by inhibiting the production of viral proteins by ribosomes. Interferons are specific to host species but are non-specific in their activity.

Inflammation is the defensive reaction of tissues to injury. It can be stimulated by many noxious agents: heat, excessive cold, chemical burns, physical injury and invasion by microorganisms. The cardinal signs of inflammation are redness, swelling, heat, pain and sometimes loss of function. Inflammation can occur in any tissue and is generally designated by the suffix '-itis'; for example, enteritis is inflammation of the intestine. In the inflammatory reaction, increased vascular permeability and a cascade release of messenger proteins increase the availability of phagocytic cells and non-specific and specific defence chemicals at the site of injury. Chemotaxis specifically draws white blood cells to the site and acute phase protein production is stimulated. These proteins include fibronectin, which coats bacteria and promotes phagocytosis, and the complement system, which is a cascade release of proteins that act on cell or microbe surfaces to enhance clumping of bacteria and cell lysis. C-reactive proteins facilitate phagocytosis. Lysozyme and iron-binding proteins remove the iron available for and necessary to bacteria for multiplication. Later in the inflammatory reaction, chemicals involved in repair and the healing process are found. Some of the features of inflammation, though it is a major defence mechanism, are undesirable in certain disease conditions, e.g. pneumonia, meningitis and arthritis. Anti-inflammatory drugs may be used to suppress some or all of the inflammatory responses.

Specific or acquired immunity is associated with either the humoral response or cell-mediated immunity. Lymphocytes are involved in both types. The B cells involved in the humoral response originate from bone marrow stem cells, develop in tonsils and intestinal lymphoid tissue (especially the bursa of Fabricius, or cloacal bursa, in birds) and then may migrate to other lymphoid tissues. Macrophages process phagocytosed antigens and present them to lymphocytes of both the humoral and cell-mediated immune systems. These specific antigens in contact with B cells stimulate the cells to divide and develop into antibody-secreting plasma cells. Plasma cells are found in lymph nodes, the spleen and at sites of infection. The antibody produced is specific to the protein shape of the presenting antigen and will bind with it. As pathogenic organisms have a range of antigenic sites (epitopes), a single pathogen will stimulate the production of a range of different antibodies. Frequent stimulation of the immune system by the same antigen leads to a build-up of antibody production and establishment of a memory cell population. This enables a rapid antibody response to be mounted if the animal encounters the same antigen in the future. The antibody response is not immediate; it takes several days from initial stimulation for significant levels to be found but antibody levels may remain high for months or years.

Lymphocytes originating from the thymus (T cells) are found in many body tissues and are responsible for cell-mediated immunity. These cells act directly on invading pathogens and infected cells. They are particularly important in some viral infections and are also responsible for tissue graft rejection. T cells sensitized to a particular antigen may kill infected cells by binding to them and secreting toxic chemicals (cytotoxic T cells). Other lymphocytes moderate the action of cytotoxic cells by releasing cytokines (T helper or suppressor cells). Exposure to antigens also leads to a build-up in memory cells in the cell-mediated immune system.

A fetus develops immunocompetence during gestation. However, infection in early gestation may not stimulate an immune response as the fetus may be too immature to recognize foreign proteins. Lack of immunocompetence in the postnatal period may be due to a primary deficiency of a component of the immune system or a secondary immunodeficiency. Some viral infections, e.g. the immunodeficiency viruses (HIV, FIV) and others (e.g. BVD), affect immunocompetence, as do severe malnutrition, radiation and use of corticosteriods. Stress is thought to play a role in reduced immune function through corticosteriod release, and some mineral deficiencies may also be involved.

Stimulation of the humoral or cell-mediated immune systems, either by natural infection or by vaccination, produces active immunity, which may provide protection to the specific antigen for months or years. This property is used in vaccination, where antigen, from inactivated pathogens or toxins, attenuated organisms, related mild strains, or genetically engineered forms, is used to stimulate an immune response with the intention of providing long-term specific protection. Vaccines may contain an adjuvant to improve the immune response. More than one dose of vaccine may be required in an initial course to provide satisfactory protection, particularly where the antigen is not a live replicating organism. The initial dose will produce a small primary antibody response, and the second a secondary or amnestic response (Fig. 2). Satisfactory establishment of a memory cell population may also need an initial course of vaccination. Booster doses of vaccine may be used to prolong the protection or to raise circulating antibody levels.

Passive immunity does not require exposure to an antigen: the antibody is given to the animal either in colostrum or in antiserum. Protection is limited to a few weeks as the protein immunoglobulin is broken down over time. Passive immunity does not aid the production of protective antibodies in the animal, as exposure to the antigen is needed. The presence of passive immunity may interfere with the immune response to a vaccine and this should be taken into consideration when a vaccine programme is drawn up. (EM)
See also: Colostral immunity

Immunoglobulin: *see* Immunity

In sacco Literally 'in a bag'. Methods of measuring the digestion or microbial degradation of feeds in a bag within the gastrointestinal tract are called *in sacco* techniques. To measure the degradation of feeds within the rumen, samples of feed are sealed in bags of woven plastic (e.g. nylon or Dacron) that has pores small enough to retain the feed particles but large enough to allow microbes to enter and the end-products of digestion to leave. The bags are suspended in the rumen via a fistula in the rumen wall; they are retrieved at intervals and analysed to determine how much of the original material has been lost. The same approach can be used to measure digestion in the stomach and a 'mobile nylon bag' technique is also used to measure digestion in the intestine. The bags are usually introduced via a cannula and recovered either through another cannula further down the intestine, or from faeces, according to which part of the digestive process is being studied. (MFF)

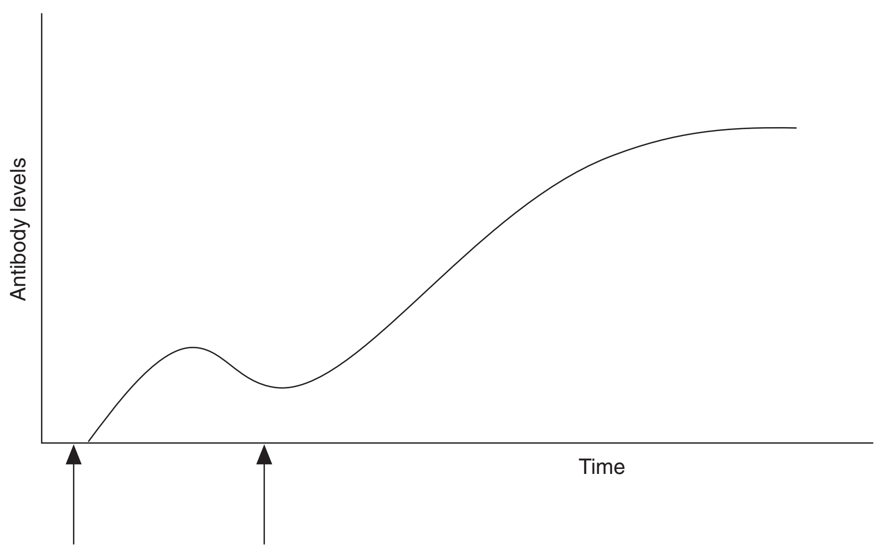


Fig. 2. Antibody response to two doses of vaccine (indicated by ↑).

***In vitro* digestibility** Digestibility determined in the laboratory by simulating the *in vivo* digestion. Commercial enzyme preparations or appropriate inocula (e.g. digesta or rumen liquor) are used in controlled incubations. To derive reliable predictions of *in vivo* digestibility from *in vitro* assays requires equations describing the relationship between *in vivo* and *in vitro* digestibility values obtained with identical feed samples. (SB)
See also: Digestibility

Further reading

Boisen, S. (2000) *In vitro* digestibility methods. History and specific approaches. In: Moughan, P.J., Verstegen, M.W.A. and Visser-Reyneveld, M.I. (eds) *Feed Evaluation. Principles and Practice*. Wageningen Pers, Dordrecht, The Netherlands, pp. 57–76.

Inborn errors of metabolism Inborn errors of metabolism (IEMs) are congenital abnormalities of metabolic pathways. Most are due to enzyme deficiencies or defects in metabolic transport. In the human population there are over 300 identified IEMs but far fewer are known in farm animals. Because farm animals are bred from a smaller gene pool than humans, there are probably fewer IEMs but they may individually be more prevalent because of the high level of inbreeding. Most are inherited through the monogenic recessive mode and may go undetected in farm livestock because farmers accept a high level of neonatal mortality. Examples in cattle include carbonic anhydrase deficiency syndrome, citrullinaemia, an inborn error of urea-cycle metabolism characterized by deficiency of argininosuccinate synthetase and consequent life-threatening hyperammonaemia, and deficiency of uridine monophosphate synthase. In sheep there is an inherited lysosomal storage disease that involves deficiencies of β-galactosidase and α-neuraminidase. There are also copper storage diseases and depressed biliary transport of conjugated sulphobromophthalein (SBP) compounds. Glycogen storage diseases have been recognized in cattle, quail and laboratory animals and are among the most widespread of IEMs. (CJCP)

Incubation The time taken for the embryo to develop *in ovo* and then hatch varies from species to species, but there is a trend for the time required for incubation to increase as the size of the hatchling increases (see table).

Typical incubation times for different species.

Species	Incubation time (days)
Chicken (standard)	21
Chicken (bantam)	20
Duck (except Muscovy)	28
Muscovy duck	33–35
Goose, small (e.g. Chinese, Canada)	30
Goose, large (e.g. Emden, Toulouse)	33–35
Guinea fowl	28
Japanese quail	17
Ostrich	42
Partridge	23
Pheasant	24
Pigeon	17
Turkey	28

The times shown are intended as a guide only. For example, when incubating chickens under commercial conditions, the incubation period may be extended by 12 or more hours to allow time for the hatching process to be completed and the hatchlings to dry off. Similarly, extra time will be required if the eggs have been stored for more than 1 week, for example, or come from older parent stock or are incubated at a suboptimal temperature. (NS)

Indicator A substance that shows a change in chemical conditions (e.g. pH), often by a change in colour. In nutrition, indicators are simple measures that change with more complex or deep-seated alterations in metabolism. Examples are the use of blood urea concentration as an indicator of protein utilization and the activity in plasma of the enzyme glutathione reductase as an indicator of riboflavin status. A method of estimating the requirement for an amino acid also uses the oxidation of a non-limiting ('indicator') amino acid: with increasing intake of the limiting amino acid the oxidation of the excess indicator amino acid decreases up to the point at which the requirement of the test amino acid is met. (MFF)

Indirect calorimetry Indirect calorimetry is used to measure the rate of metabolic heat production. Heat represents a high proportion of the total energy intake and it is generated in a complex chain of chemical reactions. Despite this, it can be estimated with remarkable accuracy from the rates of exchange of **oxygen consumption** and **carbon dioxide production** in respired air. This is possible because of a natural law first discovered by Germain Hess in 1838. Hess's law states that the heat produced in a chemical reaction is always the same regardless of whether it proceeds directly or via a number of intermediate steps. It means effectively that the heat of metabolizing a nutrient through the complex web of metabolic reactions may be duplicated by measuring the heat produced by burning the same nutrient in a **bomb calorimeter**.

Food energy is supplied by proteins, carbohydrates, fats and indigestible matter. The last is excreted in the faeces and takes no part in the consideration of the heat produced. Carbohydrates, as their name implies, are composed of the elements of carbon and water. Their oxidation may be represented chemically as:

$$C_n(H_2O)_m + nO_2 \rightarrow nCO_2 + mH_2O + \text{Heat of combustion (mol}^{-1}\text{)}.$$

Although the heat of combustion varies between one carbohydrate and another, the heat produced per litre of oxygen consumed is found to be nearly the same for all carbohydrates (21.2 kJ l^{-1}); also, as seen from the formula of the chemical reaction, the respiratory quotient (RQ), i.e. the volume ratio of carbon dioxide produced to oxygen consumed, is equal to 1. Similarly for fats, which are triglycerides, the heat per litre of oxygen is remarkably consistent at 19.8 kJ l^{-1} and the RQ is 0.711.

Proteins include nitrogen in their composition, in addition to oxygen, hydrogen and carbon. Unlike carbohydrates and fats, they cannot be completely oxidized to carbon dioxide and water; additional compounds of nitrogen are formed, such as urea, ammonia and uric acid. Again, it is found that the heat per litre of oxygen consumed in the conversion of proteins to carbon dioxide, water and urea is consistent at 19.2 kJ l^{-1} and the RQ is 0.809.

These calorific factors relevant to oxidation of carbohydrate, fat and protein are summarized in the table.

Indirect calorimetry thus requires measurement of the amounts of oxygen consumed, of carbon dioxide produced and of nitrogen excreted in the urine. From the values in the table, it is then possible to take the following steps.

1. Calculate the quantities of oxygen produced and carbon dioxide consumed by protein metabolism in forming the observed quantity of nitrogen excreted.

2. Calculate the remaining volumes of oxygen consumed and carbon dioxide produced (which are attributable to carbohydrate plus fat metabolism).

3. From their ratio (the non-protein RQ), calculate the proportions of the 'non-protein' oxygen that are attributable to metabolism of carbohydrate and of fat.

4. Calculate the heat produced by carbohydrate and fat metabolism.

5. Add together the heats of metabolizing all three food constituents to arrive at the total heat production.

In practice these tedious calculation steps may be replaced by a simple formula. Also, the calculation may be extended for herbivorous animals by incorporating a term to allow for the energy expelled as methane. The final equation (known as the **Brouwer formula**) for the heat produced (M, kJ) is:

$$M = 16.18 \times O_2 + 5.02 \times CO_2 - 5.99 \times N - 2.17 \times CH_4$$

where O_2 is the volume (l) of oxygen con-

	Approx. heat of combustion (kJ g^{-1})	Heat/oxygen ratio (kJ l^{-1})	Respiratory quotient
Carbohydrate	17.6	21.2	1.000
Fat	39.8	19.8	0.711
Protein (to urea)	18.4	19.2	0.809

sumed, CO_2 and CH_4 are volumes of carbon dioxide and methane produced and N is the mass (g) of urinary nitrogen. This equation was first proposed by Brouwer in 1958 and later endorsed by an international committee as applicable to all farm animals. The oxygen term contributes almost 75% and the carbon dioxide 25% to the total estimate of heat production; the nitrogen and methane terms each usually contribute less than 1%. For poultry, which excrete waste nitrogen as uric acid, the formula is:

$$M = 16.20 \times O_2 + 5.00 \times CO_2 - 1.20 \times N$$

and for fish, whose waste product is ammonia, it is:

$$M = 15.94 \times O_2 + 5.15 \times CO_2 - 9.14 \times NH_3$$

where NH_3 is weight (g) of ammonia.

Indirect calorimetry is performed by confining an animal inside a **respiration chamber** or making it wear a face mask. Either technique may be adapted to closed- or open-circuit operation. In closed-circuit systems air is circulated, either by the respiratory effort of the animal or by a fan, around a circuit that contains absorbers for carbon dioxide and water vapour, and into which a measured amount of oxygen is added to replace that used up. Carbon dioxide consumption is obtained from the weight gain of its absorber. The system must be leak-proof, which is difficult to ensure with animals wearing masks. Closed-circuit systems using chambers are called respiration chambers.

In open-circuit indirect calorimetry, fresh air is continuously drawn through the face mask or chamber, usually by a fan, and its volume measured as it is exhausted again. Sampling and analysis of outlet air are usually continuous, using electronic gas analysers. Leakage is not important so long as it can be ensured that all leaks are inward (i.e. of fresh air). For open-circuit calorimetry, calculations are of the rate of heat production, rather than the total heat produced over a lengthy period of measurement. The Brouwer equation is modified to:

$$M(W) = V_E \times (-20.47 \times dFO_2 + 0.73 \times dFCO_2 - 6.46\ dFCH_4) - 5.99 \times N$$

where V_E is exhaust air ventilation rate (l s^{-1}), N is nitrogen excretion rate (g s^{-1}) and dFO_2, $dFCO_2$ and $dFCH_4$ are differences between concentrations (fractions) of the gases in exhaust air and fresh air (note that, because oxygen is consumed rather than produced, dFO_2 has a negative value). In this equation the term involving carbon dioxide has a multiplying factor that is small compared with that for oxygen; consequently it, like the terms involving methane and urinary nitrogen, has very little influence on the final result. Little accuracy is sacrificed in open-circuit calorimetry by measuring only oxygen concentration and using the equation:

$$M = -20.5 \times V_E \times dFO_2$$

This type of approximation is *not* permissible with the Brouwer equation in closed-circuit calorimetry. It is important to note that ($V_E \times dFO_2$) is not synonymous with oxygen consumption, because inlet and outlet ventilation rates are only equal when RQ=1.

The above description has centred on the metabolism of protein, carbohydrate and fat from food, without reference to energy retention as growth, i.e. the formation of animal protein and fat. The quantities of protein, carbohydrate and fat are in reality net quantities (i.e. digested minus retained protein, carbohydrate and fat) and the arguments are still valid when applied to growing, productive or even starving animals.

It has been shown that indirect calorimetry is based on assuming fixed values for the RQs and heats per litre of oxygen consumed in the metabolism of protein, carbohydrate and fat in both food and animal tissue. These are certainly gross approximations, though averaging throughout the body over all the wide range of compounds involved helps to reduce variation. It is nevertheless hard to prove accuracy for the method on theoretical grounds. Perhaps the best proof of its accuracy and consistency lies in the fact that repeated observations over the last 100 years have failed to show any unexplainable difference between the results of indirect calorimetry, where heat is inferred from measurement of chemical quantities, and **direct calorimetry**, where the measurement is of the heat given up by the animal to its environment. (JAMcL)

See also: Calorific factors; Energy balance

Further reading

McLean, J.A. and Tobin, G. (1987) *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, 338 pp.

Indispensable amino acids: *see* Essential amino acids

Individual feeding Provision of food to individual animals, usually housed separately, for specified feeding treatments or measurement of food consumption. Animals may also be fed individually using equipment that identifies the individual electronically by a coded tag and either dispenses a set amount of feed or records the animal's voluntary consumption. (JSav)

Indoles Indoles (C_8H_7N) and skatoles (methyl-indol) are produced by fermentation of tryptophan ($C_{11}H_{12}N_2O_2$) in the intestinal tract. Both give rise to the powerful odour of faeces. Some can be absorbed from the intestine and excreted in the urine. (NJB)

Infertility: *see* Fertility

Inositol A compound with the empirical formula $C_6H_{12}O_6$. It may exist in one of seven optically inactive forms and in two optically active forms. Of these, only myo-inositol is biologically active. Inositol is widely distributed in plant and animal cells. In the rat, myo-inositol is not required under normal dietary conditions. However, rats treated with antibacterials have been shown to benefit from supplemental myo-inositol. The positive effect of added myo-inositol is presumably due to suppressed intestinal microfloral synthesis of it. No information is currently available for chicken, pig or horse.

In the animal, inositol is found in the inner leaflet of cell membranes as phosphatidylinositol and phosphatidylinositol 4,5-bisphosphate. Phosphatidylinositol 4,5-bisphosphate is the chemical connection between certain cell membrane hormone receptors and rapid changes in cellular concentrations of calcium. The hormone receptor in the plasma membrane activates phospholipase C, which cleaves phosphatidylinositol 4,5-bisphosphate to inositol 1,4,5-triphosphate (IP3) and diacylglycerol. IP3, a soluble compound, diffuses through the cytosol and binds to specific IP3 receptors on the endoplasmic reticulum to cause the release of stored calcium. The increased calcium binds to and activates any of several different classes of regulatory proteins to initiate a physiological effect. The diacylglycerol remains in the cell membrane and together with the elevated calcium is a potent activator of protein kinase C, another important signalling protein. (NJB)

Key references

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Rodwell, V.W. (2000) Metabolism of purine and pyrimidine nucleotides. In: Murray, R.K., Granner, D.K., Mayes, P.A. and Rodwell, V.W. (eds) *Harper's Biochemistry*, 25th edn. Appleton and Lange, Stamford, Connecticut, pp. 386–401.

Insecticide residues: *see* Pesticides

Insects as food Locusts (*Schistocerca gregaria*) are used as animal feed in Africa, provided that they are not killed by arsenic. After sun-drying to remove the offensive smell the ground locust meal is palatable to pigs and poultry. However, in pigs it will taint the meat with a fishy smell. Ground locust meal (see table opposite) has been used at < 20% of total diet in pig rations and < 16% in poultry rations. Locust meal has a dry matter (DM) content of 890–895 g kg^{-1} and its nutrient composition (g kg^{-1} DM) is crude protein (CP) 510–520, crude fibre 140 and ether extract (EE) 105–110. Lakefly from Lake Victoria have a DM of 910 g kg^{-1} and contain CP 620, minerals 180 and EE 39 g kg^{-1}. Small quantities of silkworm pupae can be included in pig and poultry diets, and silkworm pupa meal has been use to replace fish meal. Pupae contain chitin and of their high crude-protein content only about 75% is true protein. Pupae are best utilized separated from their cocoons, thus reducing the fibre content. They are high in unsaturated fats and this can affect the taste of the meat. (JKM)

Insulin A peptide hormone with a molecular weight of 5808, containing two chains.

The composition of various insects used as animal food.

	Dry matter (g kg^{-1})	Nutrient composition (g kg^{-1} DM) Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Whole locusts								
Raw, Kenya	294	635	135	87	141	2	–	–
Dried, Tanzania	895	516	140	–	109	–	–	–
Silkworm (*B. mori*)								
Solvent extracted	925	776	43	73	10	98	1	15
Raw	200	542	39	52	303	64	1	11
Silkworm (*A. mylitta paphia*)								
Solvent extracted	928	742	102	69	11	76	2	8
Raw	200	563	77	53	300	7	2	7

Source: FAO (2002) http://www.fao.org/ag/AGA/AGAP/FRG/AFRIS/Data/239.HTM
NFE, nitrogen-free extract.

The A chain has 21 amino acids and the B chain 30 amino acids. The chains are linked by two disulphide bridges. Insulin is synthesized in the β-cells of the islets of Langerhans in the pancreas. It is synthesized in the rough endoplasmic reticulum, transported to the Golgi and packaged in membrane-bound granules. Its half-life in plasma is about 5 min. Its action is initiated by binding to insulin receptors on the cell surface. Insulin is anabolic, increasing the cellular storage of glucose, fatty acids and amino acids. An excess of insulin results in hypoglycaemia, coma and death. Continuous low concentrations of insulin result in diabetes mellitus, leading to high circulating levels of glucose which, if left unchecked, results in a debilitating disease that ultimately becomes fatal. (NJB)

Insulin-like growth factor (IGF) Insulin-like growth factors are designated as IGF-I and IGF-II. IGF-I is a polypeptide of 70 amino acids whereas IGF-II has 67 amino acids. A significant degree of amino acid sequence homology exists between insulin and IGF-I and IGF-II. IGF-I is regulated by growth hormone and nutritional status. It is synthesized in the liver and other tissues and is involved in skeletal and cartilage growth. In plasma it is found bound to IGF-binding proteins (five or more), which inhibit its action. IGF-II is synthesized in many tissues and factors involved in its regulation are not known. As with IGF-I in plasma, IGF-II is bound to binding proteins. It is thought to be involved in embryonic development. (NJB)

Key references

Ganong, W.F. (1999) Chapters 19 and 22. In: *Review of Medical Physiology*, 19th edn. Appleton and Lange, Stamford, Connecticut.

Granner, D.K. (2000) Pituitary and hypothalamic hormones. In: Murray, R.K., Granner, D.K., Mayes, P.A. and Rodwell, V.W. (eds) *Harper's Biochemistry*, 25th edn. Appleton and Lange, Stamford, Connecticut, pp. 550–560.

Intake: *see* Feed intake

Interactions: *see* Environment–nutrition interaction; Genotype–nutrition interaction

International units The International System of units is abbreviated as SI (Système Internationale d'Unités), a coherent system based on seven basic units and two subsidiary units, the radian and steradian. These are listed in the table overleaf along with a number of derived SI units. SI units replace the British FPS (foot, pound, second) system and the metric CGS (centimetre, gram, second) system. SI units are based on the MKS (metre, kilogram, second) system; they are decimal and coherent. Coherent means that all derived units are formed by multiplication or division of the basic SI units without the introduction of any numerical factor, or even a power of ten. This has the advantage that when measurements expressed in basic SI units are substituted into an equation, the result is automatically in the appropriate basic unit of the SI. SI units are given unit symbols that follow all the usual rules of algebra. They do not need a full stop as in abbreviations, nor do they need an 's' to form a plural (i.e. two centimetres is 2 cm, not 2 cms). Multiplying prefixes listed below can be used to indicate decimal subunits or multiples of units to allow convenient and manageable numbers in the range 0.1–999.9.

Dimensionless numbers

Since SI unit symbols follow algebraic rules, dimensionless numbers can be created by dividing a quantity symbol by an appropriate unit symbol. If h = 5 m, where h denotes height, we may write h/m = 5, so that the right-hand side has no unit and is dimensionless. This is useful for heading columns of figures or labelling axes of graphs, making the numbers on the axes more manageable; for example, an axis labelled wavelength/nm can be labelled wavelength/10^2 nm, thus removing two zeros from every number along the axis.

The International System of units.

Property	**SI unit**	**Symbol**
length	metre	m
mass	kilogram	kg
time	second	s
electric current	ampere	A
temperature	kelvin	K
amount of substance	mole	mol
luminous intensity	candela	cd
angle	radian	rad
solid angle	steradian	sr

Derived SI units

frequency	hertz	Hz	=	s^{-1}
force	newton	N	=	$kg\ m\ s^{-2}$
energy	joule	J	=	$kg\ m^2\ s^{-2}$
power	watt	W	=	$kg\ m^2\ s^{-3}$
luminous flux	lumen	lm	=	cd sr
illumination	lux	lx	=	$cd\ sr\ m^{-2}$
pressure	pascal	Pa	=	$kg\ m^{-1}\ s^{-2}$
electric charge	coulomb	C	=	A s
e.m.f.; p.d.	volt	V	=	$kg\ m^2\ s^{-3}\ A^{-1}$
resistance	ohm	Ω	=	$kg\ m^2\ s^{-3}\ A^{-2}$
capacitance	farad	F	=	$A^2\ s^4\ kg^{-1}\ m^{-2}$
magnetic flux	weber	Wb	=	$kg\ m^2\ s^{-2}\ A^{-1}$
flux density	tesla	T	=	$kg\ s^{-2}\ A^{-1}$
inductance	henry	H	=	$kg\ m^2\ s^{-2}\ A^{-2}$
conductance	siemens	S	=	Ω^{-1}

Decimal multiple and sub-multiple prefixes

10^{18}	exa	E	10^{-1}	deci	d
10^{15}	peta	P	10^{-2}	centi	c
10^{12}	tera	T	10^{-3}	milli	m
10^9	giga	G	10^{-6}	micro	μ
10^6	mega	M	10^{-9}	nano	n
10^3	kilo	K	10^{-12}	pico	p
10^2	hecto	H	10^{-15}	femto	f
10	deca	D	10^{-18}	atto	a

Note the following:

- The mole is based on the gram, not the kilogram.
- SI thermodynamic temperature is the kelvin symbol K (not °K). The Celsius scale is more often used in practical measurements: 273 K is approximately 0°C. The Celsius scale has intervals of 1 kelvin.
- In the USA, metre is spelt 'meter' and litre 'liter'.
- A number of non-SI units persist in usage: litre, calorie, per cent, parts per million. A number of these are listed in the table below.

International Units

International Units (IU or i.u.) are used to express the quantities of vitamins A, D and E in terms of their biological activity. They are older units, devised before these vitamins could be separated by HPLC and their isomers measured accurately. However, their use persists and they can be converted by the following factors.

0.3 micrograms (μg) retinol equivalent = 1 IU vitamin A

0.6 μg beta carotene = 1 IU beta carotene

1.0 μg vitamin D = 40 IU vitamin D

1.0 mg natural vitamin E (D-alpha tocopherol) = 1.49 IU vitamin E

1.0 mg synthetic vitamin E (DL-alpha tocopherol acetate) = 1.0 IU vitamin E (IM)

Intestinal absorption The process by which nutrients, including vitamins, minerals and water, enter the body from the lumen of the gastrointestinal tract. Nutrients can enter the body by transcellular absorption, which involves transport through the epithelial cells to the extracellular fluid (ECF), from where they pass to the lymph and blood, or by paracellular absorption, by which the nutrients move directly to the ECF through the tight junctions between the epithelial cells.

Absorption into the epithelial cells can be performed by simple diffusion, facilitated diffusion (by the help of a carrier protein in the membrane), active transport, secondary active transport (coupled transport) and pinocytosis (amoeba-like engulfing of macromolecules and ions).

Complex carbohydrates, proteins and lipids are generally not absorbed intact: they have to be broken down (digested) to absorbable units, which must diffuse across the unstirred water layer to reach the epithelial cells where the mucous coat of the cells also constitutes a barrier to diffusion.

The membranes of the epithelial cells contain glycoprotein enzymes that hydrolyse oligosaccharides and disaccharides into monosaccharides and oligopeptides into di- and tripeptides and amino acids before absorption. Hexoses and pentoses are rapidly absorbed across the wall of the small intestine; the latter by simple diffusion.

Non-SI units		
atmosphere	atm	101,325 Pa (definition)
Torr	torr	133.322 Pa = 1/760 atm
atomic mass unit	amu	1.66054×10^{-27} kg
bar	bar	1×10^{5} Pa
electron volt	eV	1.602178×10^{-19}J
poise	P	0.1 kg m^{-1} s^{-1}
litre	l	1×10^{-3} m^3 = 1 dm^3
ångström	Å	1×10^{-10}m
debye	D	3.335641×10^{-30} C m
calorie	cal	4.184 J (definition)
Calorie (kilocalorie)	Cal	4.184 kJ
inch	in	0.0254 m (definition)
pound	lb	0.4536 kg
per cent	%	0.01 kg kg^{-1}; 0.01 kg l^{-1}
part per million	ppm	mg kg^{-1}; mg l^{-1}
part per billion	ppb	μg kg^{-1}; μg l^{-1}

Glucose is transported across the intestinal epithelium coupled to sodium (Na^+) transport, utilizing a common carrier protein. Na^+ is then actively transported out of the cell, and glucose enters the interstitium by simple diffusion or facilitated diffusion. From there it diffuses into the blood. The energy for glucose transport is provided by the active transport of Na^+ out of the cell, which maintains the concentration gradient across the luminal border of the cell so that more Na^+ and glucose can be transported across the membrane. Glucose is transported out of the cell to the ECF by diffusion, either by simple diffusion or by a carrier, i.e. by facilitated diffusion. *Galactose* is transported by the same carrier as glucose. **Fructose** is transported by a different carrier, which is independent of Na^+ and is not energy requiring, i.e. facilitated diffusion. Some fructose is converted to glucose in mucosal cells.

Amino acids are in many cases transported in a similar way to glucose with co-transport of Na^+. A neutral amino acid carrier, a phenylalanine and methionine carrier and an amino acid carrier in the brush border are Na^+ dependent. The Na^+-independent carriers in the brush border include one for basic amino acids and one for neutral amino acids which prefers hydrophobic side chains. A separate system transports di- and tripeptides into the mucosal cells, where they are hydrolysed to amino acids. The transported amino acids, as well as those produced by intracellular hydrolysis of di- and tripeptides, accumulate in the mucosal cells and from these cells they enter the ECF by simple diffusion and facilitated diffusion. Only about half of absorbed amino acids come from ingested food. The other half comes from endogenous sources, mainly proteins in digestive juices and desquamated mucosal cells. A number of specific factors in the food may influence the reabsorption of endogenous protein in the ileum. In the large intestine, most unabsorbed protein, in particular endogenous protein, is utilized by the microflora and excreted in faeces as microbial protein.

Some **small peptides** may also enter portal blood; only those from gelatine that contain proline and hydroxyproline and those from certain meats that contain carnosine and anserine are known. **Protein antigens**, particularly from bacteria and viruses, are absorbed in specialized intestinal epithelial cells that overlie aggregates of lymphoid tissue (Peyer's patches). These cells pass the antigens to the lymphoid cells. **Nucleotides**, produced from the hydrolysis of nucleic acids (DNA and RNA) by pancreatic nucleases, are split into nucleosides and phosphoric acid and further to their constituents' pentoses, purine and pyrimidine bases by enzymes located on the luminal surfaces of the epithelial cells. The liberated bases are absorbed by active transport.

Lipids are absorbed by passive transport after formation of micelles in the intestinal lumen. The micelles consist of fatty acids and monoglycerides, liberated from triglycerides by pancreatic lipase, with bile salts secreted via the pancreatic duct from the liver. Fatty acids with fewer than 10–12 carbon atoms pass directly from the epithelial cells into the portal blood, where they are transported as free (unesterified) fatty acids, whereas fatty acids with more than 10–12 carbon atoms are re-esterified to triglycerides. In addition, some of the absorbed cholesterol esters are esterified. These esters are then coated with a layer of protein, cholesterol and phospholipid to form chylomicrons, which leave the cell by pinocytosis and enter the lymphatics.

Vitamins are readily absorbed: most are absorbed in the proximal small intestine. Fat-soluble vitamins are absorbed together with other lipids after the formation of micelles. The absorption of vitamin B_{12} is dependent on intrinsic factor, a protein secreted by the stomach, and the complex is absorbed across the ileal mucosa by pinocytosis.

Sodium is actively absorbed in the small intestine either with glucose, galactose or amino acids or alternatively by a sodium/potassium pump. Furthermore, sodium can diffuse into and out of the small intestine, depending on the concentration gradient throughout the small and large intestines. The sodium concentration in the intestinal lumen is maintained by a high sodium concentration in the digestive secretions. **Potassium** is absorbed primarily by passive diffusion. **Chloride** is absorbed in a coupled transport with sodium or by exchange with bicarbonate.

Calcium is absorbed primarily in the proximal small intestine by active transport, but there is also some passive transport. Active transport is facilitated by 1,25-dihydroxycholecalciferol, a metabolite of vitamin D, which induces the synthesis of a Ca^{2+}-binding protein in the epithelial cells. The synthesis of the metabolite from vitamin D is controlled hormonally and related to the concentration of calcium in the blood. Thus, calcium absorption is adjusted to the body's needs. The absorption of calcium, as well as of magnesium, is also facilitated by the presence of protein and is inhibited by phosphates and oxalates, because these anions form insoluble salts with Ca^{2+} and Mg^{2+} in the intestine.

Iron is absorbed primarily in the proximal small intestine and primarily in the ferrous state (Fe^{2+}). However, most dietary iron is in the ferric form (Fe^{3+}), which can be reduced by ascorbic acid and other reducing agents once dissolved at the low pH in the stomach. Haem is also absorbed and the Fe^{2+} it contains is released in the epithelial cells. The mucosal cells contain an intracellular iron carrier, but the polypeptide transferrin is also important for iron transport in the plasma. Apoferritin is a protein in the epithelial cells that bind iron. The resulting ferritin is lost when the epithelial cells are shed into the intestinal lumen at the end of their life cycle. Absorption of iron is inhibited by phytic acid, phosphates and oxalates that form insoluble complexes with iron in the intestine.

Phosphorus in feeds is either organically bound or as inorganic phosphates. Phosphorus in the phytates (inositolphosphates) is not available unless the phytate is degraded. Absorption of phosphorus is inhibited by calcium.

Water moves freely into and out of the intestines and maintains an osmotic pressure that equals that of the plasma. Almost all the water entering the digestive tract, whether from intake or secretions, is absorbed in the intestine. (SB)

See also: Absorption; Digestion; Lipid absorption

Further reading

Cunningham, J.G. (1992) *Textbook of Veterinary Physiology*. W.B. Saunders, Philadelphia, 655 pp.

Intestinal diseases: *see* Digestive disorders

Intestinal fluid: *see* Chyme; Digesta

Intestinal microorganisms: *see* Gastrointestinal microflora

Intestinal motility: *see* Motility

Intestinal mucosa The tissue between the muscularis mucosae and the intestinal lumen. The mucosa is made up of the muscularis mucosae, the lamina propria, vascular bed, lymphatic system and the enterocytes that cover the intestinal villi. In the small intestine the enterocytes are of at least three types: columnar, goblet cells and argentaffine cells. Goblet cells secrete mucin, a glycoprotein that provides protection to the intestinal surface. The columnar cells have microvilli that face the intestinal lumen; these microvilli are where the disaccharidase enzymes and peptidases are found. Argentaffine cells are found in the crypts of Lieberkühn. (NJB)

Intolerance: *see* Food intolerance

Inulin A fructose polymer found in tubers of the **Jerusalem artichoke**. It is soluble in warm water. Inulin is the preferred substance to test the kidney glomerular filtration rate because it is not reabsorbed by the kidney and can be quantified in the collected urine. After infusing inulin IV to obtain a steady state in body fluids, a sample of urine is taken and the inulin concentration determined. By comparing the plasma concentration of inulin with the amount recovered in the urine over a specific time, the volume of blood cleared of inulin can be calculated. In an average man the glomerular filtration rate determined by use of inulin is 125 ml min^{-1}.
(NJB)

Iodine Iodine (I) is a non-metallic element with a molecular mass of 126.9045 that exists in the elemental state as I_2. Iodine is an essential nutrient for all species of farm animals. The I content of plants can vary widely: forages contain from 0.5 to 2.5 mg kg^{-1} while seeds, such as soybeans and groundnuts, contain only 0.1–0.2 mg kg^{-1}. In feeds, I occurs mostly as the inorganic iodide, which is readily absorbed in all parts of the gastrointestinal tract. Both organic and iodate salt forms of I are degraded to the iodide form before absorption can occur.

Upon absorption, I is distributed to all parts of the body but most of it is concentrated in the thyroid gland as mono- and triiodotyrosine and thyroxine, with a small amount of 3,5,3′-triiodothyronine. The latter is the active form of the thyroid hormone.

Iodine deficiency in farm animals is demonstrated most vividly by reproductive impairment. Development of the fetus can be slowed and death *in utero* can occur, or the newborn can be weak and hairless. In adult animals, enlarged thyroid glands can develop. Iodine deficiency also can affect male fertility, primarily as a result of deterioration in the quality of the semen. The US National Research Council (NRC) recommends approximately 0.6 mg I kg^{-1} dry diet for cattle and horses, approximately 0.14 mg kg^{-1} diet for pigs and 0.35 mg kg^{-1} diet for poultry.

Tolerance to I in the diet varies among species of farm animals. As little as 50 mg I kg^{-1} diet for young calves reduced growth rate; older animals tolerated as much as 200 mg I kg^{-1} diet. As a safety measure, the US NRC set the upper tolerance level for dietary I for cattle and sheep at 50 mg kg^{-1} diet. Swine and poultry can tolerate higher amounts of I, up to an estimated 300 mg kg^{-1} of diet. Horses, on the other hand, seem to be sensitive to the concentration of dietary I and the upper tolerance limit is estimated at 5 mg kg^{-1}. (PGR)

See also: Selenium; Thyroid

Further reading

Hetzel, B.S. and Maberly, G.F. (1986) Iodine. In: Mertz, W. (ed.) *Trace Elements in Human and Animal Nutrition.* Academic Press, Inc., New York, pp. 139–208.

Ion balance Ion balance involves the regulation of the amount of inorganic ions (or electrolytes) in the body, including Na^+, K^+, Cl^-, HCO_3^-, H^+, Ca^{2+} and PO_4^{3-}, in such a way that excretion matches daily intake. Some excretion of NaCl occurs through perspiration but the majority is highly regulated by the kidney. (GG)

Ion transport The movement of inorganic ions across a cell membrane by the action of a specific carrier protein. Movement may occur by primary active transport, which requires direct energy input from metabolism in the form of ATP, or by secondary active transport, using the gradient of another ion such as Na^+ to power the process. (GG)

Ionophores Ion-bearing compounds that surround cations so that the hydrophilic ion can be shuttled across hydrophobic cellular membranes to defeat the normal concentration gradient essential in living cells. Ionophores display diverse structures and profiles of cation selectivity. For example, valinomycin is a cyclic peptide which binds potassium, while monensin is a carboxylic ionophore which displays a binding preference for sodium. Both can act as antibiotics. Ionophores are produced by strains of *Streptomyces* bacteria. They are used in beef cattle to improve feed efficiency by shifting rumen fermentation towards the production of more propionic acid, which can be used by the animal, and less methane, which is lost. (JDR)

Iron A transition element with atomic number 56. The most abundant isotope of iron has an atomic weight of 55.85. Iron is one of the most abundant elements in the earth's crust. It is chemically versatile, which results in advantages and disadvantages concerning its use in biology. Iron is an essential nutrient for nearly all organisms because it is a co-factor for proteins that perform life-sustaining processes such as the production of ATP. In vertebrates and other higher organisms, iron is required for cell division. Biological forms of iron include haem iron, in which the iron atom is inserted in the porphyrin ring of protoporphyrin IX, as in haemoglobin. A variety of non-haem iron proteins also exist, the iron–sulphur (Fe–S) proteins being particularly important, with critical roles in ATP production by mitochondria. Other types of non-haem iron proteins include diferric transferrin, the serum iron transport protein, or the cytosolic iron storage protein ferritin. In vertebrates, some of the major processes supported by iron-containing proteins include DNA synthesis, respiration (ATP production) and oxygen transport (haemoglobin). Diseases of iron metabolism include iron overload and iron deficiency, which can be important for some farm animals, particularly pigs. Iron deficiency can result in reduced capacity to transport oxygen (anaemia). It can also impair the ability of skeletal muscle to generate ATP and can impair the function of the immune system. Problems with the use of iron by organisms relate to its very low solubility and its propensity to participate in chemical reactions that lead to the formation of free radicals such as hydroxyl radical. Body iron content is primarily regulated through changes in the capacity of the small intestine to absorb iron. Once iron is absorbed it is very tightly retained, as there is no regulated way to excrete it. Approximately two-thirds of the iron in the body is present as haemoglobin. Non-haem iron is transported between organs by transferrin. (RSE)

Iron deficiency anaemia Iron is required for the production of the blood pigment haemoglobin. In iron-deficient anaemia, erythrocyte numbers are reduced, as is the haemoglobin content of each red blood cell (microcytic hypochromic anaemia). Iron stores in the neonate are not high and, although the iron content of colostrum may be up to 15 times that of milk, this may not be sufficient to meet the requirements of a rapidly growing neonate until weaning. Sows' milk only provides approximately 1 mg iron day^{-1} per piglet, compared with an average requirement of 7 mg. Iron deficiency anaemia is most commonly seen in fast-growing housed piglets without access to dirt, and in young ruminants fed an unsupplemented milk-based diet with little or no roughage.

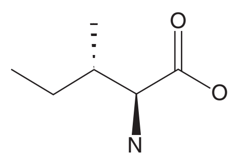
Piglets can be given iron by injection or orally. There have been deaths associated with these treatments. A turf can be supplied as a source of iron, or the sow can be supplemented with 2000 mg iron day^{-1}; she will pass sufficient iron in her faeces to supplement her piglets' diet. (EM)

See also: Anaemia; Haemoglobin

Isoenzymes: *see* Isozymes

Isoflavones: *see* Flavonoids

Isoleucine An essential amino acid ($CH_3 \cdot CH_2 \cdot CH(\cdot CH_3) \cdot CHNH_2 \cdot COOH$, molecular weight 131.2) found in protein. It is one of the branched-chain amino acids. Isoleucine is rarely deficient in common diets for pigs and poultry, but blood meal (and red blood cells per se) are quite deficient in this amino acid. The first two reactions in isoleucine catabolism, transamination followed by oxidative decarboxylation, are catalysed by enzymes that also act on leucine and valine.



(DHB)

See also: Essential amino acids

Isomaltase An enzyme found in the brush border membranes of epithelial cells in the duodenum and jejunum. Also known as α-dextrinase, it functions to 'debranch' the α-limit dextrins by cleaving α(1→6) linkages located at these branch points in starch. (GG)

Isomaltose A disaccharide, $C_{12}H_{22}O_{11}$, molecular weight 342, of two D-glucose residues joined by glycosidic α(1→6) linkage. Produced from branch points of amylopectin and glycogen during enzymatic digestion. Isomaltose is the repeating unit in dextran, an extracellular polysaccharide synthesized by some bacteria. Isomaltose is rarely found free in nature, except in honey and fermentation products. Depending on the enzymatic system, variable amounts of isomaltose are present in partially hydrolysed amylopectin, glycogen and maltodextrins. During digestion in animals, it is enzymatically hydrolysed to glucose. (JAM)

See also: Carbohydrates; Oligosaccharides; Starch

Isomers Molecules that have the same number and kind of atoms but have them in a different arrangement, making them act as a different molecule. For example, leucine and isoleucine have the same empirical formula ($C_6H_{13}NO_2$) but act like entirely different amino acids. The same is true for the monosaccharides glucose and galactose ($C_6H_{12}O_6$). (NJB)

Isozymes Different proteins that catalyse the same chemical reaction. Isozymes are found in such different organisms as human vs. bacterium. A second definition for isozymes exists in which tissues within an animal may have different subunit combinations of a multi-subunit enzyme such as lactic dehydrogenase. Lactic dehydrogenase has four subunits. There are two subunit types: H (heart) and M (muscle). The two extremes are HHHH vs. MMMM but can vary from HHHM to MMMH. This type of subunit variation has been seen for multi-subunit enzymes that are identified as dehydrogenases, oxidases, transaminases, phosphatases, etc. (NJB)

J

Jackbean (*Canavalia ensiformis* (L.) DC) A drought-resistant, annual legume, also known as sword bean, grown mainly in South and Central America. It is commonly used as green manure or cover crop in erosion control. Seeds are sources of lectins, canavanine, urease and other enzymes used in chemistry, biochemistry and medicine. Young pods and immature seeds are used as vegetables after prolonged boiling or fermentation to detoxify. Raw seed is high in protein (*c.*30% in dry matter) and nitrogen-free extract (*c.*50%), half of which is starch. Raw seeds cannot be used as a feed for pigs and poultry because of antinutritional factors (toxic amino acids, alkaloids, polyphenolics, lectins, saponins, trypsin inhibitors and immuno-proteins) which severely reduce intake and growth. Boiled jackbeans included at 10% of chick diets did not impair growth, intake or feed conversion. Pigs fed boiled beans at 30% of diet showed a large reduction in initial feed intake. Raw seed meal in cattle diets should be < 30%. Raw beans contain urease and therefore should not be included in diets containing urea. Some jackbean is grown, under irrigation, for forage but the forage is unpalatable unless dried. (EO)

Jejunum The central section of the small intestine, between the duodenum and the ileum. It is the main site for the absorption of the degradation products of organic nutrients, i.e. glucose, amino acids, small peptides, fatty acids, monoglycerides and glycerol. (SB)

Jerusalem artichoke *Helianthus tuberosus*, a perennial herb cultivated in tropical and subtropical countries for both human and animal use. The fresh tops are used as fodder and its white-, red- or purple-skinned tubers are used to fatten cattle, sheep and pigs. The storage carbohydrate in the tubers is not starch but inulin. For pigs, up to 33% can be used in place of maize but larger amounts reduce digestibility and productivity. Older pigs adapt to larger quantities of Jerusalem artichokes. (JKM)

Key references

FAO (2002) adapted from Göhl, B. (1981) http://www.feeds/.html [26.01.02] *Tropical Feeds*. www.FAO, Rome.

Duke, J.A. (1983) [www] *Handbook of Energy Crops* http://www.hort.purdue.edu/newcrop/duke_energy/dukeindex.html [26.01.02]

Nutrient composition of Jerusalem artichokes.

	Dry matter ($g\ kg^{-1}$)	Nutrient composition ($g\ kg^{-1}$ DM)						
		Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Fresh leaves, Malaysia	217	207	124	161	23	485	20.4	3.6
Fresh aerial part	323	105	167	155	34	539	–	–
Fresh tubers, Malaysia	168	83	48	60	6	803	2.1	3.5
Fresh tubers, Israel	196	77	66	61	5	791	–	–
Fresh tubers[a]	200	150	40	50	–	750	0.23	0.90

Sources: FAO (2002) and [a]Duke (1983).
NFE, nitrogen-free extract.

Jojoba Jojoba (*Simmondoia chinensis*) is a small woody tree or shrub 0.5–2.5 m tall with a taproot able to penetrate 15–25 m below the soil surface and with an expected life span of 100 years. The roots make it suitable for desert areas and it is grown in the USA and Australia. Oil is extracted from the seed and is then used for the natural appetite suppressants, simmondsins, that it contains. There is a market for jojoba for inclusion in pet foods and in cattle and chicken feed. The fruit contains approximately 50% oil and this is not degraded by bacterial activity; however, the pulp residue meal can be extracted to reduce simmondsins and trypsin inhibitor levels to produce a meal with 20–30% protein content. Extracted jojoba meal has been fed as a replacement for concentrate feeds at < 10% of total diet for lambs and beef cattle, but feed intake and weight gain were reduced. Ensiling the meal with maize can increase its palatability. (JKM)

Key references

Castleman, G. (2000) Jojoba. http://www.nhq.nres.usda.gov

Selim, E.M., Abbott, T.P. and Hiroshi, N. (1996) Simmondsin concentrate from defatted jojoba meal. Agricultural Research Service. http://www.nal.usda.gov

Joule The joule (J) is the SI unit of energy. It is defined as the work done when the point of application of a force of 1 newton is displaced through a distance of 1 m in the direction of the force (the newton being the force required to accelerate a mass of 1 kg by 1 m s^{-1}). Energy can take many forms (e.g. mechanical, electrical, chemical and heat), all of which may be quantified in joules. (JAMcL)

See also: Energy units

Jute A fast-growing prickly woody herbaceous annual (*Hibiscus cannabinus* L.), growing up to 4 m tall. Jute is cultivated mainly for its fibre but also yields 6–30 kg seed ha^{-1}. The seeds contain about 20% oil, used for salad, cooking and lubricant oils. The seed cake produced after oil extraction can be fed to cattle and sheep. The stem is largely cellulose but contains relatively high levels of ether extract, which can serve as a source of energy. The leafy parts of some varieties contain as much as 30% protein, and young plants ensile easily. (JKM)

Nutrient composition of jute products (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Fresh stem, India	–	150	199	82	58	511	20.8	5.0
Leaves dried, India	–	131	116	118	21	614	33.1	3.5
Seeds, South Africa	915	272	251	61	154	262	6.0	6.3
Dry press cake	–	330	174	60	–	376	–	–

Sources: FAO 2002 adapted from Göhl, B. (1981). http://www.feeds/html [26.01.02] Tropical Feeds. www.FAO. Rome
Duke, J.A. (1983) [www] *Handbook of Energy Crops* http://www.hort.purdue.edu/newcrop/duke_energy/dukeindex.html [26.01.02]
NFE, nitrogen-free extracts.

K

Kale An annual, *Brassica oleracea*, grown extensively in temperate areas as a feed for ruminants, to extend the grazing season in autumn. It is highly palatable for cattle and sheep and is usually fed by either strip or zero grazing, or as silage. The variety most commonly grown is marrowstem, which produces heavy crops but is not winter hardy. Thousand-headed and dwarf thousand-head are hardier and produce a large number of new shoots late in the winter. The feeding value of kale is proportional to the leaf content: the woody stems are less palatable and less digestible. Kale has 86% water; the dry matter contains 16–17% protein and 20–25% soluble carbohydrates with a metabolizable energy (ME) of 11 MJ kg^{-1} (see table). Adequate supplementation with minerals is important, particularly iodine and selenium. Kale contains *S*-methyl cysteine sulphoxide, which may cause haemolytic anaemia after conversion in the rumen to dimethyl disulphide. Glucocinolates in kale can cause lesions of the liver, kidneys and thyroid, leading to thyroid dysfunction in cattle if kale is fed in excess of 20 kg day^{-1} per head over long periods. The milk from dairy cows may be tainted if they are fed kale at high levels. Dietary inclusion rates for fresh kale are 25% for cattle and ewes, 10% for calves and 10–33% of total feed intake for lambs. Kale silage can be consumed at greater levels (< 60% of the total feed intake of lambs). (JKM)

Kaolin Kaolin and kaolinitic clays are used as binding agents to increase the durability of pellets. They are naturally occurring mixtures of minerals containing at least 65% complex hydrated aluminium silicates whose main constituents are kaolinite, bentonite and other montmorillonite clays. (MG)
See also: Binding agents

Kapok seed meal The kapok is a tropical tree of the *Bombacaceae* (Bombax) family: the main variety is *Ceiba pentandra*. Kapok seeds are by-products of lint production. They are ground and the oil is used in edible products and cosmetics. The residual oil cake is used as fertilizer and animal feed. Kapok oil cake has a high fibre content and low digestibility. It can be used up to a maximum of 70% in cattle diets, above which it is unpalatable. Kapok oil cake with 2% oil is toxic to chicks at > 20% of total diet and reduces growth rate at < 10%. It may also be toxic to pigs. The dry matter (DM) content of kapok seed oil cake is 865–890 g kg^{-1} and its nutrient composition (g kg^{-1} DM) is crude protein 290–340, crude fibre 220–320, ash 78–80, ether extract 64–88 and NFE 64–88. (JKM)

Nutrient composition of kale (g kg^{-1} DM) and metabolizable energy (MJ kg^{-1} DM).

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	NDF	EE	Ash	Sugar	Starch	ME
Fresh	130–145	157–200	175–185	243–440	21–36	125–150	170–233	5–9	11.4–12
Silage	176	201	–	232	–	–	65	–	12.3

EE, ether extract; ME, metabolizable energy; NDF, neutral-detergent fibre.

Keratins Keratins are a superfamily of proteins found in cells and their derivatives such as hair and nails. Apart from 'hard' keratins, which make up hair, nails and lens proteins, there are five major types of keratins based on genomic structure and amino acid sequence homology. Types I and II are termed 'soft' keratins and consist of at least 20 members that are specifically expressed in epithelial cells. Types III and IV are found in mesenchymal, muscle and neural tissues. Type V keratins make up the nuclear laminas. Obligate heterodimer pairs of keratins act as building blocks of intermediate filament proteins, which function in providing cell shape and protection from mechanical stress. (GG)

Keto acids Acids that are the critical intermediates in the metabolism and interconversion of amino acids. They have a structure in which a carbonyl carbon R·C=O·COOH is α to a carboxyl carbon, i.e. they are α-keto acids. The majority of these compounds are produced from related amino acids by transamination. For example, upon transamination, alanine ($CH_3{\cdot}HCNH_3^+{\cdot}COO^-$) yields the keto acid pyruvate ($CH_3{\cdot}C{=}O{\cdot}COO^-$). Keto acids of indispensable amino acids, with the exception of lysine and threonine, can be transaminated to yield the corresponding L-amino acid. Keto acids are intermediates in the utilization of D-amino acids. Many D-amino acids can be deaminated to form a keto acid by the enzyme D-amino acid oxidase. The resulting keto acid can be transaminated with the amino group from glutamic acid or another amino (-NH_3^+) donor to become the L-amino acid. This is how D-methionine is converted to L-methionine. The majority of transaminations are dependent on glutamic acid as the nitrogen source. Alanine is another source but it does not participate in as many reactions as does glutamate. The amino acids alanine, glutamate and aspartate are dispensable amino acids; their biosynthesis is dependent on a final transamination step involving the keto acids pryuvate, α-ketoglutarate and oxaloacetate, respectively. Transamination and keto acid formation are critical to the movement of nitrogen from amino acids to aspartate, which is one of the nitrogen donors in the formation of urea, the major form in which mammals excrete nitrogen. (NJB)

Ketones Substances with the general chemical structure R·C=O·R. Three ketones produced in animal metabolism are acetone ($CH_3{\cdot}C{=}O{\cdot}CH_3$), acetoacetate ($CH_3{\cdot}C{=}O{\cdot}CH_2{\cdot}COO^-$) and β-hydroxybutyrate ($CH_3{\cdot}CHOH{\cdot}CH_2{\cdot}COO^-$). They occur in high concentrations in blood of animals suffering from ketosis. Acetone is volatile and smells sweet and can be detected in the expired air of ketotic animals. Ketones are produced when the rate of production of acetyl-CoA from fatty acids exceeds the capacity of the tricarboxylic cycle to covert the carbon to CO_2. (NJB)

Ketosis A metabolic disease, also called acetonaemia, caused by excessive amounts of toxic ketone bodies in the blood. It is common in dairy cattle, particularly those with fatty liver syndrome, in early lactation when the energy demands of milk production exceed energy intake leading to a negative energy balance. Use of adipose tissue to provide energy is inefficient when blood glucose concentrations are low, leading to build-up of ketones. Some diets low in precursors of propionic acid are described as ketogenic. (EM)

Kid A young goat.

Kidney beans: *see* Bean

Kidney disease There are eight major diseases of the kidney. Renal ischaemia, or reduced renal blood flow, is usually the result of a general circulatory failure; it may be acute, e.g. following serious haemorrhage, or chronic, as in congestive heart failure, and is one of the results of severe water deprivation. Glomerulonephritis affects primarily the glomeruli; it is rare in animals, being primarily a disease of humans, but it does occur in dogs. Nephrosis involves degenerative and inflammatory lesions of the renal tubules, usually associated with the ingestion of one of a wide range of toxic substances. These range from heavy metals, such as cadmium, to overdosage with a variety of drugs that are safe in the usual prescribed dose. The urine is of high specific gravity and contains protein. Interstitial nephritis was common in the dog but is now seldom seen, because of vaccination against the causal organism. The condition has been observed in cows fed roughage treated with caustic soda. Embolic nephritis is usually associated with bacteraemia, when clumps of bacteria block the vessels supplying portions of the kidney; it is not usually a fatal condition. Pyelonephritis develops from an infection that ascends from the lower urinary tract; it is characterized by pus in the urine and inflammation of both the ureters and bladder.

Hydronephrosis is a cystic enlargement of the kidney resulting from obstruction of the ureter, often caused by a calculus. Renal tumours are uncommon in animals. (ADC)

Kilocalorie 1 kilocalorie (kcal) = 1000 calories. Formerly known as Calorie or large calorie or CALORIE. These forms, though still used, are confusing and should be avoided. (JAMcL)

See also: Energy units

Kilojoule 1 kilojoule (kJ) = 1000 joules. (JAMcL)

See also: Energy units

Kitchen waste Kitchen waste, swill or garbage waste may consist of food leftovers, spoiled food, food past its expiry date, or mislabelled food. In some countries, kitchen waste cannot legally be used in pig diets due the possible spread of swine fever and foot-and-mouth disease, while in others it can be fed after heat processing. Food that has not been in contact with meat or meat by-products can safely be fed to pigs without processing. The nutritive value of kitchen waste for pigs is adequate with respect to protein and energy but it often has a low dry matter content which tends to reduce dry matter intake and growth, principally in younger animals fed *ad libitum* (see table). The digestibility of kitchen waste is variable and related to the source. If used as part of a balanced diet, the feeding of garbage residues to pigs has no detrimental effects on carcass quality. (JKM)

Kiwifruit *Actinidia chinensis*; also called Chinese gooseberry. It grows on a vigorous, woody, twining vine or climbing shrub reaching 9 m in height. It originated in South China and was introduced commercially into New Zealand in 1934. The oval fruit is up to 6 cm long, with russet-brown skin densely covered with short, stiff brown hairs. The flesh, firm until fully ripe, is glistening, juicy and luscious, bright green, or sometimes yellow. It is grown mainly for human consumption and extraction of the enzyme actinidin for industrial food use, but can also be used fresh for animal feed or made into tropical silage. The fruit is low in dry matter and protein but rich in carbohydrate, potassium (332 mg 100 g^{-1}) and vitamin E, and extremely high in vitamin C with up to 100 mg per fruit. Overripe or poorly shaped fruits are used for livestock feed. They can be dried or fed fresh. The hairs on the skin of the fruit cause irritation when eaten and may limit intakes. The dry matter (DM) content in kiwifruit is 198 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is protein 39.9, fat 3.5, carbohydrates 883.8, ash 22.7, calcium 1.6, iron 0.51, magnesium 3, phosphorus 6.4, thiamine 0.02, niacin 0.5, riboflavin 0.05 and ascorbic acid 1.05. (JKM)

Typical composition of kitchen waste.

	Dry matter (DM) (g kg^{-1})	Crude protein	Crude fibre	Ether extract	Gross energy (MJ)
Composition (g kg^{-1} DM)	132–310	175–195	36–53	201–341	–
Digestibility (%)	80.5–87.3	61–83	56.6–72.5	77–94	23.1

Kjeldahl A procedure used to measure total nitrogen (N) in biological materials. N in a sample of the material is converted to ammonium sulphate by boiling in concentrated sulphuric acid in the presence of catalysts (mercury or selenium) and potassium sulphate (which raises the temperature of the digestion). The ammonia formed is then determined. Originally this involved steam-distillation of the ammonia, after making the digest alkaline by addition of sodium hydroxide, into a known volume of standard acid, the ammonia then being determined by titration. More convenient methods of determining the ammonia have since been developed. (CBC)

Klason lignin An analytically defined fraction of plant material, measured gravimetrically as insoluble material remaining after treatment of a sample with 72% sulphuric acid, usually heated. The lignin content of plant tissue increases as it ages, making wood one of the more lignified tissues. (JAM)
See also: Dietary fibre

Kohlrabi Kohlrabi (*Brassica oleracea* var. *caulorapa*) is a low biennial plant with green or purple skin and white flesh. Its swollen stem is a carbohydrate storage organ; it grows at ground level and is harvested for human consumption. It is a good source of vitamin C and potassium. As a stock feed, kohlrabi is similar to turnip and can be grazed by ruminants. Young kohlrabi are tender and the greens are palatable but the adult greens can become tough. The dry matter (DM) content of kohlrabi is 900 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 122, crude fibre 111, ether extract 22 and ash 78, with ME 11.2 and FME 10.4 MJ kg^{-1} DM. (JKM)

Krebs cycle: *see* Tricarboxylic acid (TCA) cycle

Krebs–Henseleit cycle An older term for the urea cycle. It was named the Krebs–Henseleit cycle because Professor H.A. Krebs proposed (in 1932) a series of reactions to account for the catalytic effect of added ornithine or citrulline on urea production by liver slices. It was shown that the sum of the concentrations of ornithine + arginine did not change appreciably during an incubation, while the amount of ammonia which disappeared roughly equalled the amount of urea produced. (NJB)

Krill Krill (*Norvegica pelagic*) is a collection of small shrimp-like crustaceans ranging from 8 to 70 mm, according to species. The main uses are as high-protein feed for farmed fish and marine tropical fish, and, in Japan, for human consumption. Krill is generally sold as a dried meal or hydrolysate. Krill should be frozen immediately after catching, since storage at room temperature results in the production of toxins. The fat is rich in highly unsaturated fatty acids, of which the omega-3 series contribute 40%. The composition varies according to season, with increased proportions of **palmitoleic** and **omega-3 acids** in spring. The unsaturated fat content can adversely affect cellulose digestion in the rumen. The high concentration of β-carotene (150–200 ppm) gives fish such as salmon their pink colour. The dry matter (DM) content of krill is 900 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 580, ether extract 180, starch and sugars 20–40, ash 130; essential amino acids: valine 53, isoleucine 50, phenylalanine 52, lysine 82, threonine 47, methionine 40, tyrosine 45, histidine 25, arginine 67; and fatty acids C14:0 117 and C18:3 n-38. (JKM)

L

Labelling A means of marking a substance so that it can be distinguished from the unlabelled substance. The labels most commonly used in nutrition research are isotopes, either radioactive or stable, of one or more of the atoms in the substance. Because the major metabolic substrates are compounds of carbon, the stable (^{13}C) and radioactive (^{14}C) isotopes of carbon are very common labels, but isotopes of hydrogen (the stable isotope deuterium, ^{2}H, or the radioisotope tritium, ^{3}H) are also frequently used and, in work on nitrogen metabolism, its stable isotope ^{15}N. Isotopes of most minerals and trace elements are also available and are used to study the metabolism of those nutrients. Radioactive labels are measured by counting their disintegrations in a beta or gamma counter; stable isotopes are measured by mass spectrometry. Labels need not be isotopic: a molecule can be labelled by tagging it with an entity that can be measured by other means such as fluorescence.

The dilution of a labelled substance in a pool of that same substance (unlabelled) in the body can provide various kinds of information. Most simply, it can give an estimate of the size of the pool (e.g. the dilution of a known amount of $^{2}H_2O$ in body water is used to estimate total body water). If the labelled compound or 'tracer' is infused at a constant known rate, its dilution can be used to estimate the rate at which the substance is passing through the pool (the 'entry rate' or 'flux'). For example, if L-[1-^{13}C]leucine is infused at a constant rate into the blood (I), the ^{13}C enrichment of leucine in the blood rises and approaches a plateau or equilibrium isotopic enrichment (E). The labelled leucine is then leaving the blood at the same rate as it is being infused and its ^{13}C enrichment is used to calculate the rate at which leucine as a whole (Q) is entering the plasma pool, from absorption (A) and from protein breakdown (B), and leaving the plasma pool for protein synthesis (S) and oxidation (O). Then, assuming a constant plasma pool size:

$$Q = I/E = A + B = S + O$$

Similar methods are used to estimate the pool sizes and entry rates of a wide range of metabolites.

Isotopic labels are intrinsic, meaning that they do not alter the chemical structure, but substances can also be made distinguishable by tagging them with an extrinsic label, e.g. by the addition of radioactive iodine. Proteins such as albumin can be iodinated (by which radioactive iodine, ^{128}I or ^{131}I, is bound to tyrosine residues in the protein) and infused at a known rate. The equilibrium dilution of the label in the blood provides a measure of the rate at which albumin is being released into the blood and being taken up from the blood.

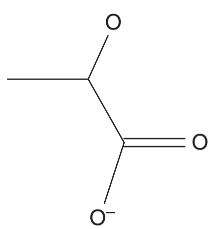
There is a danger that nutrients or metabolites with extrinsic labels may behave somewhat differently from the unlabelled substance. For example, the addition of the label may interfere with their interaction with enzymes or receptors. Isotopic labelling is not entirely free of this danger; especially with hydrogen, the large proportionate difference in mass (twofold for deuterium, threefold for tritium) means that the labelled and unlabelled substrates may behave differently in their biochemical interactions. (MFF)

Laboratory animals Most animals used for biological research are small species such as rats, mice and quail. Laboratory animals are often used as models for studying nutritional processes in humans and farm animals, being easier to handle and cheaper to keep than the latter. The validity of such studies relies on the assumption that the relevant metabolic processes are the same in different species, which may not always be the case. (MFF)

Lactalbumin: *see* Dairy products

Lactase An enzyme found in the brush border membranes of epithelial cells in the duodenum and jejunum. It splits the disaccharide lactose into glucose and galactose. The enzyme is present in most newborn mammals to assimilate the high concentrations of lactose present in milk and then may down-regulate or disappear following weaning. (GG)

Lactate A three-carbon acid. L-Lactate, $CH_3{\cdot}HCOH{\cdot}COO^-$, is derived from pyruvate in glucose catabolism. Under anaerobic conditions the NADH + H^+ produced in the catabolism of glucose is used to reduce pyruvate to lactate with the regeneration of NAD, which can again participate in reactions leading to the production of ATP in glycolysis. Under anaerobic conditions or at levels of exercise intensity that exceed the aerobic metabolic capacity, lactate concentration increases. This may decrease blood and tissue pH and decrease enzyme activity, leading to metabolic complications.



(NJB)

See also: Glycolysis

Lactation The secretion of milk by the mammary glands of mammals. Most animals provide sufficient milk to meet the requirements of their suckling offspring. Dairy cows, goats and some breeds of sheep have been selected for improved milk production. Annual milk yields are 4000–12,000 l in dairy cows, 600–1100 l in goats and 200–700 l in sheep. Lactation typically lasts for 10 months in cows and goats and 7 months in sheep. Milk yield in cattle is low following parturition and rises to a peak 6–8 weeks into lactation; it then declines steadily until milking ceases and the animal is dried off. The rate of decline is typically 2.5% per week in dairy cows, but higher-yielding animals are characterized by greater persistency.

Most lactating animals exhibit a period of negative energy balance in early lactation, because their voluntary feed intake is insufficient to meet the demands for increasing milk yield. Over this period the animal will mobilize body reserves, particularly body fat, in support of milk production. In later lactation, when appetite is more than sufficient for milk production, body fat reserves are replenished. The rate of mobilization of body fat is affected by energy intake in relation to energy requirements for milk production. It is important that animals are not overfat at parturition since excessive body fat reduces feed intake still further, leading to ketosis, fatty liver syndrome and reproductive failure. On the other hand, animals that are too thin at parturition may have insufficient body energy reserves to compensate for reduced feed intakes. This is not a problem if diets of high energy concentration are offered, since the rate of energy mobilization has a greater impact on health and reproduction than absolute levels of reserves (Garnsworthy and Webb, 1999). The recommended range of body condition scores at calving in dairy cows, for example, is 2.0–3.5 (on a 1–5 scale, where 1 is thinnest and 5 is fattest). Labile protein reserves are proportionately small, compared with fat reserves, since most body protein is found in muscles. Protein nutrition in early lactation can therefore be critical in determining the ability of the animal to support milk production from mobilized body fat.

The nutrient concentration of diets for animals in early lactation needs to be high, because of the imbalance between requirements and feed intake. However, for ruminants, the proportion of the ration dry matter derived from forage should not be allowed to drop below 30% or rumen fermentation will be impaired, leading to digestive upsets and reduced butterfat production (*see* **Concentrate**).

The energy and protein requirements for lactation are determined by milk yield, milk composition and metabolizability of the diet (which affects the efficiency of utilization of metabolizable energy). For cattle and goats, the energy value of milk is given by the equation EV (MJ kg^{-1}) = 0.0376 BF + 0.0209 P + 0.948, where BF and P are the butterfat and protein contents of the milk (g kg^{-1}). For sheep, the equation is 0.0328 BF + 0.0025d + 2.2033, where d is the number of days of lactation. The efficiency of utilization of metabolizable energy (ME) for lactation is equal to 0.35q + 0.420, where q is the metabolizability of the diet (AFRC, 1993). An average dairy cow will therefore require approximately 5.2 MJ ME l^{-1} milk produced. The requirement for metabolizable protein for lactation is equal to the true protein content of milk divided by the efficiency of utilization of absorbed amino acids for milk production (0.68; AFRC, 1993). An average dairy cow will require approximately 47 g metabolizable protein per litre of milk produced.

In sheep rearing lambs (in contrast to milking sheep), lactation lasts for 12–20 weeks. Milk yield reaches a peak in the third week of lactation and then steadily declines. Potential milk yield is impossible to measure in suckling animals, since the quantity of milk produced is determined by the ability of the lamb(s) to suckle. Estimates based on weighing lambs before and after suckling suggest that ewes with single lambs produce between 75 and 130 l in a 12-week lactation and ewes with twin lambs produce between 80 and 210 l. There is a large variation between breeds in milk yield. The energy requirement of a ewe for milk production is approximately 5.2 MJ ME kg^{-1} and the protein requirement is approximately 74 g kg^{-1} milk.

In pigs, lactation lasts for 3–6 weeks, depending on the management system of the breeding herd. Milk yield rises after parturition to peak at about 4 weeks and then declines at a rate of 9% per week. Milk yield is related to the number of piglets in the litter, averaging approximately 0.8 l per piglet. The energy requirement of a sow for milk production is approximately 8.3 MJ of digestible energy kg^{-1} and the protein requirement is approximately 100 g kg^{-1} milk. (PCG)

See also: Milk

References

AFRC (1993) *Energy and Protein Requirements of Ruminants*. An advisory manual prepared by the AFRC Technical Committee on Responses to Nutrients. CAB International, Wallingford, UK.

Garnsworthy, P.C. and Webb, R. (1999) Nutrition and fertility in dairy cows. In: Garnsworthy, P.C. and Wiseman, J. (eds) *Recent Advances in Animal Nutrition – 1999*. Nottingham University Press, Nottingham, pp. 39–57.

Lactation disorders The metabolites for the synthesis of milk constituents come from dietary nutrients and from mobilization of body reserves, principally adipose tissue, muscle and some minerals, such as calcium in bone. In high-yielding mammals such as the dairy cow, early lactation milk production is supported mainly by mobilization of body reserve, but food rapidly takes over as the main source. The extent of the mobilization depends on reserves: for fat it can last for half of the lactation but for calcium it is unlikely to last for more than a few days. If the diet continues to provide insufficient nutrients, the animal's potential milk yield will not be achieved. If such malnutrition occurs in early lactation, when new secretory tissue is still being developed in the mammary gland, subsequent increases in food intake are not likely to return milk yield to its potential level.

Specific nutrient deficiencies or imbalances reduce food intake and thereby depress milk yield. Especially important are adequate dietary supplies of nutrients required to support the synthesis of milk constituents, and of these calcium is of special importance.

Milk fever, a disease common in high-yielding dairy cows, is caused by insufficient absorption of calcium. It usually occurs within the first few days of lactation, when an affected cow collapses. Treatment is by intravenous infusion of a solution of calcium lactate or calcium borogluconate. It can generally be prevented by feeding a diet low in calcium for several weeks before calving. This increases the efficiency of absorption of calcium so that if, at calving, the dietary content of calcium is increased, an adequate amount is absorbed to support the greatly increased requirements of lactation.

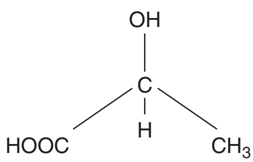
In dairy cows given rapidly fermentable diets a condition known as low milk-fat syndrome is often evident. Such a diet produces a low acetate:propionate ratio in the rumen fermentation and the relative lack of acetate limits milk fat synthesis. The condition can be alleviated by reducing the concentrate:forage ratio or by using concentrates with slower rates of fermentation.

A common lactational disorder is bacterial infection of the mammary gland, or mastitis. The gland has various defences against infection but mastitis is common in situations where the invasion of bacteria into the teat canal is facilitated by dirty conditions or sharing of milking clusters, as often occurs with the dairy cow. Mastitis occurs less frequently in sheep and goats. The prevalence of mastitis, in dairy cows at least, is influenced by the adequacy of the vitamin E and selenium status, and possibly magnesium.

A less common disorder is the failure of milk letdown in cattle. This can often be rectified by an injection of oxytocin, which stimulates the mammary epithelial cells to contract and milk to be expelled from the alveoli into the gland cistern.

Other lactation disorders include agalactia in sows. (JMF)

Lactic acid 2-Hydroxypropanoic acid, $CH_3 \cdot HCOH \cdot COOH$.



Because carbon 2 has four different substituents, lactic acid can have L and D forms. Commercially available lactic acid is usually a racemic mixture of the two. The pKa is 3.86, so at a normal body pH of ~7.4, the carboxyl carbon of lactic acid is not protonated and the molecule carries a negative charge. Under normal aerobic conditions, all cells except erythrocytes oxidize glucose to CO_2 and H_2O, generating 38 ATPs per mole of glucose. Glucose is first catabolized to pyruvate via glycolytic enzymes found in the cytosol; pyruvate then enters the mitochondria to be completely oxidized to CO_2 and H_2O. However, under a workload with limited oxygen, mitochondria are not able to oxidize NADH at a rate that matches its production, and NADH is diverted to lactate production. Production of lactate is the result of pyruvate reduction to L-lactate by L-lactate dehydrogenase, i.e. $CH_3 \cdot CO \cdot COO^- + NADH + H^+ \rightarrow CH_3 \cdot HCOH \cdot COO^- + NAD$. All cells in the body can produce lactate, which is subsequently extracted from the circulatory system for catabolism by the liver and cardiac muscle. The net yield of ATP under anaerobic conditions (when the NADH produced during glycolysis cannot be oxidized by the mitochondria) is only 2 ATPs mol^{-1} glucose converted to 2 mol lactate. Under this condition, the rate of glucose catabolism must increase 19-fold (38/2) to meet the ATP flux demands. A notable source of lactate is fast twitch skeletal muscle (i.e. white muscle) under conditions of a high workload due to, for example, sprinting, pulling or lifting. As a result of this intense exercise, lactate is produced in muscle and accumulates in the blood and tissues. Blood lactate is extracted by the liver and converted to glucose via the pathways used in gluconeogenesis. Glucose is then released to the blood and may be taken up by skeletal muscle. In the older literature, this inter-organ coordination was referred to as the Cori cycle. A relevant metabolic disorder in ruminants is acidosis.

Following an abrupt increase in the ingestion of readily fermentable carbohydrates, the rumen and intestinal microflora respond with profuse production of volatile fatty acids and DL-lactate. Clinical rumen acidosis is declared at pH 5.2. Acid absorption from the digestive tract causes an acidification of blood, and clinical systemic acidosis is declared when blood pH falls below 7.35. L-Lactate can be metabolized readily by ruminants, while D-lactate is metabolized very slowly. Until recently, D-lactic acid was considered to be the principal culprit in ruminant acidosis, but it now appears that the total acid load resulting from production and absorption of fermentation acids is responsible for the disorder.

Like several other organic acids, lactic acid has antimicrobial properties, can lower gut pH and makes an energy contribution to animals' diets. It is recognized as a preservative in EU Feeding stuffs legislation and is listed as 'E270, lactic acid, $C_3H_6O_3$, suitable for use in all feeding stuffs'.

It is a colourless, viscous liquid, miscible with water or ethanol and although stronger than most short-chained carboxylic acids, is non-fuming so is relatively easy to handle. It has a mild, fruity, acid taste that does not reduce the palatability of feeding stuffs. It is, however, liable to corrode equipment.

In common with other organic acids, its antimicrobial properties stem from its ability to enter microbial cells in its undissociated state. When inside the cell it dissociates to give hydrogen ions (H^+), which lower pH and result in wasteful energy expenditure in the effort to restore balance, and acid radicals ($CH_3 \cdot CHOH \cdot COO^-$), which disrupt DNA synthesis, in turn interfering with protein synthesis and cell replication.

In the small intestine, lactic acid helps to maintain a balanced microflora and healthy gut development. It has also been shown to stimulate pancreatic activity in newly weaned piglets and there is some evidence that it may, in part at least, replace prophylactic antibiotics by stimulating non-specific immunity in the small intestine. In poultry, lactic acid acidifies the crop and to a lesser extent the caecal contents, reducing the potential for the growth of pathogens such as salmonella.

Lactic acid is important on-farm in the ensiling process. Typically, it is produced *in situ* from plant sugars by lactic acid-producing bacteria. Often, in practice, inoculants of selected, particularly efficient strains of homofermentative lactobacilli are introduced into forage crops during harvesting for silage.

(DMS, CRL)

Key reference

Adams, C.A. (2002) *Total Nutrition – Feeding Animals for Health and Growth*. Nottingham University Press, Nottingham, UK, 248 pp.

Lactic acid bacteria: *see* Gastrointestinal microflora

Lactic acidosis The transfer of large amounts of lactic acid from the rumen to the blood, resulting in a life-threatening decrease in blood pH (metabolic acidosis). This condition is often referred to as 'grain overload' as it is generally caused by excessive ingestion of readily fermentable carbohydrates and undersupply of forages that promote chewing activity and saliva production. Rumen flora not adapted to the availability of highly fermentable carbohydrates convert a large portion of this carbohydrate to lactic acid, rather than to the other volatile fatty acids typical of rumen fermentation. As lactic acid accumulates in the rumen the pH of the rumen declines, which can kill many rumen microbes. If the lactic acid and the other organic acids produced by carbohydrate fermentation are absorbed into the blood and exceed the ability of the liver to metabolize these acids, it can create an acidic condition within the blood and body fluids. A severe decline in blood pH disturbs the protein structure of cells and causes a general failure of all systems of the body. In non-ruminants, lactic acidosis is usually secondary to anaerobic glycolysis within muscle tissue during prolonged anaerobic exercise. (JPG)

Lactitol A disaccharide of galactose and sorbitol, 4-*O*-β-D-galactopyranosyl-D-glucitol ($C_{12}H_{24}O_{11}$), produced by the reduction of the glucose component of lactose. It is not hydrolysed by mammalian digestive enzymes but is readily fermented by the intestinal microflora. (NJB)

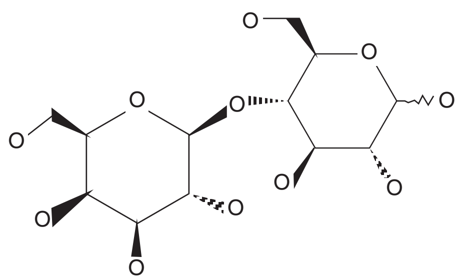
Lactoferrin A protein in milk, structurally similar to transferrin. The molecular weight of lactoferrin is 78–80 kDa and, like transferrin, it binds 2 mol of iron. Lactoferrin binds iron with an affinity 300 times that of transferrin. Lactoferrin has antibacterial properties in the gut, perhaps by decreasing iron availability to intestinal microbes. Although lactoferrin receptors have been identified on cells, its role in iron transport and delivery is not known. (NJB)

Key reference

Hutchens, T.W. and Lönnerdal, B. (eds) (1997) *Lactoferrin Interactions and Biological Functions*. Humana Press, Totowa, New Jersey.

Lactoglobulin A major milk protein accounting for more than two-thirds of the total protein found in the whey of cows' milk. It has a molecular weight of 38,000 and has 370 amino acids arranged into four separate peptide chains. On electrophoresis, lactoglobulin separates into two components: A and B. Both A and B are dimers (i.e. AA or BB) of 19,000 each so that both A and B lactoglobulins have a molecular weight of 38,000. A or B or both may be found in samples from individual cows. It has a total of 370 amino acids arranged into four separate peptide chains. (NJB)

Lactose Milk sugar, 4-(β-D-galactopyranosyl)-D-glucopyranose, $C_{12}H_{24}O_{12}$, made up of glucose and galactose. In milk of the major dairy cattle breeds, the concentration of lactose varies from 4.67 to 5.04% of liquid milk and accounts for 35.9% of milk solids. In commercial preparations lactose is a white powder and is stable, sweet and odourless. It is used in a variety of foods and as a diluent in the pharmaceutical industry.



Lactose is synthesized in the mammary gland from two molecules of glucose. One of the glucose molecules is activated to glucose-6-phosphate and in three subsequent steps is converted to uridine diphosphogalactose which, under the action of the enzyme lactose synthase, is combined with free glucose to form lactose.

The digestion and absorption of lactose occur in the small intestine. Lactase (the enzyme that hydrolyses lactose) is not uniformly distributed: its specific activity is highest in the upper jejunum and falls throughout the remainder of the small intestine. Lactase is found on the brush border (microvilli) of the enterocyte. The glucose and galactose that are released on the brush border are taken up by specific transporters into the enterocyte, then released into the bloodstream. The galactose can be converted into glucose in the liver and metabolized in the body as glucose, with all its ramifications. Mucosal lactase activity does not change with dietary lactose. The microflora of the small and large intestinal contents respond to increased dietary lactose by a doubling of lactase activity of the intestinal contents. Thus, some substantial fraction of dietary lactose may be hydrolysed by the bacteria in the intestinal contents. Lactose intolerance is a well-recognized dietary-associated complication. It is thought to be due to a decrease in the mucosal lactase activity such that a greater fraction of the lactose is fermented, producing gas and short-chain volatile fatty acids. Intestinal fermentation results in increased osmotic pressure in the intestinal contents, which results in water retention leading to diarrhoea. (NJB)

Key reference

Ekstrom, K.E., Benevenga, N.J. and Grummer, R.H. (1975) Effects of diets containing dried whey on the lactase activity of the small intestine mucosa and the contents of the small intestine and caecum of the pig. *Journal of Nutrition* 105, 851–860.

Lamb: *see* Sheep

Lameness Any imperfect use of limbs but generally excluding conditions in which the animal is systemically affected. In ruminants, most lameness arises in the feet but in young calves, lambs and goat kids it is commonly due to septic arthritis. In horses and pigs many cases of lameness arise from abnormalities of joints and tendons. (WRW)
See also: Foot diseases; Laminitis

Laminitis In acute laminitis, the laminae of the hoof separate from the interdigitating horn so that the pedal bone (third phalanx) drops, rotates or both. It is seen in horses on grass, and in cattle on concentrate feed, and may be associated with lack of exercise or toxaemia. In dairy heifers and cows fed large amounts of concentrates and living in restricted conditions, haemorrhage in the sole is very common, and is often referred to as sub-clinical laminitis. (WRW)

See also: Activity, physical; Concentrate; Foot diseases; Hooves

Lard The abdominal fat of pigs that has been rendered and clarified. The composition is dependent on diet but includes a high proportion of long-chain saturated fatty acids. It is a rich source of energy (*c*. 38.5 MJ kg^{-1}) but deficient in other essential nutrients. In some countries it is used in pig, poultry and pre-ruminant diets to increase dietary energy concentration. The major fatty acids in lard (g kg^{-1} of total fatty acids) are: 14:0 1.6; 16:0 25.5; 16:7 n-7 2.2; 18:0 16.8; 18:1 sum of *trans* isomers 0.3; 18:1 sum of *cis* isomers 39.2; 18:2 n-6 10.0; 18:3 n-3 1.2; and saturated fatty acids 43.9, monounsaturated fatty acids 41.7 and polyunsaturated fatty acids 11.2. (JKM)

Large intestine The section of the digestive tract between the small intestine and the anus. In most mammals it consists of the **caecum**, **colon** and **rectum**. Most birds have two caeca, both connected to the intestine at the ileocaecocolic junction. The large intestine is the major site for microbial activity in non-ruminants and is of particular importance for non-ruminant herbivores such as horses, rabbits and ostriches. (SB)

Larval feeding: *see* Fish larvae; Live fish food

Lathyrism A paralytic syndrome of humans and livestock characterized by spastic paraplegia, pain, hyperaesthesia and paraesthesia. Historically, lathyrism occurred under conditions of poverty and drought when people were forced to subsist on diets composed largely of seeds of *Lathyrus* spp. Horses are highly sensitive, developing a hopping gait, stiffness and pain when moving. The onset of disease ranges from several days to months depending on the dose. One identified toxin is directly neurotoxic, causing neurolathyrism (muscle rigidity and paralysis). A second toxin causes osteolathyrism by inhibiting connective tissue development (lameness). Many animals recover fully but chronically poisoned animals can develop permanent stringhalt-like signs. (BLS)

Lauric acid Dodecanoic acid, $C_{12}H_{24}O_2$, molecular weight 222, shorthand designation 12:0. This 12-carbon, monocarboxylic, saturated fatty acid, with a melting point of 44.2°C, is a major component of coconut and palm oils and is also present in human milk, dairy fat, cinnamon and laurels. (JAM)

See also: Fatty acids

Lead The nutritional essentiality of lead has only been demonstrated under laboratory conditions in ultra-trace quantities. Lead is a potentially toxic element for farm animals. It is present in many forms on the farm, but most hazardous are old paints (made before lead was removed from paint in the latter part of the 20th century), discarded lead batteries and roofing material, and soil contaminated by industry and mine tailings. Cattle are most at risk, being inquisitive and likely to eat soil, paint, etc., when their diet is inadequate. Lead is the most common cause of cattle poisoning in the UK, accounting for about 200 deaths annually. The symptoms of acute lead poisoning are blindness, excessive salivation, irritability and convulsions, often accompanied by a stiff gait and impaired vision. Chronic lead poisoning may induce loss of appetite, osteoporosis and fractures, and neurological disorders, due mainly to the strong affinity of lead for the binding sites of calcium and other essential nutrients. (CJCP)

Leaf protein In temperate regions, forage leaf is fed fresh, ensiled for winter feed or dried to produce grass, clover or lucerne (alfalfa) meal (see table overleaf). Lucerne meal is fed to racehorses and high-yielding cows. In tropical regions, the leaves of a wide range of plants are fed fresh, wilted or dried into leaf meal. Typically these are used as protein sources for cattle, goats, sheep, poultry, fish and shrimp. They also supply vitamins, minerals and trace elements, as well as pigments. *Alchornia cordifolia* meal is fed to poultry as an egg and meat colorant, while *Sauropus androgynus* (Katuk) and Tu-chung (*Eucommia*

Dry matter ($g\ kg^{-1}$), nutrient composition ($g\ kg^{-1}$) and energy ($MJ\ kg^{-1}$) contents of leaves.

	Dry matter	Crude protein	Crude fibre	Ash	Ether extract	NFE	ME
Gliricidia spp. leaf meal	930	230–240	200	85–90	35–42	400–480	–
Leucaena leucocephala meal	950	292	192	105	–	–	–
Alchornia cordifolia	950	190	164	25	51	575	–
Grass meal	930	155	220	85	35	480	9.3
Lucerne meal	930	160	240	95	25	425	8.0
Lucerne, fresh	945	230	243	83	48	396	–
Lucerne meal concentrate	951	370–420	7–30	13–16	30–69	360–423	–
Residue from lucerne	926	171	352	69	33	375	–

ME, metabolizable energy; NFE, nitrogen-free extract.

ulmoides) are used to reduce meat lipid content. Many leaves contain antinutritional factors (ANFs) which limit dietary inclusion levels. Levels of some ANFs can be reduced by simple processing such as wilting (*Gliricidia*), drying (*Cassava*) or by supplementing the diet with specific antidotes (e.g. adding iodine, copper or ferrous sulphate to leaves of *Leucaena leucocephala*). Selection and breeding of low-ANF plants is possible. (JKM)

Lean body mass The lipid-free mass of the body (excluding digesta). Lean body mass is normally calculated by subtracting fat (lipid) content from total body mass. It therefore includes body water. (MMacL)

Leaves: *see* Leaf protein

Lecithin Phosphatidylcholine, a major phospholipid in cell membranes. The *sn* 1 and 2 positions of the glycerol backbone $CH_2OH{\cdot}CHOH{\cdot}CH_2OH$ of lecithin are long-chain fatty acids while the *sn* 3 position has phosphocholine, $\cdot O{\cdot}PO_3{\cdot}CH_2{\cdot}CN^+{\cdot}(CH_3)_3$, linked to it. The fatty acid in the *sn* 2 position of lecithin is generally a long-chain unsaturated fatty acid such as arachidonic acid. (NJB)

Lectins Carbohydrate-binding proteins of non-immune origin that agglutinate cells or precipitate polysaccharides or glycoconjugates. Carbohydrates are present on most cell membranes: if their structure fits the binding site of the lectin, agglutination will occur. Lectins were first termed haemagglutinins because of their ability to cause the agglutination of human and animal blood *in vitro*. Lectins are distinguished from antibodies that agglutinate cells by being found in plants, bacteria and viruses that do not have the ability to produce antibodies. In addition, lectins are a heterogeneous group of proteins that vary in size, composition and three-dimensional structure in contrast to antibodies, which are structurally similar.

Lectins are distributed broadly throughout the plant kingdom and have been identified in moulds and lichens as well as higher plants. Ricin was the first to be isolated, extracted from castor beans in 1889 by Stillmark. Since Stillmark's discovery, lectins have been identified in more than 1000 plant species. The majority of the toxic lectins come from species of *Euphorbiaceae* and *Leguminosae*. Most lectins in higher plants are found in the seeds but they have also been found in tubers, plant saps, leaves, stems and bark. The highest concentrations of lectins are in the mature seeds of legumes, where they may constitute as much as 10% of the total protein.

Because of the broad distribution of lectins throughout the plant kingdom, they are present in most foods and feeds of plant origin. Not all are toxic to animals but many raw legume seeds are detrimental to animal performance. Ingestion of lectins can result in diarrhoea, decreased nutrient absorption, increased bacterial infection, growth retardation and death. Lectins binding to surface cells of the intestinal mucosa may cause lesions and disruption of the normal development of the microvilli. Apart from reducing nutrient absorption, such lesions may increase bacterial proliferation in the gut and infiltration via the bloodstream into internal organs. (SEL)

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Leg weakness A term commonly used to describe specific syndromes in pigs and turkeys. In pigs, the pathogenesis includes osteochondrosis, epiphysiolysis and osteoarthrosis, but generally excludes infectious arthritis. It is a condition of rapidly growing pigs between 12 and 24 weeks of age. The affected pigs generally show a progressive lameness. Osteochondrosis (dyschondroplasia) involves abnormal differentiation of the cartilage of growth plates. It is found in subclinical form in the majority of pigs sold for meat. In epiphysiolysis, the epiphysis separates from the diaphysis (shaft) of the bone, often the proximal femur. In osteoarthritis (degenerative joint disease, DJD) the articular cartilage degenerates. The causes of leg weakness are uncertain but it appears to be more common in pigs selected for growth and feed conversion and fed on a high plane of nutrition. Predisposition may be inherited (heritability of up to 0.3), the Landrace breed being particularly affected. Lack of exercise is also a suspected risk factor and exercise appears to improve the gait of pigs, though it does not reduce the joint lesions. High dietary concentrations of calcium and phosphorus are commonly advised methods of prevention. Signs of leg weakness include a short-stepping swaying gait, crossed legs, flexed carpal joints and difficulty in rising. Epiphysiolysis can cause sudden inability to rise and may be difficult to distinguish from a fractured femur. Leg weakness is a common reason for culling gilts and boars, often at the beginning of their breeding life.

The aetiology of leg weakness in turkeys is not understood. The birds show swelling of the hock joints. Osteochondrosis is also seen in young male pure-bred cattle as osteochondritis dessicans and as sub-chondral cysts, causing unilateral lameness but bilateral radiographic changes and a high rate of culling if not treated surgically. Osteodystrophia fibrosa (bran disease; miller's disease) is a condition seen in horses, pigs and goats in which bone is resorbed and weakened. It may be caused by a diet high in phosphorus and low in calcium. The animal shows shifting lameness with no pain and may have swollen upper and lower jaws. In ostriches, leg weakness is commonly encountered. Adequate calcium, grit (3–6 mm for chicks, 6–20 mm for adults) and protein between 16 and 18% of the diet are normally recommended. (WRW)

See also: Bone diseases

Legume Any plant of the family *Leguminosae*, which includes lucerne (alfalfa), clover, peas and beans. Bacteria (*Rhizobia*) colonize the roots of legumes and fix atmospheric nitrogen. (JMW)

Legume protein The protein contained in leguminous plants such as lucerne (alfalfa), clover, peas and beans. (JMW)

Legume silage The term legume (from *legere*, to gather) applies to many nitrogen-gathering plants which bear seeds in pods. The foliage of legumes is rich in protein compared with cereals or grasses. Legumes are perceived as difficult crops to ensile due to their high chemical buffering capacity. Legume silage plants include lucerne (*Medicago sativa* L.), sainfoin (*Onobrychis vicciifolia*), white clover (*Trifolium repens* L.), red clover (*Trifolium pratense* L.), vetches (*Vicia sativa* L.), field beans (*Vicia faba* L.), peas (*Pisum sativum* L.) and lupin (*Lupinus* spp). (RJ)

Lehmann system A system of feeding animals a bulky feed *ad libitum* with restricted amounts of a balancing concentrate feed given once or twice a day. It was developed in Germany about 100 years ago for feeding **potatoes** to pigs. It is well suited to feeding root crops, but can also be used with other perishable crops such as waste **bananas**, **sugarcane** juice, etc. (MFF)

Lentil (*Lens culinaris* Medik; *L. esculenta* Moench) Also known as red dahl or split pea, lentils grow on a widely cultivated bushy herb about 50 cm tall, native to Asia. The seeds are used mainly for human consumption, particularly in the Near East and Asia. Harvested vines are valuable for ruminant feed. The protein in raw lentils is inefficiently used as feed, with a ratio of body weight gain:protein consumed of 0.03, compared with 1.42 for chickpea (*Cicer arietinum* L.). The digestibility of lentil straw – 51.9 g digestible organic matter (DOM) 100 g^{-1} dry matter (DM) – in ruminants is higher than for most other straws, with a voluntary intake only 10% lower than that of lucerne hay. As with all legumes, the nutrient content and digestibility of the leaves (8–10% crude protein and 66.2% DM digestibility) are considerable higher than for other plant parts (see tables). (LR)

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Leucaena A tropical leguminous tree or bush of which the leaves, pods and seeds can be used to feed animals. It is grown to produce firewood, to stabilize and enrich poor soils and as a source of nutrients for animals, primarily ruminants. There are ten species and about 800 varieties of leucaena, some of which can produce over 100 t of forage per annum. Typically the forage has (g kg^{-1} dry matter) protein 250, fat 40, crude fibre 80 and neutral detergent fibre 600. It has adequate concentrations of minerals and is a substantial source of carotenoids, which are important in egg production. The metabolizable energy of leucaena for ruminants is about 8.5 MJ kg^{-1}, while that for poultry is only about 2.5 MJ kg^{-1}, due to its non-starch polysaccharides, tannins and the toxic amino acid mimosine. Compared with the leaves, the seeds of leucaena are higher in protein and fat (300 and 80 g kg^{-1}, respectively) but they also contain more mimosine (60–100 g kg^{-1} in comparison with 40–60 g kg^{-1} for the leaf).

Mimosine (see figure) is a non-protein amino acid that causes numerous adverse effects when consumed by animals. It causes depilation and interferes in the metabolism of other amino acids to which it is structurally related. It degrades readily in ruminants to yield 3-hydroxy-4(1H)-pyridone (see figure), which is often referred to as 3,4-DHP and which interferes with thyroid function to cause goitre. The mimosine content

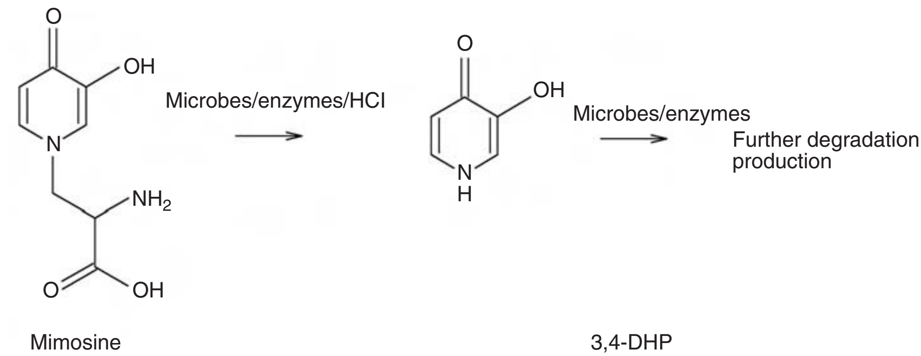
Nutrient composition (% dry matter) of lentil products.

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Bran	87.6	26.4	8.4	2.8	1.1	61.3		
Pod husks	88.0	12.6	29.0	3.5	0.8	54.1		
Straw		5.8	37.1	9.0	2.4		1.65	0.07

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Digestibility (%) and ME content of lentil products.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Pod husks	11.8	67.2	99.9	70.7	9.26
Straw					7.90



Mimosine and its degradation by *Synergisti joneseii* and enzymes.

varies with the variety of leucaena but is a deterrent to its use as a fodder (especially as the sole source) in some parts of the world. The value of leucaena as a forage for ruminants depends greatly on the presence or absence of certain rumen microorganisms (*Synergysti joneseii*) which degrade mimosine and 3,4-DHP to innocuous compounds within the rumen. In some areas of the world (notably Australia) the rumen microflora are cultured and administered to cattle and sheep and they can then browse leucaena with impunity and grow well on leucaena-based diets.

Leucaena meal, included in poultry diets at about 50 g kg^{-1}, increases egg yolk pigment in hens and provides protein for growing chicks. Higher inclusion rates tend to cause poorer performance, presumably due to the tannins and non-starch polysaccharides. Pigs appear to be able to tolerate about 50 g kg^{-1} in their diet without detrimental effects but the digestible energy of leucaena leaf meal for pigs is only about 5 MJ kg^{-1}. (TA)

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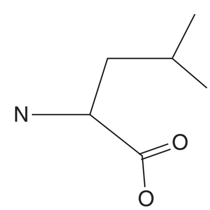
Leucaena leaf meal: *see* Leaf protein

Leucine An essential amino acid $(CH_3)_2{\cdot}CH{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$, molecular weight 131.2) found in protein. It is one of the branched-chain amino acids. Leucine is generally found in considerable excess in most plant proteins, so in practice a deficiency is rare. Leucine is purely ketogenic; it cannot be used in gluconeogenesis. Catabolism of leucine involves transamination followed by oxidative decarboxylation to a coenzyme A derivative, and these first two steps in leucine catabolism use the same enzymes that are used for the first two steps in isoleucine and valine catabolism.



(DHB)

See also: Essential amino acids

Leukotrienes Lipid-based compounds derived from arachidonic acid, a 20-carbon unsaturated (20:4 n-6 $\Delta^{5, 8, 11, 14}$) fatty acid synthesized in most mammals from linoleic acid (18:2 n-6 $\Delta^{9, 12}$) except in cats, where arachidonate is an essential fatty acid. Arachidonate in the *sn*-2 position of the glycerol moiety of phospholipids in cell membranes is released by phospholipase A_2. It can then be used in the biosynthesis of series 4 leukotrienes. This conversion is dependent on a lipoxygenase which facilitates the incorporation of molecular oxygen into arachidonate, forming an intermediate (5-HPETE), which ultimately leads to formation of A_4, B_4, C_4, D_4, E_4 and F_4 forms of leukotrienes. Four of the leukotrienes are amino lipids. Leukotriene C_4 contains glutathione (x-glutamyl-cysteinyl-glycine); D_4 derived from C_4 contains glycine and cysteine; E_4 derived from D_4 contains cysteine; and F_4 derived from E_4 after addition of glutamic acid has cysteine and glutamic acid. These substances act as local hormones and have short half-lives. They are chemically similar to prostaglandins and thromboxanes but are involved in hypersensitivity and allergic responses. They are vasoactive, and produce bronchoconstriction and are involved with counteracting the effects of asthma (Drazen *et al.*, 1999). Two other series, 3 and 5, are identified but their functions are little understood. The series 3 leukotrienes are derived from Mead acid (20:3 n-9 $\Delta^{5,8,11}$). The series 5 leukotrienes are derived from timnodonic acid (20:5 n-3 $\Delta^{5,8,11,14,17}$).

(TDC)

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Level of feeding: *see* Plane of nutrition

Lieberkühn's crypts: *see* Crypts of Lieberkühn

Light Electromagnetic radiation with a wavelength of 400–780 nm which, when received at the retina and neurally transferred to the brain, makes sight possible. Light also has a profound effect on the physiology and performance of farm animals, whether artificial light in indoor production systems or natural light for grazing livestock. For avian species, light influences sexual activity by directly penetrating the skull and tissues to the hypothalamus. Since farmed birds are reared typically in indoor systems, knowledge of the components of the artificial lighting regime that affect behaviour and performance is critical. These are photoperiod (day length), light intensity (illuminance) and spectral composition (colour balance or wavelength). Photoperiod has the strongest influence, affecting growth rate and skeletal integrity, rate of sexual maturation and all reproductive characteristics.

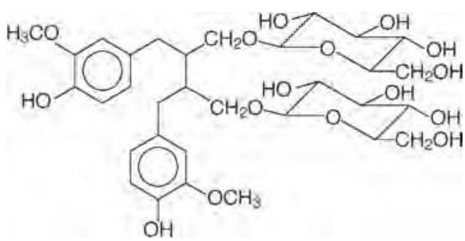
Light intensity also has a strong influence on bird behaviour and, to a lesser extent, bird performance. Activity and energy expenditure are positively correlated with intensity, together with the incidence of cannibalistic behaviour and its related mortality. A minimum intensity of 2 lux during rearing ensures that sexual maturity is not retarded, whilst maximum egg production in modern hybrids is achieved with a minimum intensity of 5–10 lux. Unexplainably, feed intake and egg weight decrease, though at a low rate, with increasing illuminance. Growth rate and feed conversion in modern broilers and turkeys are not significantly affected by light intensity, provided that the illuminance during the first week is sufficiently bright to allow the birds to find feed and water.

Spectral composition minimally affects egg production, despite longer wavelengths (red) penetrating to the hypothalamus more effectively than shorter wavelengths of light. This is inconsequential to birds given white light, because white includes all wavelengths of light. Birds are more active and tend to exhibit more aggression under red light and this might explain why body weight gain in broilers and turkeys is reduced under red light. Though not light in human terms, UVA ultraviolet radiation is important for poultry because they have a fourth retinal cone that is sensitive to UVA. As a consequence birds can see objects and plumage markings that reflect UVA, though these will be invisible to humans. Injurious pecking in growing turkeys is reduced when birds are given supplemental UVA concurrently with environmental enrichment.

Light affects reproductive activity, growth, food intake and pelage growth in mammalian species, with photoperiod rather than light intensity or wavelength being the key factor. Seasonal changes in natural photoperiod provide the major influence in largely outdoor production systems, but artificial lighting regimes during periods of housing can clearly be important. Deer, sheep and goats demonstrate the most pronounced seasonal changes in physiology whereas cattle and pigs are less seasonal. In addition, within the diurnal period, whatever the time of year or photoperiod, animals preferentially eat more during the day than at night. Thus, in freely feeding cattle and sheep, meals are longer and more frequent during daylight than during darkness.

(PDL, CLA)

Lignans A class of secondary plant metabolites. Lignans are oligomers of hydroxy cinnamic acids ($C_6H_5CH{=}CHCOOH$). Unlike lignin, lignans are soluble and may be absorbed from the digestive tract of mammals. Lignans have post-absorptive physiological effects such as oestrogenic activity. For example, consumption of the lignan secoisolariciresinol diglycoside (shown here) in flaxseed is associated with a decreased risk of breast cancer.



(JDR)

Lignin An insoluble polyphenolic compound associated with polysaccharides in the plant cell wall. Lignin makes the cell wall rigid and hydrophobic. It is formed by the oxidative polymerization of monolignols (hydroxy cinnamyl alcohols). The polymerization process occurs outside the cell after monolignols are transported across the plasmalemma. The structure of lignin is complex and difficult to determine by traditional biochemical techniques. Lignification of the cell wall occurs after cell elongation is complete and is associated with a decrease in the digestibility of cell wall polysaccharides. Lignin in the cell walls of grasses is cross-linked with polysaccharides through esters of two cinnamic acids: *p*-coumaric, $HOC_6H_4CH{=}CHCOOH$; and ferrulic acid, $HOC_6H_3(CH_3O)CH{=}CHCOOH$. These esters are saponified by alkali treatment, which leads to an increase in the degradability of the polysaccharides. This process is used to increase the digestibility of cereal crop residues. The cell walls of legume forages have fewer ester cross-linkages and alkali treatment has little effect on the degradability of their cell wall polysaccharides.

Lignin is indigestible and is negatively correlated with digestibility of the cell wall. Certain aerobic fungi are capable of degrading lignin through oxidative cleavage of the phenolic rings through the action of phenol oxidases and Mn^{2+} peroxidases. The degradation of lignin in anaerobic environments is too slow to occur in the digestive tract of mammals. (JDR)

Lignocellulosic waste Waste products such as sugarcane bagasse, yam peel, cocoa bean shells and paper milling waste are used as animal feeds, as carriers for low-dry-matter feeds, or as substrates for bio-conversion into protein-enriched feed by cellulolytic fungus. Lignocellulosic wastes are used most frequently in ruminant diets. (JKM)

Lignoceric acid Tetracosanoic acid, $CH_3{\cdot}(CH_2)_{22}{\cdot}COOH$, molecular weight 368.6, shorthand designation 24:0. A 24-carbon saturated fatty acid found in sphingolipid and glycosphingolipid of animal tissues and in seeds of *Leguminosae* and *Sapindaceae*.

(DLP)

Limestone A sedimentary rock found in vast deposits throughout the world, usually formed from the exoskeletons of marine creatures and consisting mainly of calcium carbonate ($CaCO_3$). It is typically white or off-white. In a ground form it is used as a source of calcium in animal feeding stuffs. A common type of limestone is dolomite, in which some of the calcium is replaced by magnesium, CaMg

$(CO_3)_2$. The availabilities of calcium and magnesium from dolomite are relatively low.

(CRL)

Linamarin A simple cyanogenic glycoside found in linseed, cassava and white clover. Its structure is $C_6H_{12}O_6 \cdot C \cdot (CH_3)_2 \cdot CN$. In the gastrointestinal tract it readily undergoes acid or enzymatic hydrolysis to yield glucose and cyanic acid (HCN). HCN is extremely toxic, inhibiting cytochrome oxidase activity and ultimately causing death. (TA)

Linear programming Method of minimizing or maximizing a mathematical function, linear in a number of variables, subject to linear constraints on these variables. Primarily used in animal nutrition to minimize the total cost of a feed, subject to restrictions on its nutrient composition. (RG)

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Linoleic acid *cis*-9,12 Octadecadienoic acid, with molecular structure $CH_3(CH_2)_4(CH{=}CHCH_2)_2(CH_2)_6COOH$, molecular weight 280.4, shorthand designation 18:2 n-6. An essential fatty acid of the n-6 family and a metabolic precursor of many physiologically active eicosanoids. It is found in high concentration in many oil seeds.

(DLP)

Linolenic acid *cis* 9,12,15 Octadecatrienoic acid, with molecular structure $CH_3(CH_2)(CH{=}CHCH_2)_3(CH_2)_6COOH$, molecular weight 278.4, shorthand designation 18:3 n-3. An essential fatty acid of the n-3 family and a metabolic precursor of many physiologically active eicosanoids, it is highly susceptible to spontaneous oxidation. It is the major fatty acid in linseed oil; there are also significant amounts in soybean oil. (DLP)

Linseed Linseed (*Linum* spp.) is grown for its fibre (flax) and the oil of its seed. Linseed oil is high in unsaturated fatty acids, especially linolenic acid, and is therefore subject to oxidation. Consumption of linseed oil, especially by non-ruminants, makes the tissue lipids soft and subject to oxidation, with an undesirable flavour and smell. Linseed cake or meal (the residue after the oil has been extracted) is used as a protein concentrate in animal diets, mainly for ruminants and horses. It is less useful in diets for non-ruminants because it contains up to 100 g kg^{-1} of non-starch polysaccharides (NSPs) known as mucilaginous gums. They are essentially indigestible by non-ruminants and tend to absorb large quantities of water, increasing digesta viscosity and producing wet sticky faeces. Enzyme supplementation may reduce some of the effects associated with these NSPs but this is not necessary in ruminants as the gums are degraded by the rumen microflora. Linseed meal also contains the cyanogenic glycoside linamarin, which can yield HCN after ingestion.

The apparent metabolizable energy values of linseed meal for poultry, pigs and ruminants are about 8, 13 and 14 MJ kg^{-1}, respectively. The crude protein concentration is 300–400 g kg^{-1}. It contains factors that antagonize vitamin B_6 in poultry. The protein is relatively low in lysine, which may be made less available by heating due to the formation of Maillard products. Inclusion levels of linseed in diets are usually less than 20 g kg^{-1} diet for poultry or 110 g kg^{-1} for other species.

(TA)

Lipase A class of hydrolytic enzymes that degrade lipids. Lingual lipase is present in the saliva of calves when they are on a milk diet but disappears when they mature. Pancreatic lipases are secreted into the duodenum.

Lipids are hydrophobic and, before they can be digested, most dietary lipids need to be emulsified, i.e. their lipid droplets are reduced to a size that forms stable suspensions in water. Emulsification is begun in the stomach by the higher temperature and intense mixing, which decrease the droplet size before the lipid enters the small intestine. In the duodenum the emulsification is completed by the detergent action of bile acids and phospholipids secreted via the bile duct from the liver.

Lipase itself cannot penetrate the coat of bile products surrounding the droplets of triglyceride, the major dietary lipid component. The enzyme colipase, a relatively short peptide, is needed to make a path through the bile products, giving lipase access to the underlying triglycerides. Lipase then cleaves the fatty acids from each end of the triglyceride molecule, but does not attack the central fatty acid. Thus, the hydrolysis products of one triglyceride are two fatty acids and one monoglyceride.

Other lipid-digesting pancreatic enzymes include cholesterol esterase and phospholipase. The hydrolysis products are non-esterified fatty acids, cholesterol and lysophospholipids. (SB)

Lipid absorption Because lipids do not dissolve in water they have first to be emulsified; they can then be hydrolysed by lipases in the duodenum and must then be formed into micelles before they can be absorbed into the enterocytes of the intestinal mucosa.

Emulsification is achieved mainly in the duodenum by exposure to bile, which leads to the production of emulsified droplets. In the jejunum the combined actions of lipase, colipase and bile lead to the formation of micelles consisting of the hydrolysis products – fatty acids and monoglycerides. The micelles diffuse through the unstirred water layer to the brush border of the enterocytes through which all the components except the bile acids are absorbed by diffusion. The bile acids pass down the intestinal tract to the ileum, where they are absorbed by a specialized sodium co-transport.

In the enterocytes, triglycerides are reformed and packaged into chylomicrons. These are complex aggregates also consisting of cholesterol esters, with a surface layer of phospholipid and cholesterol molecules with their hydrophobic ends towards the centre and their hydrophilic ends facing the surface, which makes the chylomicrons water-soluble. A small number of protein molecules help to stabilize the surface and also to direct the metabolism of the particle.

Fatty acids containing fewer than 10–12 carbon atoms are not packaged in chylomicrons but pass from the mucosal cells directly into the portal blood, where they are transported as free (non-esterified) fatty acids (NEFA).

Chylomicrons are too large to pass through the basement membrane of the intestinal capillaries and cannot be absorbed through the intestinal blood system. Rather they travel through the intestinal lymphatics to the thoracic duct which empties into the vena cava; in this way chylomicrons reach the blood vascular system.

Lipid absorption is greatest in the jejunum, but appreciable amounts may also be absorbed in the ileum. (SB)

See also: Gastrointestinal tract

Lipid metabolism The digestion, transport, storage and oxidation of dietary lipids as well as the *de novo* synthesis and utilization of lipids. Processes include emulsification and lipolysis of dietary fats, absorption of fatty acids, resynthesis of triacylglycerol and phospholipids in the intestine and their packaging into chylomicrons with cholesterol and apoproteins for transport in the lymph and blood. *De novo* fatty acid synthesis is limited to certain tissues. These differ between species: liver and adipose tissue are the major sites in rodents and pigs, liver in humans and avian species, adipose tissue in ruminants and the mammary gland in all mammals. Cholesterol is synthesized in many tissues and is regulated by feedback inhibition from cholesterol taken up from plasma lipoproteins by a receptor-mediated process.

The water-insoluble triacylglycerol from intestinal absorption is transported in plasma in bulk as chylomicrons and from liver as very low density lipoproteins; the fatty acids of triacylglycerol are released by lipoprotein lipase activity of specific tissues. Removal of triacylglycerol from lipoproteins results in a dynamic remodelling in plasma of lipoprotein particles of differing lipid and protein content, brought about by exchange of phospholipid, cholesterol, cholesteryl esters and specific apoproteins of different particles.

Fuel supply and energy balance of the animal are maintained by deposition of lipid, especially in adipose tissue during energy surplus, and by mobilization in deficit; the frequency of such cycles may be hours, days or months, depending upon nutrient supply and energy demands. Mobilization of stored fatty acids is mediated by hormone-sensitive lipase; fatty acids are transported to tissues by association with serum albumin. Though muscle and other tissues may utilize mobilized fatty acids directly, the bulk is taken up by liver in a concentration-dependent manner. In liver, fatty acids are oxidized to ketone bodies (acetone, acetoacetate and β-OH butyrate) which are exported for energy by extrahepatic tissues. Excessively rapid mobilization and oxidation of fatty acids may lead to ketosis, a condition in which the supply of strongly acidic ketone bodies exceeds the capacity of tissues to oxidize them. In such conditions ketone bodies are excreted by the kidneys, accompanied by equimolar quantities of base, causing the animal to become acidotic.

Though quantitatively the major role of lipid metabolism is to match energy supply to demand, many lipid components are essential to the healthy function of the body. These include cholesterol metabolism to form bile acids and hormones and to aid in lipid transport, essential fatty acids for membrane function and as precursors of the prostaglandins that provide many regulatory functions, and sphingolipids as essential components of cell membranes and nerve tissue. Many inherited disorders of lipid metabolism are known to occur, some of which lead to degenerative conditions of the body and others that are more lethal in the short term. (DLP)

Further reading

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Lipid peroxidation Generally a chain reaction that leads to the degradation of unsaturated fatty acids with the formation of multiple oxidized products. There are three phases: (i) initiation, whereby an electron is abstracted from a reactive carbon of the fatty acid molecule, usually by a metal ion (such as copper) or by a hydroperoxide product of the chain reaction, to form a free radical; (ii) propagation, whereby the free radical combines with oxygen to form a peroxy free radical, which in turn may abstract hydrogen from another unsaturated molecule to yield a peroxide and a new free radical, thus initiating the chain reaction, which may be repeated several thousand times; and (iii) termination, which occurs by free radicals reacting with themselves to yield inactive products, or by introduction of a chain-breaking antioxidant (e.g. vitamin E). The methylene groups adjacent to double bonds are most susceptible to abstraction of electrons, thus the methylene-interrupted diene system of polyunsaturated fatty acids is most reactive and susceptible to oxidation. (DLP)

Lipids Low molecular weight (generally < 1000) substances of biological origin that are relatively more soluble in non-polar than polar solvents. They are characterized by their low oxygen content and are therefore energy dense. Neutral lipids (fats, oils) are generally found as energy storage molecules whereas the more polar lipids (phospholipids, sphingolipids) are key components of cellular and subcellular membranes. (DLP)

Lipogenesis The metabolic process whereby non-lipid substances (carbohydrates and some amino acids) are converted to fatty acids. Acetyl CoA is a key intermediate. (DLP)

Lipolysis The process whereby glycerides are hydrolysed and released as fatty acids and glycerol by the action of a lipase enzyme. Most commonly this involves triacylglycerol as the substrate. Phospholipases hydrolyse the constituents of phospholipids at specific bonds, yielding products differing according to the specificity of the phospholipase. (DLP)

Lipopolysaccharide A complex component of the cell wall of Gram-negative bacteria. Lipopolysaccharides contain a lower proportion of lipid than do glycolipids. The toxic lipid moiety (lipid A) contains a high proportion of 3-OH myristic acid; other fatty acids of 10–22 carbons may be present, as well as glucosamine, ethanolamine and phosphate. A polysaccharide core links lipid A to the O-polysaccharide moiety which designates specificity. Various structural models have been presented. (DLP)

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Lipoprotein lipase A lipolytic enzyme secreted from capillary endothelial cells. It hydrolyses the triacylglycerol of triacylglycerol-rich lipoproteins (chylomicrons, VLDL) in serum, thus releasing fatty acids to be taken up by tissues. It requires specific activating peptides found in circulating lipoproteins. The lipoprotein lipase of milk is identical to that of serum. Regulation of the expression of the enzyme differs among tissues. (DLP)

Lipoproteins Protein–lipid complexes that solubilize neutral lipids so that they can be transported in an aqueous medium, such as the blood. Particle size (75 to >1000 Å) and molecular weight ($0.2–100 \times 10^6$ daltons) are inversely related to density. Larger, less dense particles contain > 80% triacylglycerol and only 1–2% protein, whereas the smallest and most dense particles are > 50% protein with most of the lipid being cholesterol and phospholipid. Large particles have a central core predominantly of triacylglycerol and some cholesteryl ester, surrounded by a thin film of phospholipid, free cholesterol and protein. Major classes of lipoproteins are commonly classified according to hydrated density (triglyceride content decreasing as density increases) and electrophoretic mobility into: chylomicrons (density < 0.94 g ml^{-1}, produced by the small intestine to transport dietary lipid), very low density lipoproteins (VLDL; density 0.94 to < 1.006 g ml^{-1}, produced by the liver, and to a lesser extent the small intestine); low density lipoproteins (LDL; density 1.006–1.063 g ml^{-1}, created by the metabolism of VLDL); and high density lipoproteins (HDL; density 1.063–1.20 g ml^{-1}). These classes may be further subdivided on the basis of lipid or protein content. The protein components are called apoproteins and are responsible for signalling the metabolism, transport and cellular uptake of lipoproteins. (DLP, JAM)

Liquid diets Liquid feeding systems allow higher feed intakes and as a consequence pigs fed liquid diets have faster growth rates. Fermented liquid feed given to weaned piglets has the potential to reduce disease in the gastrointestinal tract and improve the performance of weaners. Calves are fed various liquids after their initial colostrum, including whole milk, surplus colostrum, waste or discarded milk and milk replacer, some of which are specifically formulated for *ad libitum* intake. Sugarcane juice and by-products such as molasses and condensed solubles from fermentation (*see* **Yeast**) can be fed to ruminants. Such products can be part of a multi-component diet and they can be processed to increase palatability or to provide an appropriate feed to utilize urea. The addition of oil can increase the energy concentration; protein, vitamins and minerals may also be added. Liquid feed has a low replacement rate and cows fed on whey will consume approximately two-thirds of their normal water intake as whey. The use of liquid feed requires some form of storage and feeding equipment which can, depending on cost, be prohibitive to the economical use of liquid feeds. (JKM)

Lithium Lithium (Li) is a highly alkaline metal with an atomic mass of 6.941, and is present in the earth's crust at about 20 mg kg^{-1}. The natural lithium content of feed ingredients is probably very low. One study found < 3 μg kg^{-1} in whole ground maize. Although there is no known dietary requirement for any farm animal, there is evidence that low concentrations of dietary lithium are essential for the support of maximal reproductive efficiency and birth weight in rats. Rats maintained on diets containing 0.6 μg lithium kg^{-1} for three generations had significantly lower litter size and weights than similar rats maintained on 500 μg dietary lithium kg^{-1}. (PGR)

Further reading

Pickett, E.E. and O'Dell, B.L. (1992) Evidence for the dietary essentiality of lithium in the rat. *Biological Trace Elements Research* 34, 299–319.

Litter Animal bedding. The central function of poultry litter is to provide bedding for birds (broilers and turkeys) so that they may grow well, remain comfortable and be free from blemishes when slaughtered. Litter may also act as an insulation material, reducing heat transfer through the floor of the poultry house. The litter must absorb by admixture all excreta and convert it to a drier and more manageable material. The degradative processes in litter and the exchanges with the poultry house environment must maintain both a proper litter moisture level and good air quality. Bacteria and other microorganisms are essential components of litter but the qualities of the medium also necessitate consideration of the role of litter in pathogen maintenance and transmission and recycling of drugs and toxins.

Whilst the provision and management of litter appears to be a simple technology, the material is actually an important dynamic component of the poultry house environment. Thus, any analysis of litter problems, including 'wet litter', will reveal a multiplicity of causes, factors and complex interactions that may underlie the aetiology of the difficulty. Litter management involves choice of material (and availability), depth of litter to be used, supplementary additions and frequency, litter stirring and the use of chemical additives and of course litter removal, disposal and/or re-use. A global calculation based on 1998 figures suggests a world broiler meat production of 52 million tonnes, requiring approximately 25 Mt of litter and resulting in 100 Mt of used litter for disposal. Used litter, with or without composting, may be employed as a fuel or fertilizer or as the base for ruminant feedstuffs.

The choice of litter material must be based upon the ability to absorb water, decomposability, freedom from toxins and contaminants, availability and cost. In use, the litter should be dry and friable; there should be no caking or capping and the ammonia content should remain low. Materials frequently used as litter include wood shavings, sawdust, wheat straw, oat straw, papyrus straw, peat moss, newsprint, cardboard, rice hulls, groundnut hulls, maize cobs and vermiculite.

An important feature of the litter material is moisture content. Many raw materials have an initial moisture content of 10–15% and in use this falls between 25–50%. Litter moistures of 40% are considered satisfactory but caking will occur at 45% and severe wet litter problems will occur at 50% or greater. Perhaps the most important chemical transformation taking place in active litter is the conversion of uric acid to ammonia via allantoin and urea by bacterial degradation. This process can be accelerated in high moisture conditions and this will have serious consequences for the poultry house environment. Wet litter is a major problem occurring under production conditions around the world; thus, understanding the water relations of litter and the factors precipitating wet litter is essential. Water added to the litter from any source is either retained in the litter or evaporated into the air and ultimately is removed by ventilation. For any litter material and set of conditions it is necessary to define the equilibrium moisture content – equilibrium relative humidity relations between the litter and the air in the poultry house. These relationships facilitate the prediction of litter moisture and therefore litter quality from a knowledge of relative humidity and temperature and can form the basis of calculations of ventilation rates required to control litter condition.

Wet litter is usually identified by caking or sealing of the surface. This condition will influence growth rate, carcass quality and disease status. There is a wide range of possible causes, several of which may contribute to the problem in any situation and all of which must be considered when seeking a solution. They include: external climatic conditions (e.g. high temperature associated with high humidity), inadequate ventilation, condensation (poor insulation), disturbances in bird water intake or water balance, diseases producing diarrhoea, dietary effects, water quality and composition, the use of some anti-coccidial drugs, inappropriate use of evaporative cooling and fogging and poorly maintained and leaky drinkers and pipes. In most modern commercial poultry (broiler) facilities production is operated close

to the limiting conditions and an interaction of two or more of these variables can precipitate a very rapid deterioration in litter conditions. To optimize litter quality it is necessary to pay close attention to these factors and in particular to understand litter water relations and the principles of ventilation control. (MMit)
See also: Poultry droppings

Litter size The number of piglets born during a single farrowing. Litter size may be influenced by the nutrition of the sow at critical stages. '**Flushing**' (providing a high feed level, 3–4 kg day^{-1} of a high quality diet) in the 10–14 days prior to service can increase ovulation rate in gilts. A similar result can be obtained in young sows by preventing excessive loss of body condition in lactation and achieving a high feed intake between weaning and service. After service, reduction of feed level is also important, because giving excessive feed to gilts and young sows at this time can impair implantation and reduce embryo survival. Once the implantation period has passed and pregnancy has progressed beyond 3 weeks, nutrition has little further effect on litter size. After farrowing, the litter size that a sow is nursing will exert a major influence on her nutritional requirements during lactation, since milk output increases with the number of piglets that are suckling. (SAE)

Litter weight The total weight of piglets nursing a single sow. The litter weight at birth may be influenced by nutrition during gestation, when an increased level of feed intake can increase piglet birth weight. Increased feed allowance in the last third of pregnancy is especially beneficial if the sow is in poor body condition, since low-birth-weight piglets are at much greater risk of neonatal mortality. However, giving extra feed to the sow in order to increase birth weight is a relatively inefficient process; it requires about 100 kg of extra sow food during pregnancy to give an increase of 0.1 kg in average piglet birth weight. The litter weight in the first 3 weeks of lactation is determined by the milk yield of the sow, which in turn depends on her body condition at the start of lactation and her ability to consume the large amount of feed necessary to meet the demands of milk production. Litter growth rate increases by about 9 g for each additional megajoule of digestible energy consumed by the sow. After 3 weeks of age, the suckling piglets will eat increasing amounts of solid feed, and provision of an appropriate **creep feed** will increase litter weight. (SAE)

Live fish food Many fish larvae at the time of initial exogenous feeding have a short, rudimentary digestive tract and lack a functional stomach (gastric glands). Generally, formulated diets do not meet the nutritional requirements of these larvae and thus may lead to poor growth and survival. Live food organisms are required during the first feeding stages. Live foods are more attractive than inert formulated feeds to first-feeding fish larvae, which are visual predators. These live food organisms also contain high amounts of digestible nutrients (e.g. free amino acids) and enzymes, which allow for autolysis (self-digestion of the live food).

Rotifers (*Brachionus plicatilis*) and brine shrimp (*Artemia* spp.) are the most commonly mass-cultured zooplankton for use as live food for fish larvae as well as for the early juvenile and larval stages of crustaceans (shrimp). Most species of marine fish larvae are initially reared on a diet of rotifers followed by the larger brine shrimp, after which formulated feeds are introduced. The development of a functional stomach (around metamorphosis) determines when weaning will take place.

The best live food is the natural prey of the larvae but copepods, the natural prey of marine fish larvae, are not suitable for intensive culture because of their longer growth period and culture at low density levels. The harpacticoid copepods such as *Tigriopus* and *Tisbe* spp. are better suited for mass culture than calanoid copepods (e.g. *Acartia* spp.). Since these benthic organisms do not swim in the water column, larvae cannot easily locate them. The use of captured wild zooplankton (i.e. copepods) is limited because of variations in both quality and quantity. Other live foods include freshwater cladocerans (*Moina* and *Daphnia* spp.), bivalve larvae (trochophores) and various protozoan species.

Fish larvae are sensitive to dietary deficiencies of n-3 polyunsaturated fatty acids (PUFAs). Eicosapentaenoic acid (20:5 n-3) and in particular docosahexaenoic acid (22:6 n-3) are essential for proper functioning of the cell membranes in the rapidly developing neural and optical systems of the larvae. Arachidonic acid, the major precursor of eicosanoids, is also thought to be essential for fish larvae. Copepods contain high amounts of these essential fatty acids (EFAs), whereas rotifers and brine shrimp must be enriched in these EFAs before being fed to fish larvae. Commercial EFA enrichments commonly consist of either marine oils containing an emulsifier (lecithin) or concentrated, spray-dried algal products. Live food organisms are fed these enrichments in aerated water baths for a short period of time (< 24 h) before being fed to the fish larvae.

Cultured phytoplankton or micro-algae (e.g. *Isochrysis* and *Nannochloropsis* spp.) are often used directly as a food source for shellfish and the early larval stages of some fish and crustacean species. Phytoplanktons are also fed to live food organisms to feed larval fish, with the species selected depending upon their nutrient composition. Phytoplankton in larval fish tanks also provide essential nutrients to live food organisms, scatter incoming light (possibly enhancing visualization of live food prey) and supply enzymes, feeding stimulants and unidentified compounds with properties of immunostimulants to larvae. (DN)

See also: Aquatic organisms; Fish larvae; Phytoplankton; Rotifer

Liver Liver meal is produced from condemned livers, which are dried at a low temperature and then ground. Liver meal can be included in small amounts in poultry and pig feeds as a source of B vitamins and vitamin A, but it is also a source of high quality protein and reduces the need for inorganic mineral supplements in the diet. The use in animal foods of animal by-products, including liver, is banned in the EU. Fish liver oils are rich sources of vitamins A and D and of essential fatty acids and are used in animal feeds. The dry matter (DM) content of liver meal in Uganda is 921 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 732, crude fibre 0, ash 104, ether extract 94, NFE 70, calcium 0.2 and phosphorus 0.7 (source: FAO (2002) Feed resources information service, http://www.fao.org/ag/AGA/AGAP/FRG/AFRIS/Data/318.HTM). (JKM)

Liver diseases Liver disease can be caused either by direct damage to the cells of the liver or by damage to the bile secretory system, e.g. blockage of the bile duct. The liver can be affected by primary infectious disease, caused by viruses or bacteria, parasitic disease caused by liver fluke, the larval stage of tapeworms, ascariasis in pigs, toxic damage from pathogens (e.g. aflatoxins, clostridial toxins), toxic products of metabolism or poisonous plants, such as ragwort. Signs of liver disease include weight loss and inappetence but are generally non-specific and a laboratory diagnosis may be required. Damage to the liver may include fatty change, inflammation (hepatitis), neoplasia, necrosis or atrophy. Some liver diseases have a nutritional aetiology. Fatty liver disease (hepatic lipidosis) is seen in overfat animals. If these animals are subjected to high energy demands, inefficient fat utilization leads to a build-up in ketones. Liver abscesses are more common in cattle fed high-carbohydrate, low-roughage diets. Hepatosis dietetica in fast-growing pigs is associated with vitamin E and selenium deficiency. Hepatic necrosis can be caused by aflatoxins, particularly in pigs and ducklings. (EM)

Liver function The liver is a multifunctional organ that is responsible for regulating: (i) the metabolism of carbohydrates, lipids and proteins; (ii) the production of important plasma proteins, including albumin and fibrinogen; (iii) the synthesis and release of bile acids; (iv) the storage of certain vitamins and iron; (v) the detoxification and excretion of many drugs and toxins; (vi) the production of hormones including growth hormone; and (vii) the degradation of certain hormones.

The liver is a major storage site for **glycogen** which, when broken down by glycogenolysis, releases glucose into the blood. It is also the primary site of gluconeogenesis, which converts certain amino acids, propionate and glycerol into glucose. These processes are tightly controlled by the hormone glucagon. In regulating lipid metabolism, the liver is the primary site of remnant chylomicron absorption from the circulation and the synthesis of very low-density lipoproteins (VLDLs). Liver hepatocytes are the principal source of **cholesterol** in the body, where it is used to produce **bile** acids. Bile secretion into the small intestine is the major route of cholesterol excretion from the body and plays a pivotal role in controlling serum cholesterol levels. (GG)

Liveweight The weight of the live animal at a particular time. This includes the weight of gut contents, which varies with diet and feeding pattern. Liveweight is therefore distinct from empty body weight (total weight minus gut contents) and deadweight or carcass weight, which refer to the weight of the eviscerated animal, often with other parts such as feet or head also removed. (MFF)

Lobster A name applied to various species of large decapod crustacea in the class Malacostraca, characterized by: a large carapace enclosing the thorax; five pairs of thoracic walking legs, the first of which is frequently specialized as claws; a highly muscularized abdomen designed for strong ventral flexion of the tail fan; and movable stalked eyes. There are four families of lobsters: clawed lobsters (Nephropidae, including the European, American and Norwegian lobsters), spiny lobsters (Palinuridae), slipper lobsters (Scyllaridae) and coral lobsters (Synaxidae). (RHP)

Lobster culture: *see* Shellfish culture; Crustacean feeding

Locust bean Properly the fruit of the African locust bean tree (*Parkia filicoidea*) but the name is frequently applied to the fruit of the carob tree (*Ceratonia siliqua*). The latter originated in the eastern Mediterranean region and is also found in the subtropics. The fruits are thick, fleshy (more so in the carob) pods each containing about a dozen seeds. The seeds are tough and must be crushed before feeding. The resulting meal has a high sugar and energy content and is very palatable but is low in protein (42–54 g kg^{-1}). (JKM)
See also: Carob

Key reference

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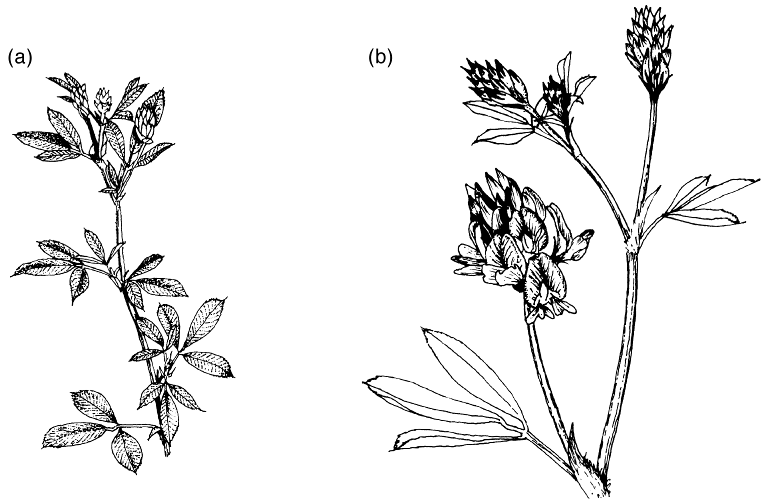
Long-chain fatty acids Fatty acids containing 14–20 carbon atoms, as distinct from short-chain (4–8 C), medium-chain (10–12 C) and very long-chain (> 20 C) fatty acids. They may contain other functional groups (e.g. double bond, hydroxyl or methyl branch). (DLP)

Long-chain triacylglycerols The high molecular weight fraction of fat. Triacylglycerols contain three fatty acids, with a total carbon number > 50. The term most commonly refers to a fraction of milk fat. (DLP)

Lordosis A common degenerative condition of the connective tissues forming the spinal column in which the affected animal develops a hollow-backed or sway-backed appearance. It can be caused by deficiencies of micronutrients, including vitamin D and tryptophan. Deficiency of copper can cause 'swayback' in sheep. (DS)

Lucerne (*Medicago sativa* L.) Also known as alfalfa, lucerne is a perennial herb with deep roots, trifoliate leaves and purple flowers, requiring sunshine and high temperatures. It can be grown alone or mixed with grasses or other legumes. Drier leaves are friable and leaf loss is high during haymaking. In lucerne-growing areas, green forage is used to feed high-producing animals as it is highly palatable and contains sufficient protein, calcium and vitamins not to require concentrate supplements. As with many forage legumes, the nutritive value declines with age and lucerne should be harvested before the flowers mature. Stage of maturity has the most influence on nutritive value of irrigated lucerne at first cutting. A rotational system is recommended for grazing animals. Hay can be harvested to separate leaf from stem. Stems can then be used as roughage and the dried leaves included in concentrate mixtures. There is a danger of young lucerne causing bloat in grazing ruminants if they consume too much; this can be avoided by using wilted material – cutting in the morning and feeding in the afternoon – or allowing grass grazing before access to the legume. Dried lucerne leaf has a high vitamin A content and 2–5% can be included in layer rations to ensure a good yolk colour. Lucerne can be used as pasture for pigs, and lucerne meal can be included in concentrate mixtures. (LR)



Lucerne. (a) A leafy shoot; (b) an inflorescence.

Nutrient composition of lucerne (% dry matter).

		DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh:	pre-bloom	17.0	25.3	23.5	11.8	2.9	36.5	2.41	0.35
	early bloom	22.7	22.9	26.0	11.5	3.5	36.1	2.56	0.31
	mid-bloom	29.0	19.0	30.0	10.3	3.4	37.3	1.76	0.24
Fresh:	1 year old	20.3	17.1	19.4	12.6	2.7	48.2		
	2 year old	21.4	16.5	21.3	11.5	2.8	47.9		
	3 year old	21.4	16.2	22.3	10.8	2.7	48.0		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Digestibility (%) and ME content of lucerne.

		CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant						
Fresh:	pre-bloom	89.0	45.0	50.0	76.0	10.35
	early bloom	79.0	49.0	38.0	78.0	9.89
	mid-bloom	69.0	45.0	50.0	61.0	8.42
Fresh:	1 year old	85.9	68.4	59.6	80.7	11.10
	2 year old	87.4	79.5	55.6	76.7	11.23
	3 year old	88.1	70.8	33.9	80.5	11.15
Leaf meal		79.4	59.9		77.7	9.51

Further reading

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Lupinosis A mycotoxicosis caused by ingestion of toxins (phomopsin A and B) produced by the fungus *Diaporthe toxica* (anamorph *Phomopsis* spp.) which colonizes domestic lupin stubble in Australia. The phomopsins are hepatotoxic hexapeptides and the severity of the disease is dose related. Lupinosis affects livestock that graze 'sweet' (i.e. low alkaloid) lupin stubble and limits the use of this animal feed in Australia. Phomopsis-resistant lupin cultivars are available but, in spite of their increasing use, lupinosis is still a major limitation to the full utilization for feed of the millions of hectares of sweet lupin stubble. Lupinosis is not to be confused with lupin poisoning caused by ingestion of 'bitter' (high alkaloid) lupins, which contain the toxic quinolizidine and piperidine alkaloids. In the western USA after the early 1900s, there were extensive losses of sheep grazing lupin pastures; these rarely occur now but lupin-induced skeletal defects in cattle ('crooked calf disease') is still a major cause of economic loss to cattle producers. Certain quinolizidine (anagyrine) and piperidine (ammodendrine) alkaloids in these lupins are responsible for the skeletal defects and cleft palate in the calf when ingested by pregnant cows during days 40–100 of gestation. (KEP)

Lupins Over 200 species of flowering plants, members of the *Leguminosae* family, grown primarily for their seed and also used as forage. The whole plant, the seeds and the residue after harvesting the seed can be used as feedstuffs for animals. Three species constitute the majority of commercial production of lupin seed for animal use: *Lupinus angustifolius*, *L. albus* and *L. luteus* (sometimes identified by their flower colour as blue, white and yellow lupin, respectively). Others have also been investigated and used to lesser extents. Australia is the largest producer of lupin seed.

Lupin seeds contain up to 450 g crude protein kg^{-1} in the dry matter and are relatively low in the sulphur amino acids. Lupin seeds have a fat content of 40–60 g kg^{-1}. They have an insignificant amount of starch; their major carbohydrate is α-galactans, which are essentially indigestible in non-ruminant animals but, if fed at too high a concentration in the diet, tend to increase water-holding capacity and viscosity of digesta and excreta, substantially alter microbial profiles in the gastrointestinal tract and reduce performance. The apparent metabolizable energy of lupin seed for poultry is 8.5–10.5 MJ kg^{-1} and for ruminants 12–16 MJ kg^{-1}. The digestible energy for pigs is 11–17 MJ kg^{-1}, with the higher value determined in the ileal digesta. Digestibility of the amino acids in poultry is between 0.7 and 0.8. Diets containing lupin seed can be supplemented with enzymes to improve their nutritional value for non-ruminants, although adverse effects are small in diets with 150–200 g of 'sweet' lupins kg^{-1}. Some lupin species and cultivars contain quinolizidine alkaloids; these are bitter and reduce food intake, especially in pigs but much less so in poultry and ruminants. So-called sweet varieties have a low total alkaloid content (< 20 mg kg^{-1}). The forage, and in some cases the seed, of lupins can be infested by a fungus, *Phomopsis leptostromiformis*, which produces phomopsin toxins; these may cause lupinosis, a mycotoxicosis seen in sheep that have grazed lupin stubble. (TA)

Lupins, grown for their seed and as forage, contain alkaloids. Photo courtesy of T. Wierenga.

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Lutein A yellow carotenoid pigment ($C_{40}H_{56}O_2$, xanthophyll) widely spread in plants and found in animals in body fat and egg yolk. It is not a precursor of vitamin A. (NJB)

Luteinizing hormone (LH) A glycoprotein hormone produced by the anterior pituitary. In females, LH stimulates the maturation of follicles, the final rupture of the follicle to release an ovum, the production of follicular progesterone and the development of the ruptured follicle into the corpus luteum. In males, LH stimulates the testes to produce testosterone. (JRS)

Lychnose An oligosaccharide, 1-α-galactosylraffinose, molecular weight 666. Carbon 1 of the fructose of raffinose is linked to an α-D-galactopyranose residue. Found in roots of members of the *Carophyllacea*. (JAM)

See also: Carbohydrates; Oligosaccharides

Lycopene An aliphatic hydrocarbon carotenoid ($C_{40}H_{56}$) with 11 conjugated double bonds. Natural plant sources are predominantly all-*trans* but the *cis* isomers predominate in many human tissues. Found predominantly in the chromoplast of plant tissues, especially tomatoes, but high also in fruits. Among the biological carotenoids, lycopene is the most efficient quencher of singlet oxygen. Clinical studies suggest it is an anti-carcinogen. (DLP)

Further reading

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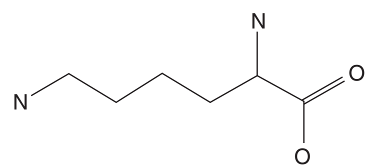
Lymphocytes: *see* Immunity

Lysine An essential amino acid ($H_2N^+{\cdot}(CH_2)_4{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 146.2) found in protein. Lysine is generally the most limiting amino acid in the food supply of both animals and humans. It is produced commercially as L-lysine·HCl, L-lysine·SO_4, or L-lysine free base. Virtually all cereal grains and their by-products are first limiting in lysine, and most oilseed meals, with the exception of soybean meal, are deficient in lysine. In addition to its use in protein synthesis, lysine, as protein-bound trimethyllysine, is a precursor of carnitine in the body.

Both protein-bound lysine and free lysine can react with free carbonyl groups such as those existing on reducing sugars to form **Maillard reaction** products. Heat and humidity promote the Maillard reaction in stored feeds and feed ingredients. Also, under alkaline conditions and heat, lysine in feeds or feed ingredients can react with dehydroalanine (produced from serine) to form the cross-linked amino acid lysinoalanine. Neither lysinoalanine nor Maillard-bound lysine have lysine bioactivity.



(DHB)

See also: Essential amino acids

Lysolecithin Generally, a phospholipid, but specifically phosphatidyl choline, from which a fatty acyl chain has been removed by hydrolysis or acyl transfer, e.g. 1-acyl or 2-acyl lysolecithin. So named for its ability to lyse erythrocytes. (DLP)

Lysozyme A protein, also called muramidase, present in milk, tears, saliva, body fluids, leukocytes and other cells. It is an antibacterial enzyme acting on the peptoglycans found in bacterial cell walls. (EM)

M

Macronutrients Nutrients required in the largest amounts. The six major classes of nutrients are carbohydrates, lipids, proteins, water, vitamins and minerals. Those that make up the greatest fraction of foods are carbohydrates, lipids and proteins and are called the macronutrients. (NJB)

Magnesium Magnesium (Mg) is an alkaline metal with an atomic mass of 24.305. It is an essential dietary component for all farm animals. Its metabolic function centres on reactions involving phosphorylation and energy transfer with ADP and ATP. About 60% of body Mg is found in bone, where it forms salts of phosphate and carbonate, but its exact function there is not known. Magnesium is also involved in the dampening of nerve impulses and muscle contraction and is antagonistic to calcium, which is stimulatory. In Mg deficiency, if the plasma concentration drops to low levels, muscle spasms, or tetany, may result. Acute Mg deficiency often occurs in cattle during lactation when there is a shift in Mg distribution in the body brought on by the consumption of forages low in Mg and the need for Mg for milk production.

In most non-ruminant animals, Mg is absorbed primarily from the upper small intestine; ruminants can absorb Mg from the ruminoreticulum and omasum. Body balance of Mg is controlled by excretion in both the urine and lower intestine. Plasma Mg concentration (about 20 mg l^{-1}) is sensitive to the amount of Mg consumed. Most common forages and seeds contain variable amounts of Mg, and although Mg deficiency is not common in grazing animals, feedlot animals sometimes require Mg supplementation. The US National Research Council recommends 1000 mg Mg kg^{-1} diet for growing beef cattle, 1200 mg kg^{-1} during gestation and 2000 mg kg^{-1} in early lactation. For dairy cattle the requirements are 1600, 2000 and 2500 mg Mg kg^{-1} diet for similar stages. The Mg requirement for pigs is approximately 400 mg kg^{-1} diet and for poultry it is 400–600 mg kg^{-1} diet. For horses it ranges from 800 mg kg^{-1} diet for growth to 1300 mg kg^{-1} for adults engaging in moderate to intense work. For sheep, it is between 1200 and 1800 mg kg^{-1} diet. (PGR)

See also: Bone density; Bone formation; Calcium; Phosphorus

Further reading

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Magnetic resonance imaging (MRI) The use of nuclear magnetic resonance (NMR) to produce images of the internal structures of the body. Nuclear magnetic resonance occurs because certain atomic nuclei (especially hydrogen) have a dipolar magnetic moment and align with an externally applied magnetic field. Image production is based on the absorption and emission of energy in the radio frequency range of the electromagnetic spectrum. Each scan produces an image of a single plane through the body so, for a complete description of body composition, images at multiple planes are needed. (MMacL)

Mahua A large evergreen or semi-evergreen tree (*Madhuca longifolia*) native to southern Asia, cultivated for its edible oil-containing fleshy seeds. The fruit seeds contain 169 g crude protein kg^{-1} and 515 g oil kg^{-1}, comprising 46% oleic acid, 18% linoleic acid, 18% palmitic acid and 14% stearic acid. The

Nutrient composition of mahua products (g kg^{-1} dry matter).

	Dry matter	Crude protein	Crude fibre	Ash	Ether extract	NFE
Oilcake						
Extracted	–	160	310	57.0	109	643
Extracted and detoxified	922	290	126	105	77.0	492
Defatted mahua seed flour	940	294	–	–	–	–
Fresh leaves	–	91	190	76	39	604
Fresh flowers	–	50	16	42	18	874

NFE, nitrogen-free extract.

meal is obtained after extraction of oil. It is high in saponins (98 g kg^{-1}), which are toxic at this concentration. These levels are reduced by treatment with isopropanol, following which the flour has an organic matter digestibility *in vitro* of 810 g kg^{-1}. (JKM)

Key reference

Singh, A. and Singh, I.S. (1991) Chemical evaluation of mahua (madhuca-indica) seed. *Food Chemistry* 40, 221–228.

Maillard reaction A **browning** reaction that occurs when proteins are heated in the presence of reducing sugars. This involves condensation of an amino acid with the carbonyl group of a hexose sugar in the open chain form to give a Schiff base. Subsequent Amadori rearrangement forms an N-substituted 1-amino-1-deoxy-2-ketose (ADK). This compound enolizes to either a 1,2-eneaminol or a 2,3-enediol. The former is degraded to 5-hydroxymethyl furfural (HMF), the latter to a methyl α-dicarbonyl intermediate that in turn rearranges into maltol, methyl reductones and α-dicarbonyls such as 2-oxopropanal, acetol, diacetyl and hydroxydiacetyl. A third pathway known as the Strecker degradation can arise in which a dicarbonyl compound reacts with an amino acid to yield CO_2, an aldehyde with one less carbon than the amino acid and pyrazine heterocyclic ring compounds. Heating molasses with ammonia or urea or the treatment of straw with ammonia can similarly form imidazoles, which cause neurological disease in cattle known as ‘bovine bonkers’.

Of the large number of compounds formed by Maillard reactions, some are reductones having an enediol conjugated with a carbonyl group. This structure is the same as that in L-ascorbic acid and such compounds are strong reducing agents in acid solution. Brown-coloured polymeric melanoidins are formed from reactions between carbonyls and amines. These have variable structure and solubility and have strong UV absorbance and fluorescence, due to unsaturated nitrogen heterocyclic rings. Some Maillard products, such as maltol, are volatile and impart a caramelized flavour. The free amino group of lysine in proteins is particularly likely to be involved in Maillard reactions, often leading to loss of availability of this essential amino acid. As this amino acid is often the most limiting amino acid in animal diets, damage to lysine by overheating high-protein foods, especially in the presence of sugars, can impair their nutritional value. (IM)

Maintenance The state in which an animal is in energy equilibrium, neither productive nor losing weight. It is then said to be on a maintenance ration. The terms half-maintenance, 2 × maintenance, etc., are sometimes used to describe feeding levels. Although growing animals are also considered to have a maintenance requirement, its definition and measurement are more problematic. (JAMcL)

See also: Energy balance

Maize Maize (*Zea mays*), also called corn or Indian corn, is probably the most important cereal plant of the *Gramineae* (grass) family. Maize may have yellow, white or red grains. It is a tall, annual grass having stout, erect and solid stems with large narrow leaves spaced alternately on opposite sides of the stem. The main stem axis is terminated by a 'tassel' which bears the staminate (male) flowers. The pistillate inflorescence, which matures to form the ear, is a spike with a thickened axis, bearing paired spikelets in longitudinal rows, each row of paired spikelets normally producing two rows of grain. The spike is enclosed by modified leaves, called husks.

Maize grain is used for both livestock and human food, and as a raw material for several industries.

Based on kernel texture, maize may be classified commercially as dent, flint or flour. For dent types, the kernel is composed of a mixture of hard and soft starches, while flint types contain little soft starch. For flour types, the kernels are composed largely of soft starch, which is easily processed by grinding. Sweetcorn is unlike other types since the plant sugars are not converted to starch. Popcorn is an extreme form of flint that is characterized by small, hard kernels devoid of soft starch. During heating, popcorn kernels explode due to the expansion of the moisture within the cells.

Maize grain (see table) is used for both livestock and human food and as a raw material in the manufacture of starch and glucose. Although the overall digestibility of the nutrients is high, the protein content, as crude protein (CP), of the grains (90–140 g kg^{-1} dry matter (DM)) is lower than that found in barley and wheat grains. Maize kernels contain two main proteins: zein is the most important and is found in the endosperm: maize glutelin occurs in the endosperm, but at lower levels than zein, and also in the germ. Zein protein is deficient in the two essential amino acids lysine and tryptophan, and this fact contributes to the overall poor quality of maize protein. Higher levels of these two essential amino acids are found in maize glutelin. One recent objective of plant breeders has been to produce new varieties with better amino acid profiles (e.g. improved lysine content).

Chemical composition of maize grain and maize by-products (as g kg^{-1} DM unless stated).

Maize product	DM (g kg^{-1})	CP	EE	Starch	NDF	GE[a]	ME[a]	DE[a]	AME[a]
Maize grain	873	102	39	700	117	18.9	13.8	16.5	15.9
Maize germ meal	879	108	82	532	224	19.7	14.5	–	14.3
Maize gluten meal	904	669	29	155	84	23.7	17.5	–	17.9
Maize gluten feed	885	220	44	186	383	19.1	12.9	–	9.2
Maize fibre	378	147	31	181	538	19.9	13.4	–	–
Distillers' dark grains (maize)	889	317	110	24	342	22.4	14.7	–	–
Maize silage	251	101	29	206	480	20.2	10.5	–	–

[a] As MJ kg^{-1} DM. Source: MAFF (1990) UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs.
AME, apparent metabolizable energy; CP, crude protein; DE, digestible energy; DM, dry matter; EE, ether extract; GE, gross energy; ME metabolizable energy; NDF, neutral-detergent fibre.

The 'gluten' proteins in maize are of poorer quality than those in wheat. Maize flour is therefore not used in bread making but is widely used throughout Latin America in the preparation of food products such as tortillas. Maize is rich in starch (range 661–755 g kg^{-1} DM) and is more slowly degraded in the rumen than the starch from other cereal grains. Maize grain contains low levels of fibre (as NDF, 91–176 g kg^{-1} DM) and the oil content varies from 22 to 51 g kg^{-1} DM and comprises mainly oleic and linoleic fatty acids (23% and 57% of total fatty acids, respectively). Maize grains generally have the highest energy value of all cereals, owing to the high oil and low fibre levels.

In addition to the use of whole maize grain for livestock feeding, the grains may also be ensiled at an average DM content of ~ 700 g kg^{-1}. Finely ground grains can be ensiled either alone (ground maize silage) or following processing of the whole ear (including husks) (ground ear maize). Maize grains, like other cereal grains, may also be processed prior to feeding using 'cold' processing methods (including grinding, rolling, cracking or crimping, and cold pelleting) or 'hot' processing methods (including steam-flaking, micronization, roasting and hot pelleting).

Maize grains are an excellent feed resource for ruminants and are commonly used in compound feeds and total mixed rations. 'Hot' processed maize grains, containing gelatinized starch, may be used for feeding high-yielding dairy cows requiring high amounts of concentrates. In certain countries maize is an important cereal fed with oats to horses. Feeding maize to poultry is important in countries where the grain is commonly grown and the use of yellow varieties promotes a yellow pigmentation in the egg yolk and tissue fat. Maize may also be grown as a forage crop and fed fresh (maize forage) or following preservation by ensiling at a grain DM content of about 350 g kg^{-1} (maize silage).

The processing of maize grains in the manufacture of starch and glucose results in the production of three main by-products: maize germ, maize bran and maize gluten, for use in livestock feeding (see table). Maize germ is separated from the kernel by coarsely grinding cleaned maize grains that have been soaked in a dilute acid solution. The germ is very rich in oil, which is mostly extracted for use in the human food industry prior to producing maize germ meal. Maize bran is separated by wet screening of the finely ground de-germed grain. The remaining solution comprises a suspension of starch and protein (gluten), which are separated by centrifugation.

Maize gluten meal, also known as prairie meal, is a high-protein feed (about 669 g CP kg^{-1} DM), produced by drying the protein (gluten) fraction to a DM content of about 900 g kg^{-1}. It is suitable for feeding most livestock species; for ruminants the protein fraction is largely undegraded in the rumen but overall the protein is deficient in lysine. Feeding maize gluten meal to laying birds increases egg yolk pigmentation. Processing the degermed kernel also gives white fibres which are mixed with corn steep liquor, and sometimes variable amounts of maize germ meal, to produce maize gluten feed. The protein quality of maize gluten feed generally limits its use to ruminant rather than pig and poultry diets. For mature beef and dairy cattle it may be included to about 40% of a concentrate ration. The composition and nutritive value of maize gluten feed is variable, owing to differences in the proportion used in the mixing process and the amount of germ meal added.

Grain distilleries using maize (*see* **Barley**, for description of distillation process and by-products) also produce a number of by-products for use in livestock feeding, including maize distillers' dark grains, which may be fed either as a meal or following pelleting. These products are very palatable to livestock and are widely used in proprietary compound feed manufacture or for feeding as a coarse mixture of feed ingredients. (ED)

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Malabsorption: *see* Digestive disorders

Malate Malate or malic acid ($HOOC{\cdot}CH_2{\cdot}CHOH{\cdot}COOH$) is one of the intermediates in the conversion of citric acid to oxaloacetic acid in the **tricarboxylic acid cycle**. (NJB)

Malic acid: *see* Malate

Malnutrition Insufficient supply of food, or of one or more specific nutrients, to meet requirements. An inadequate intake of food usually results in mobilization of body reserves to maintain essential bodily functions. Initially fat reserves are mobilized but, before this is complete, muscle protein is also mobilized, to supply amino acids for maintenance and also as a source of energy. (JMF)

Malt: *see* Brewery by-products; Distillers' residues

Maltase An enzyme found in the brush border membranes of epithelial cells in the duodenum and jejunum. Also known as glucoamylase, it breaks down malto-oligosaccharides (repeating $\alpha(1\rightarrow4)$ glucose units) into single glucose units. (GG)

Malting The process in which cereal grain, predominantly barley, is soaked and germinated under controlled conditions to activate the natural amylase of the grain. This in turn hydrolyses the starch, producing mainly the disaccharide sugar maltose, with some dextrins and other sugars. Germination is allowed to proceed for several days, during which there is some development of the radicle (root). The process is then terminated by kiln drying and removal of the rootlets (malt culms). Typically, hydrolysis of the starch is only partial but it continues to completion when the malt is re-wetted (mashing). (CRL)

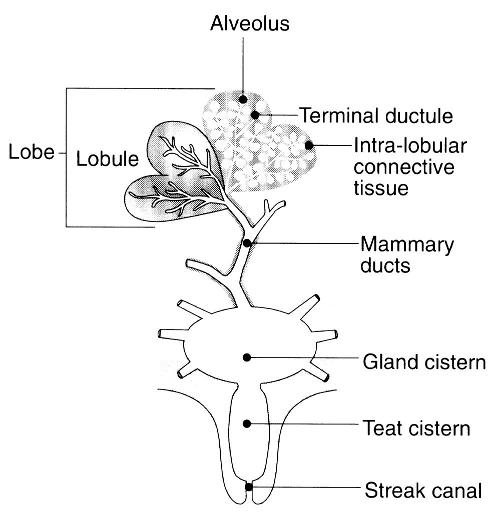
Maltodextrin Mixture of glucose, maltose and higher oligosaccharides of glucose, usually not exceeding ten glucose units. It is commonly produced by controlled enzymatic hydrolysis of starch as in partially hydrolysed maize syrups. Time, temperature and the type of α-amylase used in hydrolysis determines the mix of monomers to polymers. Molecular weight range 180–1800. (JAM)
See also: Carbohydrates; Isomaltose; Maltose; Maltotriose; Oligosaccharides; Starch

Maltose A disaccharide, $C_{12}H_{22}O_{11}$, molecular weight 342, consisting of two D-glucose residues joined by glycosidic $\alpha(1\rightarrow4)$ linkage. It is produced in the enzymatic digestion of starch, in which it is the repeating unit. (JAM)
See also: Carbohydrates; Maltodextrin; Starch

Maltotriose An oligosaccharide, $C_{18}H_{32}O_{16}$, molecular weight 504, consisting of three D-glucose residues joined by $\alpha(1\rightarrow4)$ linkages. (JAM)
See also: Carbohydrates; Starch

Mammary gland The milk-producing gland of female mammals, derived from epithelial cells under the skin. Cows have four mammary glands; sheep, goats and horses have two; pigs have 10–14. A group of mammary glands is called an udder.

Each mammary gland consists of thousands of secretory (alveolar) cells, arranged like bunches of grapes, which drain into small ducts. The ducts lead to the gland cistern, where milk is stored until milking or suckling. Milk is expelled from the gland cistern through a teat. The tissue surrounding the alveolar cells is elastic and contracts during milking, under the influence of oxytocin. Alveolar cells are closely associated with blood vessels, from which nutrients are absorbed for milk synthesis.



Diagrammatic representation of mammary duct and lobular–alveolar system.

The udder is rudimentary in males and young females, but enlarges in females after puberty. During the first pregnancy, mammary cells differentiate and become most active after parturition. (PCG)
See also: Lactation

Manganese Manganese (Mn) is a transition element with an atomic mass of 54.938. It exists in 11 oxidation states but Mn^{2+} is the predominant form in biological systems. However, Mn^{3+} plays an important role in the enzyme Mn superoxide dismutase located in mitochondria. Manganese is absorbed throughout the small intestine but Mn homeostasis is controlled primarily by biliary excretion and not by intestinal absorption, as it is with most other elements. The Mn concentration in blood plasma is approximately 5 μg l^{-1}, while in liver, where most of it is in the mitochondria, the concentration is approximately 3 mg kg^{-1}. Iron and Mn apparently share a common transport mechanism in the intestine such that each can affect the rate of absorption of the other. Manganese is also readily bound by transferrin, thus iron status of the individual can influence the amount of Mn absorbed.

Manganese is an essential mineral element for all farm animals. It is known to be an essential part of mitochondrial superoxide dismutase that plays a role as an antioxidant factor in cells. The activity of this enzyme is depressed in animals fed diets low in Mn. Pyruvate carboxylase, arginase and glutamine synthetase are all Mn-dependent enzymes. Manganese is involved in bone metabolism, where it functions in the synthesis of mucopolysaccharides through Mn-dependent glycosyltransferase. Manganese deficiency can result in perosis and 'slipped tendon' syndrome in poultry. Other signs of Mn deficiency in mammals include severe ataxia (especially if the deficiency occurs before birth), disturbances in glucose metabolism and reduction in growth and reproductive rates.

The dietary requirement for Mn is variable among farm species. The US National Research Council recommends 20 mg Mn kg^{-1} diet for growing cattle and 40 mg kg^{-1} for lactating animals; a similar requirement is recommended for sheep. The Mn requirement for poultry is set between 30 and 60 mg kg^{-1} diet, depending on age: young growing chicks require more Mn than adults. The requirement for horses has been set at 40 mg Mn kg^{-1} diet. For swine, the requirement has been set much lower than for other species: 4 mg kg^{-1} diet for growing animals and 2 mg kg^{-1} for adults.

Manganese toxicity occurs in farm animal species but the element can be tolerated to a greater extent than many other elements. In many species, the outward signs of Mn toxicity, such as weight loss and reproductive failure, do not appear until the Mn concentration in the diet exceeds 1000 mg kg^{-1}. However, swine seem to be more susceptible to Mn toxicity and 500 mg kg^{-1} has been shown to reduce weight gain. Although no outward signs appear, biochemical signs such as reduced concentrations of haemoglobin in the blood, and of iron in the serum, can appear at dietary concentrations of Mn below 1000 mg kg^{-1}. (PGR)
See also: Iron; Superoxide

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Leach, R.M. Jr and Harris, E.D. (1997) Manganese. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements.* Marcel Dekker, New York, pp. 335–355.

Mango (*Mangifera indica* L) A large evergreen tree cultivated throughout the tropics for its fruit, which has a large fibrous seed. The kernel constitutes about 15% of the weight of the fruit. The kernels contain tannins; increasing rates of inclusion in pig and poultry diets progressively reduce growth rate and feed conversion. Ruminants have been shown to tolerate up to 50% inclusion of kernels in concentrates without adverse effects on performance. Mango fruit is readily eaten by cattle and pigs. Fruit gluts can be conserved by ensiling with 1% salt and the silage can be fed to pigs. (EO)

Key reference

Gohl, B. (1981) *Tropical Feeds*. Food and Agriculture Organization, Rome, 515 pp.

Mannans Linear or branched homo- or heteropolysaccharides of α- or β-D-mannose residues. Present in the cell walls of most yeasts. Some cell surface or extracellular mannans are phosphorylated and appear to have immunological properties. Mannans in plant cell walls or endosperm virtually all contain some galactose. Many are gums and are viscous in aqueous solutions, e.g. guar gum. Water-soluble galactomannans are found in the endosperm of many leguminous plants. Mannans, glucomannans and glucuronomannans are also the principal food-reserve polysaccharides in algae. (JAM)

See also: Carbohydrates; Dietary fibre; Galactomannans; Gums; Storage polysaccharides

Mannitol A polyol or sugar alcohol, $C_6H_{14}O_6$, molecular weight 182, a reduction product of mannose. It occurs in algae, lichens and bacteria and in mountain ash berries. It is a normal constituent of silage, where it is formed by bacterial reduction of the fructose moiety of sucrose. (JAM)

See also: Carbohydrates; Mannose

Mannose A hexose monosaccharide, $C_6H_{12}O_6$, molecular weight 180, an epimer of glucose in which the bond at carbon 2, containing the hydroxyl group, is inverted. Mannose does not occur free in nature but is widely distributed in hemicellulosic polysaccharides. (JAM)

See also: Carbohydrates; Dietary fibre; Hemicelluloses; Monosaccharides

Mare An adult fertile female horse or pony: as a foal's mother she is described as its dam. A female ass or donkey is a jenny. The mare may be non-breeding, pregnant, lactating, or lactating and pregnant.

Under natural conditions the mare is a seasonal breeder, influenced particularly by **light**. The gestation period normally lasts 335–345 days but lactation length depends on management and under more intense farming it is restricted to 6 months or less. Most of the fetal growth occurs during the last 90 days of gestation but the mare's energy requirement increases during that period by only 10–20% above **maintenance**. An average lactation requires approximately eight times as much energy above maintenance as is required above maintenance by a normal pregnancy at term. However, the daily milk yield of a healthy mare may be altered by varying her daily feed intake during late pregnancy, or lactation, and by the extent of her fat stores at parturition.

During the first 8 months of her gestation period the mare has a digestible energy (DE) maintenance requirement (zero body weight change plus normal activity of the non-working horse) similar to that of the non-breeding animal. This requirement is directly proportional to body weight and for mares ranging in size from 125 kg to more than 600 kg the requirement accords to the relationships given under '**Horse feeding**' (equations 1 and 2). During the 9th, 10th and 11th month of pregnancy the DE requirement rises by 1.11 DE, 1.13 DE and 1.20 DE, respectively. The minimum nutrient requirements of the mare are given in 'Horse feeding' (Tables 1, 2 and 3). (DLF)

Marine environment The marine environment comprises the complex physical, chemical and biotic factors (temperature, salinity, living things, etc.) of the sea that act upon an organism or group of organisms and determine their function, form and survival. The surface of the earth is approximately 361 million km^2 and interconnected bodies of sea water cover about 71% of this area. Wave action, tides and vertical and horizontal ocean currents produce a continuous mixing of sea water and maintain relatively little fluctuation in the concentration of dissolved gases and salt. Oxygen is usually available and the salinity of the open ocean is relatively constant, ranging from 33 to 37 parts per 1000 ($g\ kg^{-1}$), depending on the latitude. Light and temperature vary greatly, mainly due to depth. In turbid coastal waters, the yellow-green wavelengths commonly penetrate furthest, dwindling to 1% at about 16 m. Sunlight not only illuminates but also warms the water it penetrates. A thermocline describes the rapid transition between a warm

surface layer and the cooler, denser water beneath. In unproductive areas such as tropical or temperate regions in summer, these layers are stabilized and the surface layers become depleted of nutrients, reducing primary productivity. In shallow temperate waters, mixing of the water layers in the autumn and better growing conditions in the spring cause seasonal increases (e.g. algal blooms) in productivity. (DN)
See also: Freezing

Marine fish Fish show obvious differences from terrestrial farm animals as subjects for production in captivity. They are cold blooded and so significant amounts of dietary energy are not used in maintaining body temperature; life in water means that fish do not need the large anti-gravity muscles characteristic of birds and mammals (nor do they need the heavy skeleton on which these muscles hang). The main excretory product of protein metabolism, ammonia, can be excreted directly into the surrounding water, so energy does not have to be expended in converting it to non-toxic compounds. On the other hand, respiration in water necessitates having permeable surfaces in contact with the aqueous environment. Thus marine fish risk dehydration from a hyperosmotic medium while freshwater fish face hydration from a hypotonic environment. In both cases energy has to be expended in controlling the osmotic problem. The balance of these differences indicates that fish convert food energy to carcass energy more efficiently than do mammals or birds.

Several species of wholly marine fish are either being cultivated, or are soon to be cultivated, on a commercial scale. These include yellowtail (*Seriola quinqueradiata)*, Asian sea bass (*Lates calcarifer*), European sea bass (*Dicentrarchus labrax*), gilthead sea bream (*Sparus aurata*), red drum (*Sciaenops ocellatus*), cod (*Gadus morhua*) and several flatfish, such as Atlantic halibut (*Hippoglossus hippoglossus*). They are mainly warm- or temperate-water fish, only the marine flatfish being genuine cold-water fish. Most fish are carnivorous but this is especially so in the marine environment, where they lie at the head of a food pyramid, consume a high-protein diet and rely on diet to provide all nutrients in their most active form. Thus, the capacity to modify certain nutrients to more metabolically active forms is absent (e.g. the capacity to transform linolenic acid to eicosapentaenoic or docosahexaenoic acid with full essential fatty acid activity has been lost).

Marine fish are not domesticated in the sense that rainbow trout (*Oncorhynchus mykiss*) is domesticated; consequently hard, dry pellets are rarely acceptable as food. For yellowtail, a casein-based diet with 40% moisture and containing taste attractants (inosinic acid, alanine and proline) has been found to be suitable (Shimeno, 1991). The use of casein-based defined diets has been less successful with other marine species in attempting to quantify nutrient requirements. Precise requirements for these species, therefore, remain to be established.

There is also a dearth of information on the digestibility of the major dietary components – protein, carbohydrate and fat. The absence of such data for different feedstuffs makes for difficulties in assessing both the available energy density of experimental diets that have been used and the energy requirement of the fish. Making reasonable assumptions it can, however, be inferred that the energy density of food given to marine fish is in the range 17–23 MJ kg^{-1}. Dietary protein levels are high, usually of the order of 50% of the dry matter and sometimes in excess of this value. These levels appear to provide 25–30 g protein MJ^{-1} 'digestible energy'. At these concentrations, much of the protein would be used as an energy source; there may also be a substantial heat increment of feeding but the magnitude of this in fish remains controversial. Essential amino acid requirements of marine fish are qualitatively similar to those of rainbow trout. Few, if any, attempts have been made to quantitate essential amino acid requirements. At the levels of dietary protein in use, amino acid deficiencies are unlikely to arise if a good quality fish meal is the main source of dietary protein. Carbohydrates are not well utilized by marine fish; they have limited amylolytic activity in the digestive tract and a limited capacity to metabolize glucose that is absorbed. Dextrin or pre-gelatinized starch are better utilized than is raw starch; even so, dietary concentrations of the former materials rarely exceed 20% of the dry matter.

As indicated above, marine fish have little capacity to modify 18C dietary fatty acids metabolically. Their natural diet contains a luxus of polyunsaturated long-chain fatty acids of the (n-3) series and sufficient of the (n-6) series to meet their dietary needs. Essential fatty acid requirements of marine fish are therefore met by using a marine oil (e.g. cod liver oil, pollock liver oil, menhaden fish oil) in the diet. These oils are highly digestible. Lipid is the main non-protein energy source and levels in the diet are usually in the range 10–15%. The very high energy (lipid) diets used in salmonid rearing have not found favour in the cultivation of wholly marine fish.

The vitamin requirements of yellowtail have been studied in detail (Shimeno, 1991) but few data are available for other species of marine fish. It is generally assumed that these species have a requirement for vitamins similar to that of salmonids and a vitamin pre-mix based on that used in salmonid diets is included as a component of diets for marine fish. No requirement for *p*-amino benzoic acid, menadione or cholecalciferol was found in yellowtail (Shimeno, 1991). Requirements for other vitamins were not greatly dissimilar from those of salmonids; specific vitamin deficiency diseases were described. It may be noted here that L-ascorbyl-2-monophosphate, a water-stable form of vitamin C but which is fully available to the fish, is especially useful in studies where diets of high moisture content are necessary.

Investigation of the mineral requirements of marine fish is complicated because some minerals are obtained from the sea water they drink to counter the osmotic problem arising from life in sea water (excess salt is excreted through the gills). Studies indicate the absence of a dietary requirement for sodium, potassium and chloride and a definite requirement (as yet unquantified) for phosphorus, iron and zinc, but there is no certain information on calcium, magnesium and trace element needs.

A special need in marine fish cultivation is live food for the rearing of larvae. Marine fish larvae are very small, generally less than 3 mm, and, despite numerous efforts with artificial foods (e.g. diets in microparticulate, microencapsulated and microbound form), it has not been possible to rear them without live food. Rotifers are an important live food and, in Japan, mass production of *Brachionus plicatus* makes fish larvae production possible. Newly hatched larvae (body length 2–3 mm) are given rotifers as the starting diet and this is continued for about 30 days. Thereafter other live food, in particular brine shrimp (*Artemia salina*), is substituted as rotifers tend to become too small for larvae of 7 mm or so in length. Larvae larger than 10–11 mm may be fed on minced waste fish or, more usually, an artificial diet.

Problems were encountered initially over the nutritional quality of the rotifers; these were related to the food organisms used in the rotifer culture. When grown on a marine *Chlorella*, rotifers of high nutritional value resulted; but if other organisms such as baker's yeast or a freshwater *Chlorella* were used, the *Brachionus* produced were of variable and often inadequate nutritional quality for marine fish larvae. The problem was resolved with the realization that marine fish larvae require long-chain polyunsaturated fatty acids of the (n-3) series, i.e. 20:5(n-3) and 22:6(n-3), for normal development. The fatty acid profile of the *Brachionus* reflected that of the organisms on which it was grown and while marine *Chlorella* contained high levels of the required polyunsaturated fatty acids the other organisms tried did not. Similar problems occur with the brine shrimp. Freshly hatched *Artemia* nauplii contain very low levels of (n-3) highly unsaturated fatty acids and various enrichment methods are now available to enhance their content of these nutrients. These methods include feeding the nauplii on liposomes or microencapsulated diets, all with an appropriate fatty acid profile, or a fatty acid emulsion. (CBC)

See also: Cod; Halibut; Rainbow trout; Salmon culture; Salmonid fishes

Reference

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Marine fouling The attachment of marine micro- and macroorganisms to netting, lines and floats. Common fouling organisms include seaweeds, mussels, tunicates and sponges. Problems of fouling include increased drag in currents, reduced water flow through nets, increased net weight, and provision of a reservoir for wastes and pathogens. Remedial and preventive measures include treatment with anti-foulants (copper or zinc compounds), high-pressure spray, drying and biological controls (e.g. use of crabs as predators). (RHP)

Marine oils Marine oils are made up of at least 65 fatty acids but, by ignoring minor saturated fatty acids and pooling the different isomers of monounsaturated fatty acids, this can be reduced to about 50 and about 90% of the mass of fatty acids can be described simply in terms of about 12. These can be grouped as:

Saturated	Monounsaturated
14:0	16:1
16:0	18:1
18:0	20:1
	22:1
Polyunsaturated	Long-chain polyunsaturated
18:2 n-6	
18:3 n-3	20:5 n-3
18:4 n-3	22:6 n-3

The saturated fatty acids usually total 20–30% of a marine oil, the monounsaturated 30–50%, the polyunsaturated (PUFA) $<$ 10% and the long-chain PUFA (LCPUFA) 10–30%. These are bound in various combinations to glycerol, hence oils are triacylglycerols. The mixture may be such that some fish oils, for example menhaden oil, can be readily 'winterized', with a solid layer, containing a higher total of saturated fatty acids, settling out. On the other hand, oils high in 22:1, such as herring or capelin oil, solidify evenly. Most marine triacylglycerols are probably 95% digested by fish and mammals but shark liver oils, which sometimes also contain the hydrocarbon squalene or diacylglyceryl ethers, may be less digestible. A few marine invertebrate oils may have wax esters, which can be digested by fish but not necessarily by higher animals, and some whale oils are also rich in wax esters. Freshwater fish oils from cold climates are usually similar to marine oils in fatty acid composition but may be higher in PUFA and lower in LCPUFA.

The monounsaturated fatty acids are readily digested and used for energy by most animals, although 22:1 and to a lesser extent 20:1 may be excreted as calcium soaps. They are, however, quite stable towards oxidation. The LCPUFA readily oxidize and produce a variety of aldehydes, most of which are offensive and their rancidity is popularly identified as distinctively 'fishy'.

The C_{18} PUFA of marine oils are of nutritional importance in the diets of chickens and non-ruminant farm animals. The LCPUFA (and the 18:4 n-3, invariably only 1–2%) are responsible for a new interest in fish oils as human health supplements. This is a relatively small market sector for fish oils and seal oil, which must be refined to a high quality. In the last 20 years, eating fish has been repeatedly demonstrated to reduce the risk of mortality from heart attacks. This benefit is attributed to the LCPUFA in the fish, although their muscle fats have not only the same saturated fatty acids shown above, but about 1% cholesterol as well.

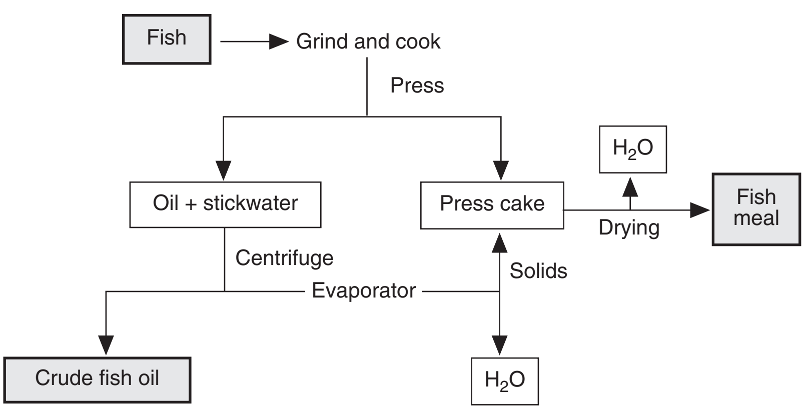
Ironically, the worldwide salmonid aquaculture industry requires the LCPUFA as a dietary component. Some may be supplied through fish meal lipids (10% by weight and containing 20–30% LCPUFA), but usually up to 10% of an oil is added to the diet. The marine oil LCPUFA are truly essential for salmonids at the level of 1% of the diet. Without LCPUFA, growth may be limited since new cells require membranes which are approximately 40% LCPUFA. Some allowance for use of 18:3 n-3 instead is possible, but it is not common in marine oils. A variety of other fats can be used for energy provided the requirement of LCPUFA is met and excessive linoleic acid (18:2 n-6) avoided. Conversely, the n-6 fatty acids are a staple part of diets for tilapia and channel catfish but so are 18:3 n-3 or LCPUFA at a lesser level than for salmonids. The dietary fatty acid requirements of broodstock and fish larvae may not be obvious but LCPUFA should be carefully considered in terms of essentiality.

Partially hydrogenated marine oils contain *trans* fatty acids, which are now considered undesirable in human diets. In consequence, more of the marine oils that were previously hydrogenated have become available for aquaculture feeds. Only limited use can be made for these in chicken, pigs, etc., because of the risk of oxidation and taint in the meat produced.

Fish oils are produced from a wide variety of fish, usually in conjunction with the production of fish meal (see figure). Fish meal is nominally 65% protein with lipid and moisture contents of 8–10% each, plus some salt and minerals. To provide this, the modern fish plant grinds up the fish and cooks it. Most of the free oil and some water are squeezed out, and the solids are then dried to the desired moisture level. Grinding and addition of an antioxidant follow. The oil and water are separated by a centrifuge, usually desludging, although decanters are now sometimes used, and the water phase is concentrated so that any protein and other solids can be added back to the basic meal at the drying stage. The oil is commonly sold 'as is'. The quality of the marine oils is heavily dependent on the quality of the raw material. With the operation of a fish reduction plant on a scale of up to 1000 t day^{-1}, prompt processing of fish landed after a variable period on board ship is not always possible. Enzyme activity in both muscle and viscera of long-dead fish can produce free fatty acids (FFAs), a useful index of the quality of the oil and to some extent of the protein in the associated meal. An FFA content of up to 3% is probably acceptable as the FFAs are quite digestible and not apt to cause rejection of feeds by either fish or mammals on grounds of flavour. Oxidation products, assessed as the peroxide value (PV or POV), is often another criterion in assessing oil quality because peroxides eventually break down to aldehydes. Without being dogmatic, for fish oil from colder regions a POV of 5 or less should be considered acceptable.

Unlike fish meals, usually no stabilizing antioxidants are added to marine oils. Whole fish or fish waste (offal) is always rich in autolytic enzymes. If the basic product is ground up ('minced') and left in storage, it will be contaminated by bacteria. To prevent this a strong acid, often formic acid, is added to keep the pH below 4. In a few days enzymatic cellular breakdown is sufficient for de-oiling and a liquefied protein product called fish silage is obtained. Although easily stored in tanks, pumped or transported, fish silage may only be suitable for manufacturing moist fish feeds, pig rations, etc. Fish silages used to be popular in fish aquaculture but are now suspect for sanitary reasons, as disease has become one of the major industry problems.

Chile and Peru can produce 750,000 t of fish oil, half the world's production, but are subject to irregular disastrous years from climate changes. At these times fish meal and oil prices soar but other countries can make up some the shortfall, e.g. South Africa, Norway, Japan, Iceland or the USA and Mexico.



Schematic of a modern fish reduction plant.

Fatty acid composition of fish and whale oil. Unpublished data reproduced by courtesy of W. Schokker and H. Boerma, Unilever Research, Vlaardingen.

Fatty acid	Herring, North Sea	Anchovy, Peru	Whale, Antarctic	Pilchard, South Africa	Sardine, Portugal	Menhaden, USA	Pilchard
12:0	0.10	0.10	0.20	0.20	0.10	0.15	0.10
14:0	6.10	7.45	7.45	7.75	6.70	7.30	7.30
14:1	0.15	–	0.75	0.15	–	–	–
16:branched	0.40	0.40	0.40	0.40	0.50	0.45	0.55
15:0	0.40	0.60	0.65	0.40	0.75	0.65	0.60
16:0	10.8	17.5	13.4	15.7	17.8	19.0	15.6
16:1	7.30	9.00	10.50	8.50	6.00	9.05	9.00
16:2 ω7	0.20	0.20	0.20	0.55	0.40	0.50	0.40
16:2 ω4	0.40	1.00	0.65	1.45	0.65	1.25	1.55
16:3 ω4	6.70	2.05	0.10	2.00	0.40	1.45	1.70
16:3 ω3	–	–	0.20	–	0.20	0.20	0.15
16:4 ω4	0.10	–	–	–	0.10	0.15	0.20
16:4 ω1	1.20	2.45	0.95	3.20	1.60	2.30	2.60
17:branched	0.30	0.35	0.25	0.25	0.20	0.20	0.15
17:0	0.35	0.55	0.95	0.80	0.80	0.90	0.85
17:1	0.30	–	0.25	–	0.30	–	–
18:branched	0.80	0.70	1.10	0.60	0.60	0.45	1.00
18:0	1.40	4.00	2.70	3.65	3.60	4.20	3.45
18:1	10.3	11.6	27.6	9.25	13.0	13.2	10.4
18:2 ω9	Tr.	0.10	0.10	0.15	0.15	0.30	0.20
18:2 ω6	0.95	1.20	1.90	0.80	1.20	1.30	1.30
18:2 ω4	0.10	0.60	0.20	0.50	0.30	0.40	0.50
18:3 ω6	0.05	0.30	0.20	0.35	0.20	0.25	0.30
18:3	Tr.	0.20	0.10	0.30	0.10	0.30	0.20
18:3 ω3	2.00	0.75	0.85	0.45	1.00	1.30	0.65
18:4 ω3	3.15	3.05	1.05	2.05	3.15	2.75	2.65
18:4	0.15	0.20	0.20	0.15	0.10	0.15	0.20
19:branched	–	0.10	–	–	0.20	0.20	–
19:0	0.20	0.10	0.60	0.20	0.40	0.40	0.10
19:1	0.10	–	0.40	–	–	–	–
20:0	0.10	0.30	0.20	0.60	0.40	0.35	0.30
20:1	13.4	1.55	6.75	2.50	4.30	2.00	1.45
20:2 ω9	–	0.30	0.10	0.40	0.15	0.45	0.15
20:2 ω6	0.15	0.35	0.15	0.25	0.20	0.35	0.30
20:3 ω6	0.10	0.10	0.20	0.30	0.10	0.15	0.20
20:3 ω3	0.30	1.10	0.60	1.35	0.85	0.80	1.00
20:4 ω6	Tr.	0.10	0.25	0.10	0.10	0.15	0.15
20:4 ω3	0.75	0.70	1.30	0.70	1.05	1.35	0.80
20:5 ω3	7.45	17.0	4.70	19.3	11.0	11.0	18.3
21:0	0.10	Tr.	0.05	0.15	0.10	0.05	0.10
21:5 ω2	0.25	0.70	0.15	0.90	0.50	0.60	0.90
22:0	0.05	0.05	0.10	0.20	0.20	0.20	0.15
22:1	21.3	1.15	2.40	3.10	3.80	0.55	1.55
22:2	0.20	0.10	0.05	0.05	0.10	0.20	0.10
22:3 ω3	–	0.15	0.25	0.15	0.15	0.15	0.20
22:4 ω3	0.25	0.55	0.20	0.40	0.70	0.50	0.60
22:5 ω3	0.75	1.60	2.40	2.35	1.30	1.90	1.80
22:6 ω3	6.75	8.75	5.70	6.45	13.0	9.10	9.60
23:0	0.10	0.05	0.05	0.10	0.10	0.10	0.15
24:0	0.15	0.05	Tr.	0.15	0.10	0.15	0.10
24:1	0.75	0.50	0.30	0.50	0.60	0.35	0.70

Overfishing is endemic and production of fish meal and fish oil is regarded by some people as an undesirable way to use the resources of the oceans. In the future these socioeconomic factors will become more important. (RGA)

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Marine plants Marine plants, in the broad sense, are those vascular plants, algae and fungi that live and reproduce in the sea and associated brackish waters. Some authorities also include seaside vascular plants whose roots are exposed to sea water to some degree but whose shoots are aerial and habit essentially terrestrial, e.g. mangroves and saltmarsh species. Vascular marine plants are chiefly the seagrasses, of which there are 58 species worldwide in four families; they are not true grasses but often with grass-like leaves and having submerged flowers and fruit. They typically populate the shallow soft bottom of temperate and tropical coasts. Marine algae are a much more diverse group both morphologically and taxonomically. They range from microscopic unicells (phytoplankton, endophytes) to the tallest vegetation known, the giant kelps, and comprise many thousands of species in about 11 divisions or phyla. The multicellular algae, or seaweeds, are mainly confined to coastal shallows, but the planktonic microalgae form a huge biomass throughout the photic zone of the world's oceans. Marine fungi are the least conspicuous of the marine plants, being microscopic filamentous species in soft substrata, or forming intertidal lichens.

Marine plants are important contributors to oceanic production and coastal stability. A number of species are commercially valuable, including some seaweeds used to supplement livestock feed (e.g. *Ascophyllum nodosum*, *Laminaria digitata*) and microalgae cultured for herbivorous invertebrates in aquaculture nursery operations (e.g. *Isochrysis galbana*). Others have achieved notoriety as aggressive weeds or sources of toxins. (CB)

See also: Algae; Seaweed

Further reading

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Marine toxins Naturally occurring organic compounds produced by organisms in the marine environment that have inimical effects on other species. A wide array of toxigenic invertebrate species are involved in the biosynthesis, transfer or propagation of such toxins within marine food webs, including protists (unicellular organisms), porifera (sponges), coelenterates (jellyfish, anemones, corals), echinoderms (sea urchins, starfish), molluscs (snails, bivalves, gastropods) and various worms and marine arthropods (joint-legged animals). In addition, marine toxins are widely distributed among vertebrates, such as fish and reptiles, particularly sea snakes. Certain marine toxins are reputed for their extreme potency – the high-molecular-weight compound, palytoxin, first isolated from the zoanthid *Palythoa* and now associated with a marine dinoflagellate, is among the most potent known biotoxins.

Toxic effects to humans and other mammals can vary from simple dermal irritation, as in the case of casual exposure to certain jellyfish and anemones, to severe physiological disturbances resulting from consumption of contaminated teleost fish, such as those associated with histamine fish poisoning (scombroid) causing an 'allergic' response, and other fish-borne diseases, e.g. puffer-fish poisoning (*fugu*; tetrodotoxicity). In extreme cases, mortalities can result; for example, in mammals, death by tetrodotoxin poisoning often occurs by respiratory paralysis following blockage of sodium channels in the neuromuscular system. (AC)

See also: Algal toxins; Marine environment

Key reference

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Marker An indigestible substance used for the measurement of digestibility, or the rate of passage of digesta. A marker may be an inert substance added to a diet, such as chromic oxide, titanium dioxide or polyethylene glycol, or it may be a substance that occurs naturally in feeds, such as acid-insoluble ash. Markers may be chosen to follow either the solid components of the diet or the liquid phase. (MFF)

Mass spectrometry (MS) An analytical tool used to gain information about the elemental composition of samples and the structure of organic, inorganic and biological molecules. In addition, the qualitative and quantitative composition of complex molecules, the structure and composition of solid surfaces and the isotopic ratios of atoms in samples can be obtained. The technique involves the atomization of a sample and formation of ions followed by the separation of these ions based on their mass-to-charge ratio and the measurement of each ion produced. It is an extremely powerful technique. (JEM)

Mastication A process of chewing feed in preparation for swallowing. This is a sideways, or circular, movement of the lower jaw. Feed is ground between the lower and upper molars and premolars. The time taken to form a bolus of small feed particles with saliva, suitable for swallowing, is much greater for long hay than for cereal grains and so the bolus of grain contains much less fluid, i.e. saliva. (DLF)

Mathematical models A mathematical description of the composition and behaviour of a system under study, intended to provide an understanding of the system, predictions of its future behaviour, or a guide to its optimal utilization. In agriculture, one can distinguish between models intended for research and those intended for management.

Models for research

The purpose of these models is to provide a clear, descriptive summary of the researcher's beliefs about the qualitative or quantitative behaviour of a system. Such models can draw attention to deficiencies in knowledge of the system and so indicate future research directions. A simple example will illustrate the main principles. Consider the problem of describing the dependency of food intake of an animal on the animal's ambient temperature. The simplest description, or model, is that of no dependency: the food intake is constant, independent of the temperature. A second, more realistic model may be that food intake decreases with an increase in temperature. A mathematically clear description of this dependency may be, for example, a linear relationship: for each degree increase in temperature, food intake decreases by a fixed number of grams. Each of these two models has parameters: numbers that describe specific instances of the models while the general form remains unchanged. The first model has a single parameter, the constant food intake of the animal. The second can be described by two parameters: the food intake at some particular temperature, and the change in food intake, in grams, for each degree increase in temperature.

Model fitting is the process of estimating values for, or fitting, the parameters in the model based on empirical measurements.

Under the best choice of parameters the model may still be found to be an inadequate description of the data, in which case the model may itself need to be replaced. On the other hand, a model may be more complex than needed to describe a given situation. The principle of Occam's razor calls for the selection of the simplest model that adequately describes the data. This principle is justified by the predictive power of models: in general, a simpler model that describes a system adequately is a better predictor of future behaviour of a system than a more complex one. The complexity of mathematical models is often described, roughly, by the number of parameters in the model. The second model above is more complex than the first, and would only be selected once the first was shown to be inadequate. The process of model selection is therefore an iterative one: a model is formulated, its parameters fitted to data, and the model reformulated as necessary until an adequate fit is found.

The range of applicability of a model is the range of conditions over which the model has been tested against empirical data and found to be adequate. There is usually little justification for trusting extrapolations of the model, or predictions about the behaviour of the system under study outside of this applicable range. The model above of a linear response to temperature variation, whatever the parameters, will clearly only be acceptable over a limited range of temperatures.

An empirical model relies primarily on data from the observed behaviour of the system for its formulation. Either of the food intake models discussed above fall into this category if chosen purely through experimental data on food intake at a number of temperatures. A mechanistic or simulation model attempts to represent mathematically something of the physical state or composition of the underlying system and to deduce behaviour of the system from its internal behaviour. For example, a model that measured the heat produced by an animal through metabolism, together with the heat able to be lost under ambient temperatures, and predicted a food intake response to temperature from this is mechanistic in its approach.

Models for management

The terms and methods described above under models for research apply equally to management models. However, here the goal of understanding the system is secondary to that of using it more effectively. A model for management must have a known, and useful, range of applicability. While a research model may be speculative, and built purely from mechanistic assumptions about the system, the model must be well tested empirically before it can be used for management. Since others may use the management model besides the creator of the model, it should be robust to misuse or misunderstanding. In the food intake example above, while the researcher may be interested more in the overall pattern of intake response to temperature, linearly increasing, decreasing or otherwise, the manager's interest is clear: which temperature should I use? Management models are not restricted to biological models: farm planning, conservation and resource allocation (for example, in feed formulation) are all based on some underlying model of the behaviour of an economic system. A manager may use a model to try out a range of operational scenarios and judge which is optimal. This may be done by hand with simple models. Inferring optimal actions based on more complex models, with many inputs, may require adding a mathematical optimization component to the model. In the simplest form of this optimization, an objective function is specified which calculates a single number, representing the benefit of any behaviour of the system predicted by the model, and therefore the ultimate benefit of the management input that caused this behaviour. Various mathematical or computational optimization techniques may be used to find inputs that maximize this benefit.

Hill-climbing techniques are some of the simplest of these. The inputs to the model are varied repeatedly one by one, to see what will increase the objective. More sophisticated methods such as dynamic, linear or integer programming may be used too, depending on the underlying mathematical structure of the model. (RG)

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Maturity The stage of plant growth at which seeds and grain are developing and ripening. Maturity signifies the period between 50% flower emergence and completion of the transfer of nutrients, particularly protein and carbohydrates, from the stem to the grain or seeds. This is associated with a fall in digestibility of the plant, associated with increased cellulose, hemicellulose and lignin in the stem, in order to support the increased weight of the floret or cob. As the seeds ripen the plant dry matter increases, which can result in loss of leaf material through shattering, further depleting the nutritional value of the non-seed fraction of the plant. Grass crops are usually grazed at a young stage, when nutritive value is high. Grass for silage is also cut before the full flower stage is reached. Hay is cut at a later stage to facilitate air-drying (sometimes barn-drying). Cereal crops, usually grown for their grain with residues as a by-product, are normally harvested when the grain has dried sufficiently to be stored. By this time, the residues have reached the stage of senescence and, if to be carried and stored, care is necessary to minimize leaf loss. (TS)

Mead acid Eicosatrienoic acid, a long-chain unsaturated fatty acid of the n-9 series with *cis* double bonds at the 5, 8 and 11 positions, 20:3 n-9($\Delta^{5,8,11}$). When the diet is deficient in essential fatty acids, the same enzymes that desaturate linoleic and α-linolenic acids will desaturate eicosenoic acid to produce eicosatrienoic acid (Mead acid). It is not an essential fatty acid and will not replace arachidonic acid or alleviate the symptoms of essential fatty acid deficiency. (NJB)

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Meal frequency When food availability is unlimited, animals concentrate their spontaneous feeding in discrete meals, which can be defined by establishing a criterion for distinguishing intra- from inter-meal intervals. Meal frequency is the number of meals thus defined per unit of time, and food intake equals meal frequency multiplied by mean meal size. When food availability is intermittent, meal frequency refers to the number of times food is provided per unit of time. (JSav)

Meat: *see* Body composition; Meat production; Meat products; Meat quality; Meat yield; Poultry meat

Meat and bone meal: *see* Meat products

Meat composition Meat consists predominantly of water. The other components are protein (muscle), fat (adipose tissue), minerals and vitamins. The major variable factor is the fat content, which is affected by species, gender, age, stage of growth and nutrition. The composition of the fat is also affected by the dietary fatty acid profile, particularly with non-ruminants. Some typical values are shown in the table opposite. (KJMcC)

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Meat meal: *see* Meat products

Meat production This term refers to the farming of animals and birds for the production of meat for human consumption. The

Composition of a range of meat products (g kg^{-1}).

Meat source	Moisture	Crude protein	Fat	Saturated fat	Energy (MJ kg^{-1})
Chicken breast	744	218	32	10	4.9
Chicken thigh	745	191	55	18	5.3
Pork chop	543	159	295	109	13.6
Lamb loin chop	495	146	354	176	15.6
Lamb leg (deboned)	631	179	187	93	10
Sirloin steak	594	166	228	97	11.8
Minced steak (lean)	645	188	162	69	9.2

major sources of meat are cattle, pigs, poultry and sheep. Of several avian species used for meat production, the commonest are broiler chickens, reared from hatching to around 4–10 weeks, depending on market outlet (size, further processing). Other avian species include turkeys, ducks, guinea-fowl, quail, pheasant, partridge, ostrich and emu. Other ruminant species include goats and deer. Production systems for non-ruminants are generally intensive with control of breed, nutrition, health and environment. Extensive systems are found both in developing countries and where welfare considerations are important to consumers and they are prepared to pay for the extra costs involved. Ruminant animals are normally reared in extensive systems though at least part of the production cycle may be indoors for one of several reasons, e.g. weather conditions, land distribution or the use of 'feedlots' as practised particularly in USA. (JW)

Meat products Primarily by-products of rendering carcass material. They include meat meal, meat and bone meal, fish meal, hydrolysed feather meal, bone meal and blood meal. *Meat meal* is manufactured from carcass trim and condensed carcasses. It is a brown, slightly fibrous meal and the term meat meal normally refers to products with a crude protein value > 60%. The product should be free from hair, bristle, feathers, horn, hoof, skin and viscera. The fat may be extracted either mechanically or with solvents. Solvent extraction removes more fat (leaving < 5%) but the final product should be free from solvent residues. EU legislation also requires that the product is described as 'rich in fat' if the oil content is > 11%. *Meat and bone meal* differs from meat meal in the quantity of bone found in the processed material. Meat and bone meal is manufactured from pieces of meat and carcass with a high proportion of bone but selected to result in a finished product with 40–55% protein. The nutritional characteristics of these meals can vary enormously as the nature of the material being processed influences protein and ash content and the treatment affects the amount of oil. The protein has a good amino acid balance and is highly digestible.

Fish meals are widely accepted as excellent protein sources but they vary with origin. Originally, fish meal was produced from the trimmings and by-products of fish-processing plants. This still occurs in the UK, where white fish meal is made predominantly from cod and haddock. However, the world demand for fish meal cannot be met solely from waste and fish are caught specifically for making into fish meal. These include South American-type fish meals, manufactured from purpose-caught small fish like Spanish pilchards. In northern Europe herring-type meals are often produced from purpose-caught sprat. Fish meal is a high-protein (> 72%) feed with an excellent amino acid composition for non-ruminant animals. The protein is resistant to rumen microbial catabolism and therefore excellent for feeding to high-performance ruminant animals, particularly dairy cows. The oil fraction is particularly high in long-chain n-3 fatty acids, which are considered healthy.

Feathers contain a high level of the protein keratin, a poor source of protein for animals. However, the digestibility is increased when feathers are cooked under pressure. The product is dried and ground to make *hydrolysed feather meal*, which is a useful source of protein (89%).

Bone meal is primarily used as a source of dicalcium phosphate after the bones have been defatted, ground, treated with hydrochloric acid and precipitated with lime. This process is now tightly controlled within the EU under *The Processed Animal Protein Regulations 2001* and in practice is not frequently used.

Blood meal is a deep red/brown granular powder made by drying blood. It is a good food material, high in protein, and is readily eaten by all animals, although it can be unpalatable at first.

Poultry meat meal (poultry offal meal) is a by-product of poultry processing plants. All body parts, including head, feet, carcass and fat, may be included. The final product varies in oil content and sometimes hydrolysed feathers may be included. The meal has a high protein content (65%) and can have a very high oil content (up to 30%), depending on the carcass parts that are included. (MG)

Meat quality The overall quality of meat encompasses the sensory attributes of quality (appearance, flavour and texture), nutritional quality and wholesomeness (microbiological quality, contamination and residues). The term meat quality is often used in a more restricted sense to cover those aspects, whether measured subjectively or instrumentally, that relate to sensory attributes. The appearance of meat (which has two aspects: the amount and colour of the fat; and the colour of the lean meat) is a critical factor influencing selection by consumers. The amount of fat and its colour can be influenced by dietary factors prior to slaughter; for example, maize meal may impart a yellow colour to the fat as the pigments are fat soluble and are deposited in the subcutaneous fat. The colour of the lean meat is determined by the amount of haem pigment (myoglobin) in the muscle prior to slaughter and the form of the pigment. For example, beef is redder than pork, and poultry leg meat is redder than breast meat because in each case the former contains more haem pigment. In pigs that are sensitive to stress, or are subjected to stress just before slaughter, a rapid fall in the muscle pH as the carcass goes into rigor produces meat that is pale, soft and exudative (PSE). In all species, feed deprivation sufficient to deplete muscle glycogen reserves before slaughter or prolonged stress (e.g. long transport journey, mixing of animals, lairage) results in meat that is dark, firm and dry (DFD). The muscles do not undergo full acidification and the pH of the muscle remains high. Due to the high ultimate pH (> 6.0) the meat has poor keeping quality and should not be vacuum packed.

The initial appearance of the whole carcass is important. Poor handling both in production and before slaughter, between farm and abattoir, can result in skin blemishes and bruising in all species and in hock burns and keel bone abrasions in poultry. Meat inspection involves examining the carcass and viscera for evidence of gross pathology. The inspection and clipping of cattle before slaughter has become increasingly important in order to reduce potential microbial contamination with pathogens being carried into cutting plant operations. Hazard analysis critical control point (HACCP) schemes are applied to reduce contamination and maintain quality standards.

The tenderness of the meat depends on the age of the animal and post-slaughter chilling regimes. Meat that is chilled either too fast or too slowly results in shortening of the muscle fibres and subsequent toughening (cold shortening and hot shortening). The toughness of the meat can be measured by a range of devices that quantify the force required to shear a piece of cooked meat (e.g. Warner-Bratzler Shear).

Flavour development in cooked meat is complex, depending both on the biochemical composition of the meat and on the method of cooking. Taints in meat can be a quality problem and may arise naturally from husbandry practices (e.g. boar taint) or from contamination after slaughter (e.g. disinfectant taint). Two compounds, skatole and androstenone, which accumulate in adipose tissue, have been identified as causes of taint in boars.

Nutritional quality of meat is becoming increasingly important, particularly in relation to fat content and the fatty acid profiles of the adipose tissue. The desires and requirements of consumers vary considerably and the aim is to produce meat that is safe and of a quality desired by the target consumer group.

(BMM, JW)

See also: Poultry meat

Meat yield The proportion of an animal carcass that is edible meat. This is different from the 'kill-out' proportion, which is the weight of the eviscerated carcass as a proportion of liveweight. The yield is affected by a large number of factors, including breed and gender (particularly for ruminants), stage of maturity, nutrition, etc. The double-muscled Belgian Blue breed of cattle gives a much higher meat yield than other beef breeds, which in turn give higher yields than dairy breeds. Typical values are 36% of liveweight for British Friesian steers, rising to 46% for Continental beef crosses and over 50% for pure-bred Belgian Blue bulls. Meat yields of bulls tends to be about 2% higher than those of heifers. Considerable differences are also apparent between sheep breeds, with values ranging from about 30% up to 40% of liveweight. In both species the yield of edible meat will be affected by consumer requirements, resulting in a variable amount of trimming of fat. Differences in production systems can also affect meat yield. For example, in Europe, emphasis has been placed on breeding pigs for lean carcasses whereas in some countries the emphasis is on rapid growth with excess fat being trimmed during processing.

There is little interest in lean and fat ratios in meat from avian species. For example, in a turkey of 10 kg liveweight, with an oven-ready weight of 8.2 kg the breast meat (so-called 'white meat') makes up approximately 2.5 kg (i.e. 25% of liveweight); this component has the highest value and maximizing its content is of considerable importance. The legs (drumstick and thigh), usually referred to as 'dark meat', account for around 22.5% of a 10 kg liveweight bird. By comparison, in a broiler of 2.4 kg liveweight, breast meat is around 15% of liveweight, demonstrating the emphasis on body composition during selection programmes in turkeys. Total meat yield (breast + thighs + drumsticks) is around 36% of liveweight for a 1.5 kg poussin and 38% for a 2.5 kg bird. A further recent development in broilers has been marketing of wings, which used to be discarded but are now sold as snacks or 'starters' in many food outlets. This is a good example of how definitions of meat yield will change: an 8% waste product is now part of the yield. (KJMcC)

See also: Carcass; Meat composition

Key references

Kempster, A.J., Cook, G.C. and Grantley-Smith, M. (1986) National estimates of the body composition of British cattle, sheep and pigs with special reference to trends in fatness. A review. *Meat Science* 17, 107–138.

Wood, J.D. and Fisher, A.V. (eds) (1990) *Reducing Fat in Meat Animals*. Elsevier Science, London.

Medicated feed Foods containing added drugs intended to be fed to animals suffering from, or at threat from, various types of disease, particularly infectious disease. Some medication (e.g. antibiotics) is to enhance efficiency of production, some (e.g. coccidiostats) is to protect against disease and some (e.g. antibiotics) is to combat existing disease.

(JMF)

Medium-chain fatty acids Fatty acids, usually saturated, of chain lengths ranging from six (caproic or hexanoic acid, $C_6H_{12}O_2$, molecular weight 116) to 12 carbons (lauric or dodecanoic acid, $C_{12}H_{24}O_2$, molecular weight 222). Absorption from small intestine of mammals does not involve transport through lymph as lipoproteins; their relatively hydrophilic character allows direct transport from intestine to liver via the portal vein. They are major constituents of coconut and palm oils and are also present in human milk and dairy fat. (JAM)

See also: Capric acid; Caproic acid; Caprylic acid; Fatty acids; Lauric acid

Medium-chain triacylglycerols Triacylglycerols in which the constituent fatty acids are usually saturated and range in chain length from six (caproic or hexanoic acid, $C_6H_{12}O_2$, molecular weight 116) to 12 carbons (lauric or dodecanoic acid, $C_{12}H_{24}O_2$, molecular weight 222). Typically, the triacylglyceride consists of fatty acids of more than one chain length. (JAM)
See also: Capric acid; Caproic acid; Caprylic acid; Fats; Lauric acid; Medium-chain fatty acids

Megacalorie 1 megacalorie (Mcal) = 1,000,000 calories or 1000 kcal. (JAMcL)
See also: Energy units

Megajoule 1 megajoule (MJ) = 1,000,000 joules or 1000 kilojoules (kJ) (JAMcL)
See also: Energy units

Melatonin A hormone, *N*-acetyl 5-methyoxytryptamine, synthesized in the pineal gland from the amino acid tryptophan. Melatonin is involved in the regulation of seasonality. Its secretion is stimulated by darkness and inhibited by light and is thus sensitive to day length. Season-related behaviour and physiology, such as mating and fertility, are influenced by its pattern of secretion. (JRS)

Melibiose A disaccharide, $C_{12}H_{22}O_{11}$, molecular weight 342, of α-D-galactopyranose linked to the 6-hydroxyl of D-glucopyranose. It is produced, together with fructose, by hydrolysis of raffinose. (JAM)
See also: Carbohydrates; Raffinose

Melitose: *see* Raffinose

Melitriose: *see* Raffinose

Melon (*Cucumis* spp.) Melons belong to the gourd family, *Cucurbitaceae*, which includes cucumbers, pumpkins, squashes and watermelons. They are annual trailing plants with runners up to 2.5 m long. The yellow bell-shaped flowers require bees for pollination. Watermelons (*Citrullus lanatus* (Thunb.) Matsum & Nakai) are creeping annual plants with large round fleshy fruits with a high moisture content. Melon seeds are used in Africa for human consumption, but may be pressed to obtain oil. The resultant oilcake can be used at up to 20% in ruminant feed. (LR)

Nutrient composition (% dry matter) of melon.

	DM (%)	CP	CF	Ash	EE	NFE
Watermelon rind, boiled	93.0	7.3	36.5	1.6		
Seeds with hulls	88.0	24.4	31.6	4.2	35.4	4.4
Seeds without hulls	91.9	34.0	8.2	6.2	46.7	4.4

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Further reading

Gohl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series, No. 12. FAO, Rome.
Pearce, G.R. (1983) *The Utilisation of Fibrous Agricultural Residues*. Australian Government Publishing Services, Canberra, Australia.

Menadione A synthetic compound, 2-Methyl-1,4-naphthoquinone, also called menaphthone, used in animal feeds as a source of vitamin K activity. It is alkylated by animal tissues to a specific menaquinone, menaquinone-4. (JWS)

Menaquinone A series of compounds, 2-Me-3-polyisoprenyl-1,4-naphthoquinones, with vitamin K activity produced by anaerobic bacteria in the lower bowel. (JWS)

Menhaden oil An oil extracted from a large herring-like fish (*Brevoortia*) caught off the east coast of North America. Menhaden oil contains a high proportion of long-chain polyunsaturated **fatty acids**, particularly C_{20} and C_{22}. Refined menhaden oil has a fatty acid profile of ≤ 12:0 trace, 14:0 7–11, 16:0 12–31, 16:1 7–13, 18:0 2–5, 18:1 9–11, 20:0 trace, 20:1 1–2, 20:4 1.5–2.5, 20:5 11–14, 22:0 trace, 22:1 trace, 22:5 1–3, 22:6 7–11. (JKM)

Mercury A heavy metal, not nutritionally essential, that is potentially toxic in farmed animals, particularly fish. In nature it exists mainly in low, non-toxic concentrations but its widespread use in industry and in particular its use as a seed dressing in agriculture has led to many poisoning incidents in farm animals and to its accumulation in lakes and waterways. It is used industrially mainly in the inorganic form, which is not well absorbed by animals, but this is readily converted into the organic forms, methyl and dimethyl mercury, by microorganisms. The organic form is more soluble and is easily absorbed via the gastrointestinal tract. It is neurotoxic and accumulates in liver and muscle, being particularly attracted to cysteine-rich molecules such as metallothioneins. (CJCP)

Metabolic disorder A disease caused by a disturbance in one or more metabolic processes that may result in a deficiency or excess of a normal metabolite. Metabolic diseases include milk fever (parturient paresis, hypocalcaemia), ketosis (acetonaemia), pregnancy toxaemia and hypomagnesaemia (grass staggers). (ER)

Metabolic rate The sum of all oxidative processes in the body, equated to the rate of **heat production**. It may be measured directly as heat, or indirectly from **oxygen consumption** and **carbon dioxide** production using a formula such as **Brouwer's**. Basal metabolic rate and resting metabolic rate are measurements made under standardized conditions, which may be difficult to achieve in farm animals. (MFF)

Metabolic weight The fractional power of liveweight to which metabolic rate tends to be proportional. It is most commonly expressed as live body weight (kg) raised to the power 0.75 (kg $W^{0.75}$) because the relationship between metabolic rate (*M*) and body weight (*W*) in adults of species with a wide range of mature body weights has the form $M = aW^{0.75}$. Within a species, however, metabolic rate tends to be proportional to a lower power of body weight. (MMacL)

Metabolism **1.** The physical and chemical processes occurring within a living cell or animal that are necessary for life.
2. The changes involving a specified element, substance or attribute within the body (e.g. nitrogen metabolism, protein metabolism, energy metabolism). These changes involve biosynthesis (anabolism), uptake and excretion (transport) and breakdown (catabolism) carried out in a living cell, tissue or organ or in the whole animal. (JAMcL, NJB)

Metabolites Compounds that are used in or produced by metabolism. A metabolite is thought of as a substrate or product of an enzyme system, although this applies as well to transport systems (uptake and excretion). A metabolite can be organic (e.g. glucose or glucose-6-phosphate) or inorganic (e.g. sulphate SO_4^{2-}, or phosphate PO_4^{3-}). (NJB)

Metabolizable energy (ME) That part of the gross energy (GE) of the food that is not excreted as the gross energy of waste products (i.e. faeces, urine and combustible gases). Metabolizability is the proportion ME/GE *of the complete ration.*

A ration that maintains a non-working, non-pregnant, mature animal without fattening or production of milk, eggs, etc., is called a **maintenance** ration. At the maintenance level of feeding, all of the ME is converted into heat, i.e. the basal heat production (HP) plus the heat increment of the maintenance ration.

The ME system for estimating food requirements uses ME for maintenance as a starting point. From this point additional ME intake (*d*ME) provides for energy retention (RE) in the form of growth, fattening and the production of milk, eggs, etc. All these processes also involve additional heat production (*d*HP) as a sort of tax on the additional ME. Thus:

$$RE = dME - dHP.$$

The ratio *d*RE/*d*ME (which is the same as RE/dME, because the starting point is that of zero RE) is known as the efficiency of utilization of metabolizable energy (k). Its converse (1 − k), which is equal to *d*HP/*d*ME, is the heat increment of the additional feed. Efficiency is different for different functions (maintenance, fattening, lactation, etc.) and is also dependent on the quality (metabolizability) of the diet. Animal rations are often quantified in energy terms as multiples of the ME for maintenance.

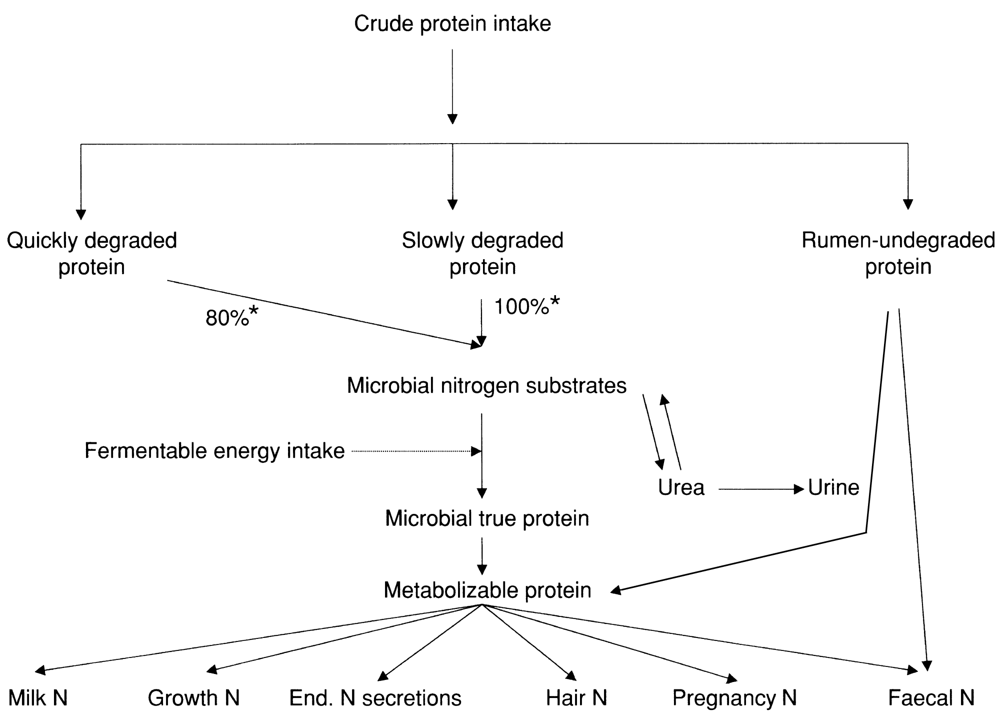
The concepts just defined for animal rations (GE, ME and RE) are also applicable to different types of food and to individual food components and this is the basis of the ME feeding system for predicting the energy requirements of animals. The values quoted in food tables are those of the ME of the different foods or food constituents. These values are not the same for all species, because of differences in their digestive systems (e.g. carnivores, omnivores, ruminants). The values may not be completely additive when feeds are combined to form diets, because of **associative effects**. (JAMcL)

See also: Calorific factors; Energy costs

Further reading

Blaxter, K.L. (1989) Metabolisable energy. In: *Energy Metabolism in Animals and Man.* Cambridge University Press, Cambridge, UK, pp. 23–37.

Metabolizable protein Protein that is usable by an animal, usually in the context of feeding ruminants. Metabolizable protein (MP) has two components: microbial true protein derived from the growth of bacteria and protozoa in the rumen and reticulum (*see* **Microbial protein**); and digested undegraded feed protein that has passed intact through the rumen and has been digested in the abomasum. The rate of production of microbial protein in the rumen depends on the supply of degradable feed protein, the supply of fermentable energy to the rumen microbes and the rate of flow of digesta out of the rumen. The supply of undegraded feed protein is also affected by the rate of flow through the rumen, which increases with the animal production level (APL). The animal's requirement for MP depends on its level of productivity. The major requirement for MP in adult female ruminants is for the production of milk during lactation, but MP is also needed for maintenance and growth, including the growth of the fetus during pregnancy, and for the production of wool. If the MP absorbed is inadequate to meet maintenance requirements, MP



The metabolizable protein system for cattle. *The proportion of the protein that is utilized to form the microbial nitrogen substrates.

is released from the breakdown of body tissues (mainly muscle), with a consequent loss of body weight. MP from body tissue breakdown is presumed to be utilized with an efficiency that varies with the use: for maintenance 1.0, for pregnancy 0.85, for lactation 0.68, for body growth 0.6, and for wool growth 0.26. (JMW)
See also: Microbial protein; Protected protein; Protein

Metalloenzymes Enzymes that, when purified by conventional means, have a repeatable molar quantity of a functional metal associated with them. These differ from metal-activated enzymes which require an added metal to function. The distinction between metalloenzymes and metal-activated enzymes lies in the affinity of the metal for the enzyme. (NJB)

Metallothioneins A group of proteins (molecular weight 6500) containing ~60 amino acids, one-third of which are cysteine. These proteins are found mainly in the cytoplasm of kidney, liver and intestine. The cysteine residues of these proteins are involved in the binding of copper, zinc, cadmium and mercury. Metallothioneins bind these metals with high affinity and participate in their storage and sequestration. In the case of copper, these proteins have the effect of decreasing the amount of free copper which participates in generation of free radicals that cause tissue damage. (NJB)

Metals Elements that tend to form positive ions in solution. In water, metal oxides tend to form hydroxides. Most conduct electricity and can be formed into a variety of shapes. In pure form they have a high specific gravity and high physical strength. About three-quarters of the elements are classified as metals. (NJB)

Methaemoglobin Haemoglobin in which the iron is in the ferric (Fe^{3+}) rather than the ferrous (Fe^{2+}) state. Also called ferrihaemoglobin, methaemoglobin is brown rather than the bright red of oxyhaemoglobin. Methaemoglobin cannot carry oxygen or carbon monoxide and thus is of little value in support of oxidative metabolism. One to two per cent of haemoglobin in blood is in the methaemoglobin form. It can be reconverted to haemoglobin in a reaction in which reduced glutathione participates. (NJB)

Methane An organic gas, CH_4. It is colourless, tasteless and less dense than air. Biogenic sources, including lake sediments, marshes, rice paddies, sanitary landfills and intestinal contents of animals, involve methanogenic bacteria, while abiogenic sources are coal mining, natural gas emissions and biomass burning. (DMS)

Methanogenesis Methane production. Methane is produced by the action of methanogens, a group of Archaea that oxidize hydrogen as a source of electrons for carbon dioxide reduction via the reaction $CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$. Methanogenesis is important as a means of electron disposal from anaerobic fermentations, notably those in the rumen and intestines. This process allows for the oxidation of reduced electron carriers (NADH + H^+, NADPH + H^+ and $FADH_2$) so that catabolic, oxidative degradation of substrates can continue. Hydrogenase enables electrons from the fermentative bacteria to be released in the form of hydrogen, and oxidized electron carriers to be regenerated. If hydrogen consumption is disrupted, hydrogen accumulates, hydrogenase is inhibited, catabolic reactions are impeded, substrate degradation is impaired, and atypical reduced products such as lactate and ethanol accumulate. Additional substrates for methanogenesis in digestive tract fermentations are formate and methylamine. Methane production constitutes a loss of digestible energy. In order to retain normal digestive attributes of gut microbes while suppressing energy loss as methane, an alternative means of electron disposal must be available to the fermentative microbes. Examples of alternative electron disposal pathways are reduction of nitrate to ammonia, fumarate to succinate, and of CO_2 to acetate. Methane is also produced from complete decomposition of the organic matter of animal excreta when held anaerobically for residence times of 4 days or longer. Under these conditions, bacteria thrive that are capable of oxidizing volatile fatty acids to acetic acid, hydrogen and CO_2. The methanogens involved have a species composition different from that of the gut. (DMS)

Methanotroph An organism that grows on methane, which serves as an electron donor and sole carbon source for cell biomass synthesis. Methanotrophs are found in microaerobic environments of soil and water. A key enzyme in these organisms is methane monooxygenase which catalyses the introduction of oxygen into methane, resulting in methanol formation. (DMS)

Methionine An essential amino acid ($H_3C{\cdot}S{\cdot}(CH_2)_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 149.2) found in protein. Methionine is a sulphur-containing amino acid that is often deficient in diets for animals, particularly poultry. Among the cereal grains, only maize is considered a good source of sulphur amino acids (methionine + cysteine). Soybean meal is first limiting in sulphur amino acids for growth of poultry and swine.

Methionine reacts with ATP to form *S*-adenosylmethionine (SAM), the most important methylating compound in the body, facilitating the biosynthesis of up to 100 different methyl-containing body compounds such as creatine, phosphatidyl choline and epinephrine. The polyamines, spermine and spermidine, also require SAM for their synthesis.

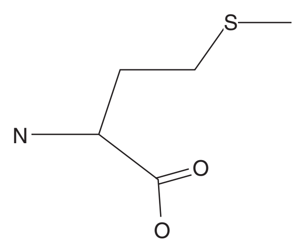
The main catabolic pathway for methionine involves trans-sulphuration of methionine to cysteine, but only the sulphur moiety of cysteine is derived from methionine. The carbon skeleton of cysteine is derived from serine.

Body protein synthesis requires both methionine and cysteine, and each compound is required in approximately equal portions for growth. Cysteine, however, dominates the total sulphur amino acid requirements for adult maintenance. Methionine can satisfy the physiological requirement for both methionine and cysteine because methionine sulphur can be converted (irreversibly) to cysteine sulphur with 100% molar efficiency. None the less, diets for animals are generally formulated in practice on a weight or concentration basis rather than on a molar basis. Thus, because of the molecular weight difference between methionine and cysteine, methionine on a weight or concentration basis is about 81% efficient in yielding cysteine metabolically.

Methionine is one of the few amino acids produced commercially by chemical synthesis (as opposed to fermentation or chemical extraction). Chemical synthesis results in the mixed DL-isomer of methionine. With the exception of primates, the D-isomer of methionine is used by animals almost as efficiently as the L-isomer. The DL-hydroxy analogue of methionine is also an important commercial product. This precursor of methionine can be converted to L-methionine in a two-step metabolic process.

Conventional acid hydrolysis procedures used to determine the amino acid concentrations in a protein result in partial destruction of methionine and cysteine. Therefore, to obtain accurate analytical estimates of methionine and cysteine concentrations in a protein, the sample must be preoxidized using performic acid. This converts methionine to methionine sulphone and cysteine to cysteic acid. Then, HCl hydrolysis of the preoxidized sample allows accurate quantification of methionine and cysteine in the protein.

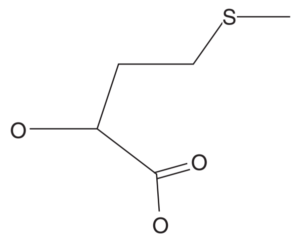
(DHB)



See also: Cysteine; Essential amino acids; Methionine hydroxy analogue

Methionine hydroxy analogue A chemically synthesized precursor ($H_3C{\cdot}S{\cdot}(CH_2)_2{\cdot}CH{\cdot}OH{\cdot}COOH$, molecular weight 149.2) of methionine that contains a hydroxyl radical on the α carbon rather than an amino group. It is available commercially as the liquid free acid (88% DL-OH-Met) or the calcium salt (86% DL-OH-Met). It is metabolized in the body to L-methionine in a two-step reaction sequence. On an isomolar basis, DL-

OH-Met is thought to be somewhat lower in biological activity than L-methionine. (DHB)



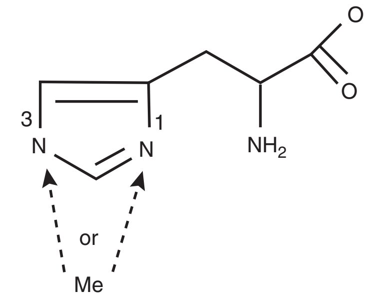
See also: Methionine

Methylamine A gas ($CH_3 \cdot NH_2$) with a strong ammoniacal odour. (NJB)

Methylation The process whereby a methyl group (CH_3-) is added to a recipient molecule. The methyl group donor is usually *S*-adenosylmethionine (AdoMet), which is the source of the methyl group for more than 50 reactions. Two other metabolites are involved in single methylations and both are related to the conversion of homocysteine to methionine. Betaine is the methyl source when homocysteine is converted to methionine by betaine homocysteine methyltransferase. The other methyl source is N^5-methyltetrahydrofolate, which is also involved in the methylation of homocysteine by the enzyme N^5-methyltetrahydrofolate homocysteine methyltransferase. (NJB)

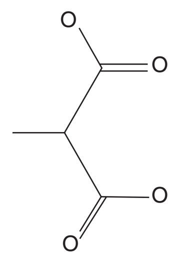
Methylhistidine Histidine that is methylated in either the 1 or 3 position. 3-Methylhistidine (also referred to as N^{τ}-methylhistidine) is formed by methylation of histidine by *S*-adenosylmethionine after it is incorporated into protein. Once released from a protein it cannot be reincorporated into protein. In those species in which it is quantitatively excreted in urine, it can be used as an indicator of protein catabolism. Because three-quarters of 3-methylhistidine in the body is in muscle (skin is also a source) it is used as an indicator of muscle breakdown. In human, rat and chicken, 3-methylhistidine is not catabolized and is quantitatively excreted in urine; it has been used as an indicator of muscle protein breakdown. However, in pigs, cattle, sheep, dairy goats, dogs and cats it is either catabolized or metabolized to balenine and not quantitatively recovered in urine.

1-Methylhistidine is also found in urine. It is the result of the methylation of free histidine and is not an indicator of protein catabolism. (NJB)



Methyllysine: *see* Trimethyllysine

Methylmalonic acid Molecular structure HOOC·CH(·CH_3)·COOH (molecular weight 118.07), an intermediate in the conversion of propionate, via propionyl-CoA, to succinate (an intermediate in the TCA cycle). Propionyl-CoA is carboxylated (CO_2 is added) by the biotin-dependent enzyme, propionyl-CoA carboxylase, to form D-methylmalonate, which is converted to succinyl-CoA and then to succinate, which is used for energy. (NJB)



5-Methyltetrahydrofolate The major one-carbon intermediate in the folic acid one-carbon system. This intermediate is critical to homocysteine metabolism because methylation of homocysteine creates methionine and produces free tetrahydrofolate, which is required for folate-dependent one-carbon metabolism. Homocysteine methylation is also dependent on vitamin B_{12}. A deficiency of vitamin B_{12} results in a significant increase in 5-methyltetrahydrofolate because of decreased methylation of homocysteine. This leads to a measurable increase in blood homocysteine and a deficiency of tetrahydrofolate. This metabolic situation is described as the 'methyl trap'. (NJB)

Micro diet Pelleted fish food with diameter of tens to hundreds of microns. Usually coated with a biodegradable polymer, such as gelatin or zein. (RHP)

Microbial ecology: *see* Gastrointestinal microflora

Microbial flora, intestinal: *see* Gastrointestinal microflora

Microbial protein The protein of microbial cells, including those of bacteria, protozoa, fungi and yeasts. Microbial protein produced in the rumen and reticulum is the principal source of amino acids for ruminants and it has a good balance of essential amino acids. Most classes of ruminant livestock can meet their total requirement for metabolizable protein from the supply of microbial true protein alone. The exception is the high-yielding dairy cow, which may require supplementary digestible undegraded feed protein to meet its requirement for metabolizable protein: it may also need supplementary essential amino acids such as methionine and lysine. Much of the dietary protein eaten by the animal is degraded to ammonia by the microbial population of the rumen and it is therefore possible to include non-protein nitrogen, such as urea, in diets that are deficient in degradable protein. Such deficiencies might arise when the dietary ingredients, such as straw or maize silage, are low in total protein, or where the degradability of the feed protein is relatively low, perhaps as a result of heat treatment during processing.

The production of microbial protein in the rumen depends on the supply of degradable protein and fermentable energy (*see* **Metabolizable protein**). Degraded protein is not used with complete efficiency for microbial protein synthesis because some (the quickly degraded fraction) is converted to ammonia, which is absorbed through the rumen wall and converted to urea in the liver. Some (about 20%) of the quickly degraded protein is lost from the rumen. The remainder is potentially available to the rumen microbial population. This is known as the effective rumen degradable protein (ERDP) and is the amount of protein (or nitrogen) available for microbial growth and metabolism. The amount of ERDP that the microbial population can utilize depends on the amount of energy available: the fermentable metabolizable energy (FME). Some sources of energy are considered to be of low value to the microbes, particularly those that yield low levels of ATP during their digestion in the rumen. In the calculation of the FME the energy of lipids, organic acids and undegraded protein is subtracted from the total metabolizable energy. The yield of microbial crude protein (MCP) per megajoule of FME depends on the animal production level (APL), because at lower APL the outflow rate from the rumen is reduced and at the lower outflow rate bacteria and protozoa die before passing out of the rumen and are digested by other rumen microbes. Their protein is recycled to produce new microbial protein. However, this process requires energy and so additional FME is utilized with no net increase in yield of microbial protein. The limit to the total yield of MCP is determined either by ERDP or by FME. If set by EDRP, MCP production equals the supply of ERDP; if set by FME, MCP production equals the FME multiplied by Y (the yield of MCP MJ^{-1} FME). This quantity ranges from 8 g MCP MJ^{-1} FME at an APL of 1.0, to 11.5 at an APL of 4.0. The lesser of the two calculated values of MCP is taken. This value is then reduced to take account of the fact that about 75% of MCP is true protein and that it is absorbed into the blood with an efficiency of about 85%. Thus microbial true protein supply is only about 64% of the MCP produced. (JMW)

Micronutrients Nutrients required in low dietary concentrations (ng, μg or mg kg^{-1}). Nutrients that fall into this category are vitamins and minerals. Using the pig as an example, copper, iron, manganese, zinc and all of the vitamins with the exception of vitamin B_{12} are required in mg kg^{-1} diet, whereas iodine, molybdenum, selenium and vitamin B_{12} are required in μg kg^{-1} diet. (NJB)

Microorganisms Small living animal or plant organisms capable of reproduction.

They can be seen only with the aid of an optical or electron microscope. They include single cells such as algae, yeast, fungi, bacteria or protozoa. (NJB)

Microvillus A submicroscopic fingerlike projection of the apical membrane (that which faces the lumen) of the epithelial cells of the **villi**, which are themselves fingerlike projections of the epithelial cell layer of the small intestine. A large number of closely packed microvilli create a brushlike surface, called the **brush border**, on the surface of the villus. Microvilli are also found in the renal tubules. The structure of villi and microvilli increases 100-fold the luminal surface of the intestine. (SB)

Microwave treatment: *see* Heat treatment

Middlings: *see* Milling by-products

Milk Milk is a highly nutritious liquid produced by female mammals for the sustenance of their young offspring. It is one of the few natural foods that can meet the total nutritional needs of humans. Dairy products are a major source of calcium and high-quality protein in the human diet. Although fats from dairy products have had a negative image since the 1980s, recent studies have shown that fatty acids in milk (especially conjugated linoleic acid) can play a significant role in reducing the incidence of cancer, diabetes and atherosclerosis, as well as partitioning energy away from body fat towards muscle tissue (Bauman *et al.*, 2001).

The major constituent of milk is water. Dissolved in the water are lactose, albumin and water-soluble vitamins, minerals and nitrogenous substances. Colloids of casein, calcium and phosphorus are suspended in the water, as are minute fat globules. Most of the constituents of milk are synthesized in the mammary gland from precursors absorbed from the blood.

Apart from water, the main constituents of milk are butterfat, protein and lactose. The proportions of these components vary between species (see table).

Butterfat, protein and lactose contents (%) of milk from different species.

	Butterfat	Protein	Lactose
Cattle	3.9	3.4	4.8
Goat	4.5	3.3	4.1
Sheep	7.4	5.5	4.8
Pig	8.5	5.8	4.8

Butterfat consists of triglycerides that are synthesized in the mammary gland from glycerol and a mixture of fatty acids ranging in carbon numbers from 4 to 22 in ruminants and 10 to 22 in non-ruminants. Shorter-chain fatty acids (up to 16 carbon atoms) are synthesized in the mammary gland from acetic acid (and β-hydroxy butyrate in ruminants); longer chain fatty acids are absorbed from the bloodstream for direct incorporation into milk triglycerides. In non-ruminants, acetate is synthesized from glucose in the mammary gland; in ruminants, acetate is absorbed from the bloodstream.

The protein fraction of milk comprises 80% casein, which is synthesized in the mammary gland from amino acids absorbed from the bloodstream. The remaining proteins are β-lactoglobulin and α-lactalbumin, which are synthesized in the mammary gland, and serum albumin and immune globulins, which are absorbed from the bloodstream.

Lactose, the only carbohydrate present in milk, is a disaccharide made from glucose and galactose, both of which are derived from glucose absorbed from the bloodstream. Lactose is the major osmotic component of milk and so its concentration varies much less than those of fat and protein. If an animal has insufficient glucose for its potential lactose synthesis, it will reduce milk yield rather than produce milk with a low lactose concentration.

Annual milk yields are 4000–12,000 l in dairy cows, 600–1100 l in goats and 200–700 l in sheep. The principal determinants of annual milk yield are genetic merit of an animal and overall plane of nutrition. Daily milk yield is affected by genetic merit, stage of lactation, milking frequency, supply of nutrients and state of body reserves. Generally, energy intake is the main factor limiting milk yield; energy and protein sources affect milk composition. In early lactation, provided that dietary protein supply is sufficient, animals will mobilize body fat reserves in support of milk production.

Fibrous sources of energy tend to increase the butterfat content of milk because cellulolytic bacteria in the rumen produce mainly acetate, which is a precursor for fatty acid synthesis in the mammary gland. Starch increases propionate production in the rumen by amylolytic bacteria. Propionate is the main precursor for glucose production, which directly influences milk yield, through the requirement for glucose as a general energy source and as a precursor for lactose synthesis. Glucose indirectly influences milk yield through the effects on circulating plasma insulin levels, which control the partition of energy between body fat and milk synthesis. Glucose also influences milk protein concentration indirectly. Essential and non-essential amino acids are required for milk protein synthesis in the mammary gland. Amino acids are also utilized for gluconeogenesis if propionate supply is inadequate. Therefore, increased propionate supply can lead to higher blood glucose concentrations, sparing amino acids from gluconeogenesis and thereby increasing milk protein content.

Dietary fat is used as a concentrated energy source for milk production and also has a direct effect on the butterfat content of milk. However, if dietary fat content exceeds 60 g kg^{-1} dry matter, rumen digestion of fibre can be disrupted through the physical and detergent effects of long-chain fatty acids on fibre particles and rumen microorganisms respectively. This problem can be overcome by feeding the fatty acids in a protected form as calcium salts, as small particles with a high melting point, or encapsulated in formaldehyde-treated casein. Dietary fat tends have a negative effect on milk protein concentration by increasing milk yield (thereby diluting milk protein), decreasing fermentable energy intake and increasing the glucose requirement for absorption of fatty acids from the gut (Garnsworthy, 1997).

In non-ruminants, milk yield is determined by genotype, age, litter size, body reserves and nutrition. Energy intake has a direct effect on milk yield in sows and protein supply influences milk protein content, since the diet is the only source of essential amino acids in non-ruminants. (PCG)

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Milk fever An acute hypocalcaemic condition of dairy cows and goats associated with the onset of lactation. Blood calcium concentration, normally maintained at 2–2.5 mM, falls below 1.5 mM, impairing nerve and muscle function and resulting in recumbency and inability to stand. Affected animals must be treated to increase blood calcium concentration (usually by intravenous calcium administration) to prevent death. Milk fever occurs because the homeostatic mechanisms that normally maintain blood calcium concentration fail. There are two major nutritional factors that increase the susceptibility to milk fever. Metabolic alkalosis, caused by diets that are high in potassium or sodium, interferes with the function of parathyroid hormone (which regulates calcium) in target tissues, preventing adequate calcium homeostasis. Addition of anions (chloride, sulphate) to the diet can counteract the alkalinizing effects of potassium and sodium and help to reduce the incidence of milk fever. Hypomagnesaemia, caused by inadequate dietary magnesium or interference with rumen magnesium absorption, can also interfere with parathyroid hormone secretion and function. (JPG)

Further reading

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Milk products: *see* Dairy products

Milk substitute Artificial milk, usually in powder form, that is reconstituted with water before use, designed to replace mother's milk in a young animal before weaning.

Many animal production systems require young animals to be artificially reared. For example, calves are removed from dairy cows within 24 h of birth so that milk can be used for human consumption; piglets may be weaned early so that the sow can be bred again; orphaned lambs often need to be reared artificially because it is very difficult to make ewes suckle lambs that are not their own.

The quality of a milk substitute depends on its ability to mimic natural milk, both chemically and physically. The newborn or young animal's digestive system is designed to digest milk and so any substantial deviation from natural milk constituents can cause digestive upsets. Of particular importance is casein, which has the ability to clot under the action of rennin and pepsin (*see* **Casein**). Once clotted, milk is slowly digested in the stomach and small intestine. If a suitable clot does not develop, milk passes rapidly to the hindgut, where it ferments and causes diarrhoea. For this reason, the best (and most expensive) milk substitutes are based on skimmed milk.

Skimmed milk is a by-product of cream and butter manufacture. The butterfat can be replaced by vegetable oils, which need to be dispersed throughout the milk substitute by an emulsifier. Milk substitutes based on whey, a by-product of cheese manufacture, plus vegetable oils and animal or vegetable proteins, historically led to poorer animal performance due to digestive upsets. Recently, the use of whey proteins, concentrated by ultrafiltration, has led to performances comparable with skim-based milk substitutes. This is because concentrated whey proteins have a very high immunoglobulin content, which helps to boost the immune system, as well as being highly digestible. Some milk substitutes have added organic acids to improve keeping quality and allow them to be fed cold. (PCG)

Milkfish (*Chanos chanos*) The only known species of the family Chanidae, widely distributed throughout the tropical and subtropical regions of the Indian and Pacific Oceans. Milkfish are euryhaline and survive in salinity of 0–50 parts per 1000. They are a popular cultured species in the tropics because of their fast growth, herbivorous food habits and tolerance of a wide range of environmental conditions. Milkfish have been cultured extensively in freshwater pens as well as brackish-water ponds. Milkfish farming is believed to have begun in Indonesia some 700 years ago and was introduced to the Philippines and Taiwan.

Milkfish find their food mainly by vision rather than chemosensory mechanisms. In natural habitats they feed on benthic, epiphytic and planktonic organisms but in culture ponds they depend on two types of natural foods, locally known in the Philippines as *lablab* (cyanobacterial mat) and *lumut* (filamentous green algae). In recent years, research has been carried out to develop artificial diets for milkfish. The optimum dietary protein for maximum growth, feed efficiency and survival has been reported to be about 40% by dry weight. In semi-intensive pond culture systems, commercial diets with 23–27% crude protein are thought to be sufficient for satisfactory growth. Milkfish do not tolerate high levels of dietary lipid and 7–10% by dry weight has been reported to be the optimum. They benefit from multiple daily feedings and are reported to gain weight 20% faster when feeding frequency is increased from four to eight times daily. (RMG)

Millet Several species of the *Gramineae* (grass) family, widely cultivated in the temperate regions of the world for their small grains (seeds). The most important members are: (i) pearl or bulrush millet (*Pennisetum americanum*), suited to soils of low fertility and a popular food crop in India and Africa; (ii) broomcorn millet (*Panicum miliaceum*), widely used in bird-seed and chicken-feed mixtures, and as a livestock feed in the USA and as a human food in Asia and Eastern Europe; (iii) foxtail or Italian millet (*Setaria italica*), used to produce hay in North America and Western Europe but also an important food source in China and other Asian countries; (iv) finger or birdsfoot millet (*Eleusine coracana*), an important food grain in southern Asia and regions of Africa; (v) kodo or ditch millet (*Paspalum scorbiculatum*); (vi) Japanese or barnyard millet

(*Echinochloa crusgalli*), grown chiefly in Japan and the USA as a hay crop; (vii) browntop millet (*Panicum ramosum*), grown in the south-eastern USA for hay, forage and game-bird feed; and (viii) little millet (*Panicum miliare*), chiefly used as a food crop in India.

Millet species usually grow to a height of 0.3–1.3 m, except for pearl millet, which grows to 1.5–3.0 m. In all species except pearl millet, the seeds remain enclosed in hulls following threshing and the hulled seeds usually have a creamy white appearance. The composition of millets is very variable (see table) but they are generally high in carbohydrates with protein, oil (as ether extract) and crude fibre contents varying from 100 to 120 g kg^{-1} dry matter (DM), 20 to 50 g kg^{-1} DM and 20 to 90 g kg^{-1} DM, respectively. About 30 million tonnes of millet are produced annually, chiefly in India, China, Nigeria and Russia. They are a staple food crop in many areas of Asia, Russia and western Africa.

Millet generally has a strong taste and millet flour cannot be used to make leavened bread. Instead, it is mainly consumed in flat breads and porridges or prepared and eaten much like rice grain. In the USA and Western Europe it is used chiefly as a fresh forage or to produce hay. Broomcorn and foxtail millets can be grown as forage for sheep and cattle and fed fresh or following preservation as hay or silage. In southern Europe, intercropping broomcorn or foxtail millet with oats and vetch grass or fodder peas is a common practice. The intercrop is usually sown in early summer in order to produce a second harvest following a winter crop. (ED)

Chemical composition of the main millet species (as g kg^{-1} DM unless specified). (Source: Göhl, 1981.)

Millet species	DM (g kg^{-1})	CP	EE	Ash	CF
Broomcorn millet, hay	866	125	25	66	339
Foxtail, fresh	356	90	22	101	337
Foxtail, hay	–	76	17	97	451
Finger millet, fresh	–	76	11	151	336
Ditch millet, fresh	–	114	14	143	288
Japanese millet, fresh (late bloom)	244	74	29	86	310
Japanese millet, hay	891	135	25	104	227

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract.

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Milling The process of grinding, crushing or pressing in a mill to comminute a material into particles of various sizes. It is an important process in both feed and food manufacturing industries, extensively used in the conversion of whole cereal grains and seeds to their various derivatives (e.g. wheat into flour). (ED)

Milling by-products When cereals, especially wheat, are milled to produce flour, the coarse fractions are separated and are often used for animal feeding. The composition of these materials varies according to the way the milling fractions are combined. Bran consists mainly of the testa, pericarp and aleurone layers of the grain. Wheatfeed, also called millers' offals, middlings or pollards, consists of fine bran particles and aleurone with some endosperm. (MFF)
See also: Flour

Mimosine A toxic amino acid from *Leucaena leucocephala*. In non-ruminants, mimosine causes poor growth, loss of hair, cataracts in the eyes and reproductive problems. Levels of *Leucaena* meal at 5–10% of the diet result in poor performance in pigs, poultry and rabbits. Ruminants grazing *Leucaena* may show poor growth, loss of hair, lameness, lesions in the mouth and oesophageal and reproductive problems. In the continental USA and Australia, consumption of *Leucaena* by ruminants causes the problems described above, but in Hawaii and Indonesia cattle and goats can consume *Leucaena* with impunity. Transfer of rumen fluid from animals in Hawaii and Indonesia to Australian ruminants resulted in a complete elimination of the toxic effects and better utilization of this high-protein (25–35% crude protein) forage. The effects of mimosine on non-ruminants can be reduced by supplementation of the diet with ferrous sulphate or mineral supplements containing zinc. (KEP)

Mineral and vitamin supplements All farm animals need a wide range of minerals and vitamins to maintain health and productivity. Mineral and vitamin supplements are formulated for inclusion in the concentrate feed so that the mineral and vitamin requirements of the particular species will be met when the animal consumes normal amounts of the feed. (KJMcC)

Mineral deficiencies Certain minerals are required in large amounts (g kg^{-1} diet) and are termed macrominerals. Others are required in minor amounts (mg kg^{-1} diet) and are termed the trace minerals. While not comprehensive, the clinical signs associated with dietary deficiency of these minerals are outlined in the table. (JPG)

Mineral supplements All farm animals need a wide range of minerals in the feed to provide a balanced diet and these are not normally available in adequate quantities in the ingredients used to formulate diets. Mineral supplements are formulated to meet the short-

Clinical signs of mineral deficiencies.

Mineral	Dietary deficiency symptoms
Macrominerals	
Calcium	Bone disease – osteoporosis (adult), rickets (young); hypocalcaemia – tetany, paresis, abnormal blood clotting, reduced eggshell thickness
Phosphorus	Bone disease – osteomalacia (adults), rickets (young); impaired growth and feed intake, appetite for unusual items (pica)
Magnesium	Impaired neuromuscular activity, tetany, impaired growth, low milk production, urinary calculi; reduced eggshell thickness and hatchability
Sodium	Depressed growth, depressed milk or egg production, pica, reduced milk fat concentration in ruminants
Chloride	Depressed growth, depressed milk or egg production, pica, decreased plasma volume
Potassium	Reduced feed and water intake, impaired growth, muscle weakness; rapid decline in milk production; sudden death in poultry
Sulphur (ruminants only)	Reduced production of microbial protein within rumen, leading to impaired growth or milk production
Trace minerals	
Chromium	Impairment of glucose tolerance, reproduction and immune response
Cobalt (ruminants only)	(Used by rumen microbes to produce vitamin B_{12} vital for efficient use of propionate.) Reduced growth and productivity
Copper	Anaemia, rough hair coat with fading colours due to inability to make melanin, impaired immune responses; defective collagen synthesis leading to impaired bone growth, osteochondrosis, stillbirths, neonatal ataxia and swayback and, in birds, aortic rupture
Iodine	Inability to make thyroid hormones; goitre; reduced growth, reproduction, milk production and cold tolerance
Iron	Anaemia, reduced growth, intolerance of exercise, reduced immune response
Manganese	Reduced reproductive efficiency, anoestrus; skeletal abnormalities and reduced growth in length of bones, perosis and slipped tendons in birds
Selenium	Degeneration of skeletal muscle, 'white muscle disease' and cardiac muscle 'mulberry heart disease', leading to muscle weakness and heart failure; impaired immune responses; retained placenta in cattle; infertility in many species
Zinc	Impaired keratin production resulting in rough hair coat, dermatitis (parakeratosis in swine), weak hooves, poor feathering; impaired immune response (lack of thymus development); impaired wound healing; reduced growth; short, thick bones; testicular hypoplasia

fall by mixing together appropriate proportions of mineral salts. These may be provided as 'licks' to which the animals (usually ruminants) have free access. More often they are added to the concentrate feed during mixing, thus ensuring uniform intake by the animals. (KJMcC)

Minerals Inorganic substances. A number of inorganic elements are essential nutrients. They include calcium, phosphorus, sodium, chloride, potassium, iron, zinc, magnesium, manganese, sulphur, copper, iodine and cobalt. All of these have known metabolic functions and requirements have been estimated for each of them, though not in all species. Other mineral elements are also known to have metabolic roles but no requirement has been established. These include selenium, molybdenum and chromium. For some other minerals – nickel, boron, lithium, fluorine and vanadium – there is no known metabolic function but there is some evidence of their beneficial role. Of those mineral elements considered essential nutrients, those for which the requirement is > 1 mg kg^{-1} diet are called macrominerals and those for which the requirement is < 1 mg kg^{-1} are called trace elements. Those for which no requirement is known, but which are thought to be required in very small amounts, are called ultra-trace elements. (PGR)

See also: Boron; Calcium; Chloride; Chromium; Cobalt; Copper; Fluorine; Iodine; Iron; Magnesium; Manganese; Molybdenum; Nickel; Phosphorus; Potassium; Selenium; Sodium; Sulphur; Trace elements; Ultra-trace elements; Zinc

Minimal metabolism There is no standard condition at which a minimal metabolic rate can be both defined and accurately measured for animals. Discounting exceptional conditions, such as hibernation and prolonged starvation, minimal metabolic rates are attained only after complete digestion of the last meal (and this takes longer than 24 h in ruminants) and whilst the animal is lying down. The conditions cannot be enforced on animals for long enough for measurement of fasting metabolism. What is usually measured is the resting metabolism of an animal provided with a **maintenance** diet. When this measurement is made continuously over a long period combined with observation of the animal's behaviour, it is possible to select periods when the animal is lying down and determine its least observable metabolic rate. All of the above have been used from time to time as estimates of basal metabolic rate, which is used as the reference level for interspecies comparisons and from which to assess metabolic increases caused by activity, feeding, thermoregulation, etc. (JAMcL)

See also: Basal metabolism; Fasting metabolism

Mobile nylon bag technique: *see* Digestion; *In sacco*

Models: *see* Growth models; Simulation models

Moisture: *see* Dry matter

Moisture content, determination: *see* Dry matter

Molasses A thick treacly liquid, a by-product of sugar production from both sugarcane and sugarbeet. (MFF)

See also: Sugarbeet; Sugarcane

Mollusc culture Molluscs are arguably the most important animal phylum for aquaculture production from marine and brackish waters. Over 80% of marine aquaculture production is accounted for by filter-feeding shellfish, the majority of which are bivalve molluscs such as oysters, mussels, clams and cockles. Their culture extends back several thousand years and it is difficult with some species to know whether they are in fact wild or cultivated. Bivalves in particular have a wide range of human intervention in their culture. Mussels, for example, may be grown by setting out lines or posts in the water for the spat (young bivalve) to settle upon, or harvested directly from wild spat that sets on cultivated oysters.

A wide range of technologies has been developed to facilitate the capture of the spat and the harvesting of the final product. Oyster culture may rely on the capture of free-living spat spawned from either wild or cultivated stocks, or upon seed produced from selected brood stock in a hatchery. The collected seed may be grown to a marketable size in racks or trays, or in suspension, or simply scattered back on to the bottom. The advantages of off-bottom culture are that there is better control over losses due to predation, survival is usually better and harvesting is more efficient, but the costs, both for capital and labour, are considerably higher.

A recent worldwide trend in scallop fisheries is the use of enhancement techniques. Scallop seed are captured by setting out collectors at an appropriate time of the year, and the small scallops are grown for a period in small-mesh nets suspended in the water. When they have grown past the size where they are vulnerable to predation, they are released back on to the scallop grounds for harvesting by traditional methods. By careful selection of the areas seeded and scheduling of the areas harvested, it is expected that growth rates and survival will be maximized, and overall harvest will increase.

Filter-feeding shellfish have the capacity to consume and become contaminated by bacteria and also by toxin-producing phytoplankton. Accordingly, technologies have been developed, and agreed upon internationally, for the testing and inspection of shellfish to ensure that they are safe to eat. In some circumstances shellfish that are marginally contaminated may be depurated (cleansed) or otherwise processed to ensure that they meet appropriate health standards and pose no risk to consumers.

Increasing harvesting pressure, and reduction of available habitat for wild marine stocks and for terrestrial species such as escargots (snails), is stimulating the rapid development of technologies for species not hitherto grown in controlled conditions, or for species introduced from other parts of the world. Examples of the former are abalones and geoducks, now being cultivated in Canada. Worldwide the most important oyster grown (3.4 million tonnes in 1998) is now the Pacific oyster, *Crassostrea gigas*, which has supplanted native oysters in many countries. Examples of other species that are successfully cultivated outside their normal range are the bay scallop, *Argopecten irradians*, into China, and the Manila clam, *Tapes philippinarum*, into western North America and western Europe.

(DJS)

See also: Mussel culture; Shellfish culture

Molluscs Molluscs have been used as food in subsistence economies since before recorded history and are extensively fished by traditional harvesting methods. They are also cultivated by a variety of technologies ranging from simple capture of juveniles for on-growing in ponds or lagoons, to elaborate procedures involving hatcheries, nurseries and complex grow-out and harvesting systems.

They have a wide diversity of life forms ranging from the free-ranging and sometimes migratory squids and cuttlefishes, with their internal shells, through the filter-feeding double-shelled bivalves, to the single-shelled snail-like gastropods. Others, such as the nudibranchs, have internal shells and external gills. They occupy all the oceans from polar seas to the tropics, and are also common in fresh water. Some of the gastropods are wholly terrestrial. Their feeding habits range from filter feeding, browsing on marine algae and epiphytes, to aggressive predation.

Total recorded landings of molluscs from all sources, wild and cultivated, in 1998 exceeded 15.6 million tonnes (Mt) (FAO data), of which over 9 Mt were cultivated. More than 3.5 Mt of these cultivated shellfish were oysters (principally the Pacific oyster, *Crassostrea gigas*), 2.2 Mt were clams and cockles, 1.4 Mt were mussels and 0.8 Mt were scallops. Many of these groups were also harvested in capture fisheries but by far the majority were cultivated. The most important group in the capture fisheries are cephalopods (squids, octopus, cuttlefish) with 2.6 Mt landed in 1998. Very few of this group are cultivated. By far the majority of molluscs are grown or fished in marine waters. Freshwater landings account for barely 600,000 t and few of these are cultivated.

Some molluscs may be eaten alive and raw; oysters particularly are considered a delicacy and support a valuable ‘half-shell’ trade, but mussels, clams and scallops may also be eaten this way. This practice requires careful attention to the cleanliness of the water in which they are grown to ensure that the shellfish are wholesome, and also to their storage and transport to ensure that quality remains high and there is no spoilage. Some may be cooked and dried; others are canned. Where distribution systems allow, many species are simply sold raw for preparation in traditional dishes.

Besides being used directly as human food, some species, e.g. the squids, are used as bait in other capture fisheries and so contribute to the fisheries economy in a different way. Some are rendered as meal. An interesting and profitable non-food use is the culture of pearl oysters for both pearls and mother of pearl. (DJS)

Molybdenum Molybdenum (Mo) is a mineral element with an atomic mass of 95.94. It exists in biological systems in a number of oxidation states, but the most common are +4, +5 and +6. Molybdenum is generally found in nature as compounds with sulphur and oxygen. It is readily absorbed from the diet via the intestinal cells; the transport mechanism seems to be passive. The mineral, at approximately 5 nmol l^{-1} plasma, is transported in the blood bound to proteins. Erythrocytes may contain 10 times the amount in plasma. Both concentrations can vary depending on the amount consumed.

Molybdenum is an essential component of at least three mammalian enzymes: xanthine dehydrogenase, aldehyde oxidase and sulphite oxidase. These enzymes catalyse redox reactions that pass electrons to cytochrome *c*, molecular oxygen, or NAD^+. Sulphite oxidase is an important Mo-containing enzyme that catalyses the final steps in the degradation of sulphur amino acids. Recent evidence suggests that each of these enzymes contains a Mo-containing co-factor called molybdopterin. The co-factor is apparently essential for full activity, because in human genetic disorders expressing Mo co-factor deficiency the activities of all enzymes are reduced. Although Mo is essential for the activity of these important enzymes, it has been rather difficult to produce Mo deficiency signs in animals. While Mo is probably essential for farm animals, no requirement levels have been set for any of the species except sheep (0.5 mg kg^{-1} diet).

Of the farm animal species, ruminants seem to be the most sensitive to Mo toxicosis, and in many cases the amount that produces toxicosis depends on the sulphate concentration in the diet. A dietary concentration of 100 mg Mo kg^{-1} diet can produce signs of toxicity, but with 0.3% sulphate present the effective Mo concentration is lowered to 40 mg kg^{-1} diet. The US National Research Council (NRC) recommends a maximum of 5 mg Mo kg^{-1} diet for cattle and 10 mg kg^{-1} for sheep. Poultry have decreased growth rates while consuming diets with 500 mg Mo kg^{-1} but pigs have shown no adverse effects at 1000 mg Mo kg^{-1} diet. (PGR)

See also: Copper; Sulphates; Sulphur

Further reading

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Monoacylglycerol Glycerol in which one hydroxyl group is esterified with a fatty acid. Also called monoglycerides, monoacylglycerols rarely occur naturally in plant or animal fats but are formed during the digestion of triacylglycerols in the small intestine. (JAM)

See also: Fats; Lipids; Triacylglycerols

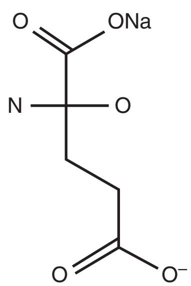
Monoenoic fatty acid A fatty acid containing one double bond written C=C or Δ. The double bond can support either the *cis* (the usual case) or the *trans* configuration. Also called monounsaturated fatty acid. Examples include palmitoleic (*cis*-9-hexadecenoic, 16:1 n-9 (Δ^9)), oleic (*cis*-9-octadecenoic, 18:1 n-9 (Δ^9)), elaidic (*trans*-9-octadecenoic, 18:1 n-9 (Δ^9)), gadoleic (*cis*-9-eicosenoic, 20:1 n-11 (Δ^9)), erucic (*cis*-13-docosenoic, 22:1 n-9 (Δ^{13})) and nervonic (*cis*-15-tetracosenoic 24:1 n-9 (Δ^{15})). (NJB)

Monoglyceride: *see* Monoacylglycerol

Monosaccharides Usually unbranched molecules of three to seven carbons, all of which bear a hydroxyl group except for one that exists as a carbonyl group. If this is on a terminal carbon it gives an aldehyde; if on an internal carbon it gives a ketone. Three-carbon aldo monosaccharides are called trioses;

those with four to seven carbons are called tetroses, pentoses, hexoses and heptoses, respectively. (JAM)
See also: Carbohydrates

Monosodium glutamate (MSG) $COOH{\cdot}(CH_2)_2{\cdot}CH(NH_2){\cdot}COONa$, the sodium salt of L-glutamic acid. It is used as a flavour enhancer. Adverse reactions to it have been reported.



(NJB)

Monounsaturated fatty acid: *see* Monoenoic fatty acid

Motilin A polypeptide hormone produced in the duodenum and jejunum under the stimulus of acetylcholine. Its function is probably to regulate the motility of the gut in the period between meals. (SB)
See also: Gastric emptying

Motility Movement of the gut wall, which can be of a propulsive, retentive or mixing nature. Changes in motility affect the retention time of the digesta and may result in diarrhoea or conversely constipation. (SB)
See also: Gastrointestinal tract

Moulds: *see* Fungi

Moulting An organized loss of feathers that occurs naturally. A juvenile moult occurs during the growing period at about 3 months of age, when the growth of new feather papillae pushes the old feathers out. An adult moult, which occurs spontaneously at the end of an individual bird's laying cycle, is caused by a complex interaction of hormones. It is accompanied by a cessation of egg production, regression of the reproductive organs and typically a 20–30% loss in body weight.

Moulting may be induced by manipulations of management when economic circumstances suggest that two shorter laying cycles are more profitable than one longer one. This is usually initiated between 50 and 60 weeks of age (prior to the age-related decline in shell quality). Possible nutritional manipulations include quantitative nutrient restriction, and *ad libitum* diets containing low sodium, low calcium or high zinc. A drastic reduction in photoperiod and illuminance also encourages the termination of egg-laying. A week before the moult, insoluble grit (5 g per bird) is given to minimize the incidence of crop impaction caused by birds ingesting feathers. For the first 10 days of the moult, the bird only receives a small quantity (15 g day^{-1}) of oats or barley, which is increased to 30–60 g day^{-1} by 3 weeks. The bird is then returned to *ad libitum* feeding of a layer diet and transferred to a stimulatory photoperiod. (PDL)

Mucin A class of large glycoproteins consisting of linear or branched oligosaccharide chains attached to a protein core, much like the bristles on a bottle brush. Mucins are secreted by epithelia of the respiratory, intestinal and urogenital tracts and, in some amphibians, the skin. Gastrointestinal mucins have 60–85% of their weight as carbohydrate, consisting of five sugars, fucose, galactose, *N*-acetylglucosamine, *N*-acetylgalactosamine and sialic acid. The protein core has a distinct amino acid composition, with serine and threonine comprising 25–60%. The hydroxyl groups on the side chains of these amino acids link to the oligosaccharides. Proline accounts for about 15% of the total amino acid residues and is thought to inhibit α-helix formation, which would prevent protein folding and limit glycosylation. Average molecular weight 2×10^6. (JAM)
See also: Carbohydrates; Fucose; Galactosamine; Galactose

Mucopolysaccharides: *see* Mucin

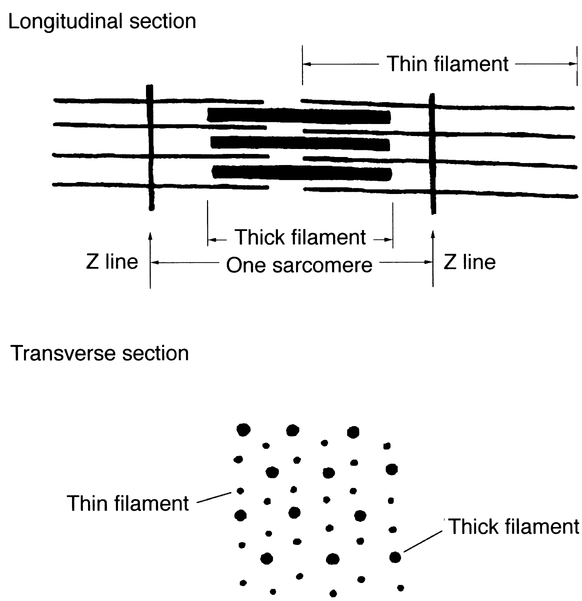
Mucoproteins: *see* Mucin

Mucosa The layer of mucosal cells covering the inner surface of the digestive tract and other body cavities. The mucosa includes several different types of specialized cells (e.g. those for the secretion of mucus (mucopolysaccharides and mucoproteins) which protects the mucosa from attack by proteolytic enzymes). In the stomach, the mucus forms a flexible gel that coats the mucosa. The cells in the surface secrete HCO_3^- which, together with the mucus, forms an unstirred layer with a pH of about 7.0. (SB)

See also: Gastrointestinal tract; Intestinal mucosa

Muscle In the live animal, muscle is a contractile tissue capable of generating force. This property therefore allows locomotion, maintenance and control of posture and regulation of the function of the heart and vascular system, respiratory, gastrointestinal, renal and reproductive tracts and other systems. There are thus three fundamental classes of muscle: skeletal, smooth and cardiac. The growth and development of muscle tissue may be understood through examination of the structure and cellular characteristics. Skeletal muscle is a syncitium formed from single nucleated mesodermal cells. During terminal differentiation these form myoblasts, which fuse to form myotubes and then give rise to the multinucleated muscle fibres. These, in turn, produce myofibrils made up of two types of contractile protein filaments: thick and thin. In skeletal and cardiac muscle the filaments are arranged in units called sarcomeres, consisting of one set of thick filaments (myosin) and two sets of thin filaments (actin). During contraction the thin filaments are pulled over the thick filaments by cross-bridge formation so that the sarcomere shortens and generates the force of contraction.

The numbers of muscle fibres present and formed from the fusion of differentiated myoblasts to yield myotubes in the developing embryo become fixed before or shortly after hatching or birth. During the postnatal growth of the animal the growth of muscle occurs only by hypertrophy (increase in cell size), not by hyperplasia (increase in cell number). Muscle cell hypertrophy occurs by two mechanisms: increase in cell circumference or 'girth' and increase in length. Myofibrillar content of growing muscle fibres increases as each myofibril reaches a critical size and then



Arrangement of the thick and thin filaments.

splits or divides into two or more daughter myofibrils. During growth the number of nuclei in the muscle also increases, due to the incorporation of satellite cells into the fibres. Satellite cells are undifferentiated precursor muscle cells or myoblasts with high nucleus:cytoplasm ratios and are located between the membrane and basal lamina of the muscle fibre. These cells fuse mainly with the growth regions towards the ends of the fibres. Increases in muscle fibre length during growth are a consequence of the addition of new sarcomeres at the ends of existing myofibrils. The growth region is thus at the myo-tendon junction. During long bone growth and muscle stretching, the insertion of additional sarcomeres allows adjustment of sarcomere length to that which is optimal for muscle contractile function.

The growth potential of a muscle may be determined by two factors. the first of which is the number of myoblasts present before fusion during embryonic development. Increased myoblast formation during the proliferative phase of development will increase the final number of muscle fibres and thus muscle mass. Secondly, as satellite cells contribute many nuclei during secondary generation of myofibres, it may be proposed that the abundance of these cells may determine the ultimate size to which a muscle can grow. Research into the regulation of myoblast proliferation and satellite cell function may provide the basis for further improvements in muscle growth in meat animals. (MMit)

See also: Body composition; Growth; Growth factors; Meat composition; Skeletal muscle

Key reference

Goldspink, G. and Yang, S.Y. (1999) Muscle structure development and growth. In: Richardson, R.I. and Mead, G.C. (eds) *Poultry Meat Science*. CAB International, Wallingford, UK, pp. 3–18.

Muscular diseases Nutritionally related disorders of the muscular tissue fall into two major categories: those associated with muscle cell degeneration and those affecting the ability of the muscle to function without altering muscle architecture. Deficiencies of selenium or vitamin E result in destruction of muscle cell membranes and proteins. This is due to an accumulation of free radicals and peroxides that are normally scavenged by the selenium-containing protein glutathione peroxidase and by vitamin E. Both skeletal and cardiac muscle are affected, though in ruminants skeletal muscle changes are more prominent, while in pigs cardiac muscle changes are more prevalent. Toxic principles from plants (e.g. gossypol in pig feed) can also induce necrosis of muscle cells. Muscle dysfunction diseases are often secondary to electrolyte imbalances that interfere with nerve transmission, resting membrane potential or action potential conduction within the muscle. Nutritionally related disorders, resulting in low blood concentrations of calcium, magnesium, or potassium, are generally characterized by muscle weakness or tetanic contraction of muscle. (JPG)

See also: Selenium; Vitamin E

Mushrooms The fleshy fruiting bodies of fungi. In North America alone, 10,000 species of mushroom exist, of which 250 are edible and 250 are poisonous while the nature of the remainder is uncertain. Most of the edible species are gathered from the wild but some are cultivated. Mushrooms can be fed to ruminants at low inclusion rates (5–10%) but large quantities are unlikely to be available for animal feeding. The nutrient composition (g kg^{-1}) of mushrooms is crude protein 201, crude fibre 135, ether extract 101, salt 31, and total free amino acids 32.96–109.69 (mg g^{-1}), and they are rich in B vitamins. (JKM)

Mussel culture Mussels grow almost everywhere on hard surfaces in shallow marine and brackish waters. They can be a nuisance to mariners, and in the cooling systems of boats and coastal generating stations. Mussels are fast growing, and have been harvested and cultivated as food for centuries.

Typically a mussel farmer will moor a series of lines suspended just below the surface of the water in anticipation of newly metamorphosed mussel larvae settling on them. These small mussels adhere to the ropes by their byssus threads and begin to grow, filtering phytoplankton from the water.

Typically mussels are cultured on lines, from which they are harvested when they reach market weight.

Depending on location and species, the mussels may be stripped off the collecting ropes when they have grown to 10–20 mm long, and transferred to other systems for grow-out. This usually requires that the mussels be wrapped, along with another rope, in a cotton gauze material that will rot and fall away after the mussels have re-fastened themselves to the rope. Alternatively the mussels may be stuffed into a plastic mesh tube of such a size that individual mussels can just crawl through the mesh. These 'socks' or 'sleeves' of mussels are suspended just below the surface of the water, while the mussels grow to marketable size. The suspension technology varies from place to place. In western France, mussel ropes are wrapped around posts (*buchots*) set in the mud. Elsewhere they may be suspended from 'tables' set into the bottom, from floating rafts, or from anchored long lines, buoyed at the surface to keep the mussels clear of the bottom. Several species of blue and green mussels are cultivated worldwide. Landings exceed 1.4 million tonnes.

There has been rapid technological development to aid farmers in setting their gear, collecting and socking spat, and in mechanical harvesting. Artisanal techniques are still effective and profitable in some areas. (DJS)

Mustard The common name of a group of related brassicas. White mustard (*Brassica hirta* Moench or *Sinapis alba* L.), black mustard (*B. nigra* Koch) and Indian or leaf mustard (*B. juncea* Coss) are cultivated primarily for their oily seeds and as a condiment. Mustard can be grown as a cover crop which may be fed green and forage mustard has a metabolizable energy content of 9.0 MJ kg^{-1} dry matter. Mustard oil cake or meal, which is a by-product of mustard oil production, is fed to animals. For animal feeding the toxic glucosides, which can affect the thyroid gland, must be removed. This can be achieved by steaming for 2 h and extraction of the ground seed with water. This causes a reaction between the enzyme myrosinase and the glucoside. In black mustard, myrosinase reacts with the glucoside sinigrin to produce a volatile irritating oil but in white mustard it reacts with the glucoside sinalbin and the oil produced is less irritating. The extracted meal can be fed to adult ruminants (< 1.5 kg day^{-1} or 7.5% of the diet in adult cattle) but must be given with more palatable feeds to prevent reduced feed intake. In diets for calves, solvent-extracted meal can completely replace soybean or groundnut meal but mustard expeller meal should not replace more than half. In poultry diets, low-glucoside mustard seed *B. juncea*, *B.*

Typical composition of mustard products.

	Dry matter ($g\ kg^{-1}$)	Nutrients ($g\ kg^{-1}$ DM)						
		Crude protein	Crude fibre	Ash	Ether extract	NFE	NDF	Glucoside ($\mu mol\ g^{-1}$)
Forage mustard	150	193	–	–	–	–	–	–
Oilcake								
Mechanically extracted	898	385	35	99	107	374	–	–
Solvent extracted	880	260	182	76	23	459	–	–
Low glucoside								
B. juncea	–	459	–	–	–	–	297	34
B. napus	–	446	–	–	–	–	132	22
B. rapa	–	431	–	–	–	–	196	25
High-glucoside meal	–	300–320	120–130	–	190–220	–	–	–
Wild mustard meal	48	260	134	44	335	–	–	92
Dehulled and defatted meal	–	480	38	70	–	–	–	230

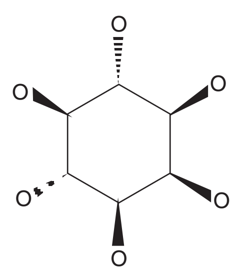
NDF, neutral-detergent fibre; NFE, nitrogen-free extract.

napus and *B. rapa* can be used as a 1:1 replacement of canola meal, but high-glucoside meals should not exceed 10% of the diet. (JKM)

Mycotoxins Toxic metabolites of fungi. Those of concern are produced by fungi that grow on grain crops in the field or during grain storage. Major fungal genera producing mycotoxins include *Aspergillus*, *Penicillium* and *Fusarium*. *Aspergillus flavus* and *A. parasiticus* produce aflatoxins (AF). The mycotoxin citrinin (CT) is a nephrotoxin, produced by several species of the genus *Penicillium* and three species of *Aspergillus*. The principal CT-producing fungus in feeds is *P. viridicatum*. Ochratoxins (OA) are produced by several *Aspergillus* and *Penicillium* species. OA is a potent nephrotoxin. Other mycotoxins produced by *Aspergillus* and *Penicillium* include cyclopiazonic acid (CPA), kojic acid and rubratoxins. *Fusarium* mycotoxins include zearalenones (Z), fumonisins (F), moniliforme, fusarochromanone, fusaric acid and various trichothecenes such as T-2 toxin, diacetoxyscirpenol (DAS) and deoxynivalenol (DON). Major pathologies induced by mycotoxins include liver damage (AF, F), kidney lesions (AF, CT, OA), hyperoestrogenism (Z), vomiting and feed refusal (trichothecenes) and neurological degeneration (F). Mycotoxins associated with forages include ergot alkaloids (endophyte-infected tall fescue) and lolitrems (perennial ryegrass staggers). (PC)

Myelin Myelin is composed of plasma membrane from Schwann cells in the peripheral nervous system and oligodendrocytes in the central nervous system of vertebrate animals. The so-called myelin sheath is composed of multiple layers of specialized membranes that are rich in glycolipids and act as insulation to promote high conduction velocities in small-diameter nerve fibres. (GG)

Myo-inositol *cis*-1, 2, 3, 5, *trans*-4, 6-Hexahydroxycyclohexane, $C_6H_{12}O_6$, one of the two optically active forms of inositol. In animals, inositol is found in cell membranes as phosphatidylinositol and phosphatidylinositol 4,5-bisphosphate. Phosphatidylinositol 4,5-bisphosphate is the connection between a cell membrane hormone receptor and rapid changes in cellular concentrations of calcium. (NJB)



Myopathy Any degenerative disease of cardiac or skeletal muscle. Most common of the nutritional myopathies are those caused by vitamin E or selenium deficiency. Vitamin E is important for protection of cell membranes as it is the only antioxidant capable of quenching free-radical peroxides generated within cell membranes during the course of muscle metabolism. Vitamin E is found in fresh green forages and vegetables. It is one of the fat-soluble vitamins, which allows it to act within the lipid bilayer of cell membranes. Selenium is an essential component of the enzyme glutathione peroxidase, which converts highly reactive forms of oxygen such as hydrogen peroxide and superoxide anion free radicals to harmless compounds such as water by donating hydrogen ions. Glutathione peroxidase protects the cytosol of the cell from free radical damage. In areas where the soil is deficient in selenium, plants may not provide enough selenium to meet the dietary requirement of the animals fed those plants. A deficiency of either vitamin E or selenium can allow free radicals to accumulate, resulting in degeneration of muscle fibres.

Selenium deficiency is most common in ruminants, particularly young calves and lambs, and causes the syndrome known as white muscle disease. The muscles of affected animals are pale and have white streaks running across them. Histologically, muscle degeneration begins at the Z lines with loss of myofibre structure and swelling of sarcoplasmic membranes. In lambs, this syndrome primarily affects skeletal muscle; in calves, the cardiac muscle is also affected. Vitamin E deficiency exacerbates the selenium deficiency but is rarely the sole cause of white muscle disease in ruminants. In pigs, selenium or vitamin E deficiency primarily affects cardiac muscle but other organ systems may also be involved. In poultry, the breast muscles are most commonly affected.

Toxic plant substances (e.g. gossypol in pig diets) can also cause degeneration of muscle. Common infectious diseases that can also cause muscle degeneration include the clostridial diseases, such as black leg and malignant oedema. (JPG)

See also: Muscular diseases; Selenium; Vitamin E

Myosin A protein found in muscle and tissues with motile function. It is the major protein component of the thick filament (about twice the diameter of actin) backbone that combines with actin to produce muscle contraction in which adenosine triphosphate (ATP) provides the energy. Myosin accounts for 55% of total muscle protein. (NJB)

Myristic acid Tetradecanoic acid, a saturated long-chain fatty acid, $CH_3{\cdot}(CH_2)_{12}{\cdot}COOH$, shorthand designation 14:0; molecular weight 228, with melting point of 53.9°C. A major component of coconut and palm oils; also present in human milk, dairy fat (e.g. 10–15% of the fatty acids in butter), poultry fat, nutmeg and myrtles. (NJB, JAM)

See also: Fatty acids

Myrosinase Beta-thioglucoside glucohydrolase (EC 3.2.3.1). The only known natural *S*-glycosidase plant enzyme, its principal activity is the hydrolysis of glucosinolates to isothiocyanates. It is activated by L-ascorbic acid and competitively inhibited by sulphate reaction products. It is a dimer with an apparent molecular mass of 120 kDa, and is isolated from *Raphanus sativus* (daikon). It is stabilized by a Zn ion and is heavily glycosylated. It has a hydrophobic pocket, ideally situated for the binding of the hydrophobic side chain of glucosinolates with two arginine residues positioned for interaction with the sulphate group of the substrate. The complete structure of a plant-specific heptasaccharide is observed at one glycosylation site. (JDO)

N

N-nitroso compounds Nitrosamines are formed by nitrosation of secondary, tertiary and some primary amines and of quaternary ammonium compounds. They can also be formed by reaction of amines with nitrate and thus may be formed within foods or feeds that are preserved with nitrates or nitrites. They are of concern because many are carcinogenic. Fish preserved with high levels of nitrite may be highly carcinogenic. Methylamines are abundant in fish tissue and readily react with nitrate to form nitrosamines. Nitrosamides are also powerful carcinogens.

(PC)

Naphthoquinones A class of aromatic diketones in which the carbonyl groups are part of the ring structure. One of the three possible quinones derived from naphthalene, $C_{10}H_{18}$, a double unsaturated ring structure, is 1,4-naphthoquinone, the ring structure of menadione, phylloquinone and menaquinone-7, all biologically active forms of vitamin K. Others are 1,2- and 2,6-naphthoquinones.

(NJB)

Near infrared (NIR) spectroscopy An analytical technique involving absorbance processes associated with overtones and combination bands of vibrational transitions in molecules that occur in the region of 730–2500 nm. The spectra observed involve mainly hydrogen-bearing groups, e.g. C-H, O-H, N-H bands.

NIR spectra of foods can provide a basis for instant multiple analyses of their composition using correlation transform spectroscopy. Sugars, starch and cellulose ($C_x(H_2O)_y$) are all polyhydroxy aldehydes and ketones rearranged as hemi-acetal ring monomers: thus, carbohydrate is characterized by -O-H stretching overtones of the hydroxymethylene group. Lipids, being long hydrocarbon chains, are characterized by predominant hydrocarbon $-CH_2-$ bands, mainly associated with the methylene group. Protein is characterized by -CONH- linkages between constituent amino acids and so the characteristic feature of protein molecules is the nitrogen in the peptide bond adjacent to a carbonyl group C=O. Spectra of an intact food are a summation of all its components.

NIR is used for the routine quantitative determination of water, proteins, low-molecular-weight hydrocarbons and fat in the agricultural, food, petroleum and chemical industries. In NIR spectroscopy, NIR light is applied to the specimen and the reflected or transmitted spectra are used in multivariate calibration models to predict the chemical composition or attributes such as digestibility of forages. NIR spectroscopy is an important tool for the routine quantitative determination of constituents in ground solids. This includes the analysis of agricultural products such as oilseed and grains for the determination of protein, moisture, starch, oil, lipids and cellulose.

NIR is calibrated by scanning large sets of typical samples of one kind having a wide range in composition. The resulting spectra are used to select a representative subset of samples for reference analyses using traditional analytical methods. The reference values obtained are then used to construct a calibration model that maps spectra on to chemical composition, using internal cross-validation to gauge performance. Multivariate statistical methods such as multiple linear regression or partial least squares are used in the modelling process. The composition or quality of any subsequent unknown sample is then predicted from its spectrum by using the calibration model. Analysis by NIR is different from separation methods such as chromatography in that the intact sample matrix is examined and contributes to the analysis. On the grounds of speed and precision, NIR is often the only cost-effective quality control method for routinely testing food commodities. (JEM, IM)

Neem (*Azadirachta indica* A. Juss) An evergreen tree, found widely in Asia and the tropics, with many medicinal uses. Leaves can be used as an emergency famine feed. Neem seed cake is the residue left after the extraction of oil from seeds; it can be used for fertilizer or feed. Approximately 100,000 t of neem seed cake is available annually in India alone. The cake contains around 15% crude protein (see table) but is not very palatable, having a bitter taste due to the presence of nimbidin. Treatment with 1% NaOH, followed by washing with water, will reduce the level of nimbidin. Levels of the cake in poultry concentrate should be limited to 5%, but higher levels can be used in rations for growing cattle. The optimum level of inclusion for sheep is 25%. (LR)

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Robards, G.E. and Packham, R.G. (1983) *Feed Information and Animal Production.* Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Nervonic acid A 24-carbon monounsaturated fatty acid, *cis*-15-tetracosenoic, 24:1 n-9 (Δ^{15}). It is found in nervous tissue. (NJB)

Net energy That part of the gross energy that is used for the animal's **maintenance**, retained as product or used for work. It is equal to the metabolizable energy minus the **heat increment of feeding**. The net energy system of assessing total feed requirements for cattle has now been largely replaced by the metabolizable energy system. (JAMcL)

See also: Energy systems

Net protein ratio (NPR) A measure of protein quality. In the assay, growing animals (usually rats or chicks) are given a diet containing the test protein (or mixture of proteins) for a set period (commonly 10 days to 4 weeks). NPR is calculated from the weight gain of the test group (T), the weight loss of a similar group of animals given a protein-free diet (C) and the amount of crude protein consumed by the test animals (P) as:

$$NPR = (T + C)/P$$

Unlike protein efficiency ratio (PER), the assay takes account of the use of the protein in meeting the animal's maintenance requirements. (NJB)

Typical composition of neem products (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh leaves	35.8	14.4	13.7	10.8	5.2	56.0	2.29	0.20
Neem seed cake		15.4	22.2	15.0	6.0	42.0		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Digestibility (%) and ME content of neem products.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Leaves	52.0	23.0	58.0	68.0	8.51

Net protein utilization (NPU) One of the systems used to evaluate the quality of protein(s) for use in human and animal diets. It is defined as the percentage of the dietary protein retained. The value of dietary protein (therefore, not a single protein) is estimated by use of an animal growth trial. This method involves measuring total body nitrogen in a group of experimental animals (groups of 4 or more rats) which have consumed a protein-free diet and another group fed a similar diet containing the test protein. After the animals have consumed the diets for the desired time (10 or more days) the value of the protein is estimated using the formula for NPU:

NPU = 100 × ((Body N of test group) – (Body N of protein-free group))/(Nitrogen consumed) (NJB)

Key reference

Hegsted, D.M. (1974) Assessment of protein quality. In: *Improvement of Protein Nutriture*. National Academy Press, Washington, DC, pp. 64–88.

Neurotransmitter A chemical that functions at the junctions (synapses) between two nerve cells (axon to dendrite) or between a nerve cell and a cell of another type such as muscle (neuromuscular junction) or a gland. The presynaptic neuron has at its termination synaptic vesicles containing neurotransmitters (e.g. acetylcholine, serotonin). In response to an impulse the synaptic vesicles release the neurotransmitter into the synaptic cleft, where it migrates 20–40 nm across the junction to affect the nerve or muscle, etc. The term neurotransmitter applies to individual chemicals such as acetylcholine or to classes of chemicals such as amines, excitatory or inhibitory amino acids, polypeptides, purines, gases or lipids. (NJB)

Key reference

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Neutral-detergent fibre (NDF) An insoluble matrix prepared by the extraction of food plants and mixed feeds in a solution of sodium dodecyl sulphate (SDS) and ethylenediamine tetraacetic acid (EDTA) in a phosphate buffer at pH 7. NDF is an estimate of the cell wall fraction of forages and mixed feeds. Cell wall polysaccharides (with the exception of pectin), lignin and cutin are the major components of NDF from forages. Proteins, lipids, non-structural polysaccharides and other cytoplasmic constituents are removed by the extraction. NDF is used to measure the amount of cell wall in foods and to determine fibre digestibility. Within the context of the detergent system of forage analysis, NDF separates completely available food components that are nutritionally uniform from those feed components that are only partially available or completely unavailable for digestion. The detergent system of forage analysis was developed by Van Soest to replace the fibre analysis of the Weende system with a more rational and easily applied system. Digestibility of a forage is estimated by analysis of NDF and an estimate of the degradability of NDF by lignin analysis, *in vitro* degradability of NDF or enzymatic degradability with fungal cellulases. (JDR)

Neutron activation analysis (NAA) An extremely sensitive, non-destructive technique used for the determination of about 69 elements. The technique involves the bombardment of the sample with neutrons to convert stable elements to radionuclides, which are subsequently measured by the radioactivity they emit as they decay. The method allows trace multi-element analyses with minimal sample preparation in various matrices such as food, fuel, drugs, fertilizers, minerals and water. (JEM)

Newborn animals The first needs of newborn animals are for food and warmth. Because they have a high ratio of surface area to body weight, and because they are wet, newborn mammals and newly hatched birds are susceptible to hypothermia, which then limits their ability to find shelter and food. The first nutritional need of newborn mammals is for **colostrum** to provide passive immunity against infections, particularly of the gastrointestinal tract. The capacity to absorb immunoglobulins intact is short-lived and ani-

The first needs of newborn animals are for food and warmth.

mals should receive adequate amounts of colostrum immediately after birth. Recommended amounts and maximal permitted delays after birth are: foal 12 hours; calf 6% of body weight within 6 hours; lamb 20% body weight over the first 18 hours; piglet 40 ml in two feeds within 4–6 hours of birth. As well as providing antibodies, colostrum of all species is rich in vitamins A, D and B_{12}, which do not cross the placenta easily, and also growth factors such as insulin-like growth factors I and II which stimulate early development.

Newborn animals have great growth potential and need sufficient dietary energy to make full use of this. For example, piglets will consume food equal to four times their basal metabolic rate for the first few weeks. A high energy intake also helps to prevent hypothermia. Iron supplementation is necessary for housed pigs.

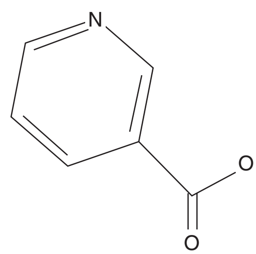
Milk replacers should closely resemble the natural product, with well-dispersed fat, and cautious use of unnatural sugars such as sucrose, which are not well digested by the newborn.

For chicks early feed intake is critical, as residual yolk is quickly absorbed. Transportation may delay feed intake and starvation of chicks at this critical point can compromise long-term growth and immune function.

(JKM)

See also: Calf; Colstrum; Piglets; Weaning

Niacin One of the B-vitamins, known as the antipellagra vitamin. The vitamin activity is possessed by niacin (nicotinic acid; pyridine-3-carboxylic acid; $C_5H_4{\cdot}COOH$) and its amide, niacinamide (nicotinamide; $C_5H_4{\cdot}CO{\cdot}NH_2$). Pellagra, a disease of humans, was once prevalent in populations who were dependent on maize as their main food. Rapid progress in the solution of the pellagra problem was made after it was realized that 'black-tongue', a condition in dogs fed a pellagra-producing diet, could be cured by nicotinic acid.



The niacin-containing coenzymes NAD^+ (**nicotinamide adenine dinucleotide**) and $NADP^+$ (nicotinamide adenine dinucleotide phosphate) are produced by all the tissues in the body. In metabolism, niacin functions in oxidation–reduction reactions as an essential component of the co-factors NAD^+ or $NADP^+$. NAD^+ or $NADP^+$ participates as a co-factor in many dehydrogenase reactions.

Generally, NAD^+ is linked to dehydrogenases that catalyse oxidation–reduction reactions in catabolic (oxidative) pathways involving enzymes such as lactate dehydrogenase in the cytoplasm or malate dehydrogenase in mitochondria. $NADP^+$-linked dehydrogenases or reductases are often connected with systems involved with reductive synthesis such as the pentose cycle, providing reducing equivalents for the biosynthesis of fatty acids from two carbon acetyl-CoA units.

Niacin is widely distributed in plant and animal tissues. Foods such as fish, meat, milk, cereals, legumes and green leafy vegetables are good sources. NAD^+ and $NADP^+$, as the vitamin co-factors in which niacin is incorporated, are found in food and are absorbed as nicotinamide after the vitamin co-factors have been hydrolysed by enzymes in the intestinal mucosa. At low concentrations they are absorbed in the stomach and intestine by a sodium-dependent facilitative diffusion process. At high concentrations they are absorbed by diffusion. Niacin can be synthesized from L-tryptophan, but not in quantities that meet the requirement. Conversion efficiency of tryptophan to niacin is affected by the vitamin B_6, vitamin B_2 and iron status of an individual. In the laboratory rat, ~ 40 mg of L-tryptophan are required to produce 1 mg of niacin.

Niacin is excreted in the urine as a methylated derivative, N^1-methylnicotinamide, and as N^1-methyl-2-pyridone-5-carboxamide and N^1-methyl-4-pyridone-5-carboxamide along with minor amounts of niacin, niacin oxide and the hydroxyl form of niacin. Urinary excretion of N^1-methylnicotinamide and N^1methyl-2-pyridone-5-carboxamide have been used to assess niacin status. The requirements of non-ruminant animals are in the range 10–30 mg kg^{-1} diet. (NJB)

Key reference

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Niacinamide: *see* Niacin

Nickel Nickel (Ni) is a transition element with an atomic mass of 58.693. It exists in six oxidation states, but Ni^{2+} is the principal form in biological systems. Nickel is found in the earth's crust at about 100 mg kg^{-1}; however, Ni concentrations in animal feedstuffs are low, ranging from 0 to 3 mg kg^{-1}. The absorption of Ni from the intestinal tract is very low relative to some other trace metals; it ranges from 1% to 10% of intake. The rate of absorption can be elevated by low iron in the diet, and various physiological states such as pregnancy and lactation can increase Ni absorption as well. As a result of the low absorption rate, tissue concentrations of Ni are relatively low, with kidney, liver, bone and hair containing the highest concentrations (0.1–0.25 mg kg^{-1} fresh tissue).

Ni is an essential component of a number of enzymes in plants and bacteria, the most notable enzyme being urease found in soybeans, rice and the jack bean. Whether Ni is an essential nutrient for biochemical processes in animals is still debated. If there is an essential requirement for Ni, it is very, very small and contamination from the air and immediate environment is enough to satisfy requirements.

Because of the low absorption rate of Ni, dietary Ni is relatively non-toxic. Dietary Ni at 250 mg kg^{-1} in the form of nickel carbonate had no adverse effects on cattle but 500 mg kg^{-1} caused a reduction in feed intake. Similarly, poultry were only affected when dietary concentrations were 500 mg kg^{-1} or more.

(PGR)

Further reading

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Nicotinamide: *see* Niacin

Nicotinamide adenine dinucleotide (NAD) Molecular structure $C_6H_6N_2O{\cdot}C_5H_8O_3{\cdot}PO_3{\cdot}O{\cdot}HPO_3{\cdot}C_5H_8O_3{\cdot}C_5H_4N_5$, molecular weight 663.44 (previously called diphosphopyridine nucleotide; DPN; coenzyme I; CoI codehydrogenase I). NAD is involved as a co-factor in oxidation–reduction reactions in both anaerobic and aerobic cellular metabolism. For example, in anaerobic glycolysis NADH + H^+ is produced and later used to reduce pyruvate to L-lactate ($CH_3{\cdot}CO{\cdot}COO^-$ + NADH + $H^+ \rightarrow CH_3{\cdot}CHOH{\cdot}COO^-$ + NAD^+). In aerobic metabolism, in the oxidation of substrates, NAD^+ is converted to NADH + H^+ (lactate + $NAD^+ \rightarrow$ pyruvate + NADH + H^+). The energy so acquired is utilized by the electron transport system in the mitochondrion to produce ATP from ADP and P_i. (NJB)

Nicotinic acid: *see* Niacin

Night blindness A condition (nyctalopia) in which the animal is unable to see in dim light and takes a long time to adjust when moved from a bright light, though able to see normally in full light. It occurs in all species of farm animals and is caused by deficiency in vitamin A, most commonly in animals deprived of green forage for long periods. Night blindness may be observed when an animal is driven through obstacles in dim light. Night blindness has also been described as an inherited condition in horses. (WRW)
See also: Vitamin A

Nipple drinkers: *see* Drinker

Nitrate The anion (NO_3^-) produced when nitric acid (HNO_3) disassociates into the cation H^+ and NO_3^-. Nitrate is a normal metabolite produced in the catabolism of L-arginine. Nitrogen from ammonium acetate is also excreted as nitrate in the rat. In plants, nitrate is taken up and reduced to NH_4^+ for use in *de novo* amino acid biosynthesis. (NJB)

Nitric oxide The nitric oxide radical (NO·) is a gas and is a potent vasodilator produced by endothelial cells. NO· has a half-life of 3–4 s in cellular systems. The enzyme nitric oxide synthase, a cytoplasmic enzyme, produces NO· from L-arginine. In the reaction, L-arginine is converted into NO· and L-citrulline. NO· plays a role in maintenance of blood pressure, as a neurotransmitter in the brain and may have a role in skeletal muscle relaxation, inhibits adhesion, activation and aggregation of platelets. Nitrite can also be converted to NO· in the process of denitrification where the end-product is dinitrogen gas. (NJB)

Nitrite An anion (NO_2^-) produced from nitrate by nitrate reductase. Nitrite can be further reduced to NO· (nitric oxide radical). It is an intermediate in the process of denitrification by which dinitrogen gas is produced. (NJB)
See also: Nitric oxide

Nitrogen An element (N, atomic mass 14) contained in the body in the form of proteins, amino acids, nucleic acids, purines, pyrimidines, vitamins, hormones, antibodies, enzymes, urea, ammonia and several other compounds. In nutrition, total nitrogen (N) in feedstuffs and body components is estimated by either the **Kjeldahl** or the **Dumas method**. In the Weende system of proximate analysis, 'crude protein' is estimated as N × 6.25 on the assumption that the average N concentration in protein-bound amino acids is 16% (100 ÷ 16 = 6.25). However, because the N concentration in amino acids actually varies from 7.7% (tyrosine) to 32.2% (arginine), other factors may be more appropriate for certain proteins (e.g. for milk and cereal proteins), depending on their amino acid composition. Nitrogen in the body is excreted primarily as undigested dietary protein and microbial protein in the faeces as well as urea in urine, which is produced primarily in the liver from catabolism of excess dietary amino acids and amino acids released by body protein breakdown.

Some urea produced in the liver enters the gut via diffusion but most goes to the kidney, where it is excreted in the urine. Not all of the urea entering the gut of mammals is excreted in the faeces, because bacterial urease breaks down some of the gut urea to ammonia, CO_2 and H_2O. Most of this ammonia is reabsorbed and then remetabolized in the liver to carbamoyl phosphate, and ultimately to urea again. Avian species excrete uric acid rather than urea as an end-product of N metabolism. The urethra of avians enters the colon such that urine and faeces are voided together.

Ruminant animals can use urea or ammonia to make bacterial protein in the rumen. Also, some of the urea produced in the liver can recycle back to the rumen, where it is catabolized to ammonia and then to bacterial protein. Thus, bacterial protein produced in the rumen together with unfermented (bypass) dietary protein are the main N sources presented to the abomasum (the true stomach) and small intestine of ruminants for digestion and absorption of amino acids.

(DHB)

See also: Amino acid; Crude protein; Protein; Urea; Uric acid

Nitrogen balance A term used to describe a calculated total body balance of nitrogen ($N_{balance} = N_{in} - N_{out}$) in animal and human experiments. The concept of balance is dependent on the premise that nitrogen cannot be stored in a unique protein in the manner that hydrogen is stored in fat. No storage form of protein is known. Nitrogen consumed in excess of needs is expected to be converted to urea and excreted. Thus, amino acid and ammonium nitrogen consumed should be a source of nitrogen for accretion of new body substance and for replacement of endogenous nitrogen that is lost from the body as skin and hair and in faeces (e.g. intestinal excretions such as enzymes, cells, etc.) and in urine. Nitrogen balance should be positive in animals gaining weight and negative in animals losing weight. In adult animals at maintenance, N balance should be close to zero; this is called N equilibrium.

N balance can be used as the criterion of adequacy in experiments designed to estimate an animal's protein (N × 6.25) or amino acid requirements for growth or maintenance. In these experiments the concentration of the amino acid or crude protein in the diet is varied and the nitrogen balance is estimated from the amount of dietary nitrogen consumed and the total amount of nitrogen excreted in urine and faeces by each of the animals fed the various diets. The maximum nitrogen balance is used as the estimate of the amount of amino acid required to maximize growth. Similar approaches are taken to estimate maintenance requirements where the balance should be zero.

Experiments designed to determine N balance require considerable effort. A number of animals must be fed the specified diets for some period of time to obtain a new steady state; then total intake and total faecal and urinary nitrogen excretion must be measured on a daily basis over a specified period of time (usually in multiples of days). The amount of time devoted to a balance experiment is critical to the repeatability of the estimate. A short time (< 1 day) would result in unacceptable error, since the nitrogen excreted may vary with time of day: faecal and urinary excretions are periodic, not continuous events. Daily variation can be 'smoothed' by carrying out the experiment for a longer period of time so that one void or defecation more or less has a small effect on the calculated answer. In experiments with humans where all apparent N consumed and N lost has been carefully assessed, calculated N balance has been positive (1.6 g N day^{-1}) in experiments over 50–220 days. In direct experiments with pigs, N balance was 16% higher than in comparative slaughters. Experimental errors in N balance experiments tend to give a positive bias, i.e. N balance tends to be overestimated. Thus, estimates of body protein accretion from N balance experiments must be treated with caution. (NJB)

Key references

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Oddoye, E.A. and Margen, S. (1979) Nitrogen balance studies in humans: long-term effect of nitrogen intake on nitrogen accretion. *Journal of Nutrition* 109, 363–377.

Nitrogen metabolism Nitrogen is a gaseous element with the atomic number of 7. It is a member of group VA of the periodic system. It is a diatomic gas (N_2) that makes up 78.084 ± 0.004% volume per cent of dry air. It has a molecular (atomic) weight of 14.0067 and oxidation states that vary from NH_3 to N_2 to NO_3^-. Atmospheric N_2 is reduced to ammonia by a process called nitrogen fixation done only by bacteria in root nodules of leguminous plants. The other source of nitrogen for use by plants is nitrate-N (NO_3^-). Plants use these sources of nitrogen in the biosynthesis of amino acids and other nitrogenous compounds (nucleic acids, phospholipids, vitamins, etc.) necessary for cellular structure and metabolism. When plants are consumed by animals or die, their nitrogenous components become available for use by other organisms. Bacteria in the soil reduce nitrate-N (NO_3^-) to dinitrogen gas N_2 in a process known as denitrification.

In animals, the majority of nitrogen is associated with the amino acids in proteins but nitrogen is also found in phospholipids, nucleic acids and a large number of other molecules. Nitrogen metabolism in animals focuses on amino acids and ammonia. Nitrogen in the form of ammonium salts can be used by animals as a source of nitrogen for the biosynthesis of dispensable amino acids. The ammonium-N is incorporated into **glutamate** by the enzyme L-glutamate dehydrogenase. Dispensable amino acids can be synthesized by transferring the nitrogen from glutamate to the keto acid of the amino acid in question (e.g. pyruvate + L-glutamate → L-alanine + α-ketoglutarate). Glutamate-N can also be used as a nitrogen source for conversion of the keto acids of the indispensable amino acids to their respective amino acids (e.g. α-ketoisocaproate + L-glutamate → L-leucine + α-ketoglutarate). The indispensable amino acids L-lysine and L-threonine cannot be formed in this way as their keto acids are either not produced or do not participate is such reactions.

The stable isotope of nitrogen, ^{15}N, is widely used as a tracer in research dealing with nitrogen metabolism. This includes the rate and extent of digestion and absorption of nitrogenous compounds, rates of synthesis and degradation of specific proteins and the metabolic transformations of amino acids to other nitrogenous constituents and the quantitative significance of these processes in relation to an animal's overall metabolism. An important dynamic aspect of nitrogen metabolism in animals involves the processes of **protein synthesis** and protein breakdown, processes that, together, are known as protein turnover. They can be measured using stable (^2H, ^{15}N, ^{13}C) or radioactive (^3H, ^{35}S, ^{14}C) isotopes. All the proteins in the animal body are involved in these processes. The half-life of proteins (a measurement with units of time^{-1}) varies from 6 min to as long as 6 months or more. The process of protein turnover allows animals to modify their metabolic potential continuously, to meet new nutritional and environmental demands. In addition to protein turnover, amino acid nitrogen is incorporated into protein that is lost from the body as milk, fetuses, skin or hair. Nitrogen derived from amino acid catabolism is directed toward the production of ammonia-N and aspartate-N used in the synthesis of **urea** ($H_2N{\cdot}CO{\cdot}NH_2$). The main nitrogen excretory product in mammalian urine is urea but up to 5% of urinary N may be in the form of ammonium-N. Ammonium-N as a percentage of total urinary nitrogen can vary because of alterations in acid–base balance, since $NH_4^+$is used as a counter ion for anions such as Cl^- that must be excreted. The main nitrogen excretion product in birds is **uric acid**, while that in fish can be urea if the fish lives in salt water or ammonium if it lives in fresh water. (NJB)

Nitrogen recycling The cyclical movement of nitrogen between the gut and the rest of the body, particularly important in ruminants. Nitrogen from amino acids catabolized in the tissues is incorporated into urea. A portion of blood urea (*see* **Blood** and **Urea**) is secreted into the gastrointestinal tract, where bacteria use it as a source of nitrogen for their growth. In ruminants, the saliva is a major route of urea entry into the rumen. The bacteria from the rumen are digested in the small intestine and the resulting amino acids are absorbed. These may in turn be catabolized, giving rise to urea which again can be secreted into the rumen, continuing the cycle. The same process occurs in non-ruminants but to a lesser degree. Similar cycling has been described for sulphur. (NJB)

Nitrogen retention An increase in the nitrogen content of the body, synonymous with positive nitrogen balance. It may be measured in a nitrogen balance experiment as the difference between the nitrogen consumed and the nitrogen excreted in faeces and urine. It may also be measured in a comparative slaughter experiment as the gain in total body nitrogen over the course of the experiment and can have units of g day^{-1} or mol day^{-1}.

(NJB)

See also: Nitrogen balance

Nitrogen-free extract Nitrogen-free extract (NFE) is an estimate of the soluble carbohydrate (i.e. sugars, starch and hemicellulose) present in a feed or other material. NFE is determined by difference: it is the substance remaining after the weights of all other assayed components (moisture, crude protein, crude fibre, ether extract and ash) have been subtracted from the weight of starting material. The accuracy of NFE measurement is questionable in that, being determined by difference, it includes the accumulated errors of other assays. It is not, in itself, an assay, but simply 'what's left'. (CBC)

Nitrogenous compounds Organic or inorganic compounds that contains the element nitrogen. In animal nutrition, those of concern include ammonia (NH_3) and oxides of nitrogen (nitrogen dioxide, NO_2; nitrous oxide, N_2O; nitric oxide, NO), water-soluble inorganic forms such as hydroxylamine (NH_2OH), nitrite (NO_2^-) and nitrate (NO_3^-) and a host of organic forms critical to the structure and function of living organisms, such as amines, amides, imines, amino acids and related compounds, nucleic acids, phospholipids, carnitine, creatine and vitamins, as well as waste products such as urea and uric acid. (NJB)

See also: Non-protein nitrogen

Nitrosamines Formed by the reaction of nitrites with amines during preservation or curing of meat, cooking or in the warm acidic conditions of mammalian stomachs. Although nitrosamines are potent hepatotoxins and carcinogens, only a few poisonings have been reported when sheep and mink were fed nitrate-treated fish meal. Nitrite and nitrate were formerly widely used as preservatives in cured meat products. Currently, sodium erythrobate and ascorbic acid are added to nitrite-preserved meats to limit nitrosamine production. (LFJ)

Nivalenol: *see* Deoxynivalenol

Non-essential amino acids Non-essential (or dispensable) amino acids are those amino acids that can be synthesized in the body (e.g. from essential amino acids, glucose, or pyruvate) in a quantity that allows for maximal growth. The non-essential amino acids include glycine, serine, alanine, aspartic acid, asparagine, glutamic acid, glutamine, proline, hydroxyproline, cysteine and tyrosine. All of these are components of protein, and are therefore required for protein synthesis. In addition, hydroxy lysine, trimethyl lysine, phosphoserine and cystine are sometimes also considered non-essential amino acids. They are not, however, required for protein synthesis, because the hydroxylation of proline and lysine, the phosphorylation of serine, the methylation of lysine and the oxidation of cysteine to cystine occur only after proline, lysine, serine and cysteine have been incorporated into peptide chains during protein synthesis. Avian species and some reptiles and fish cannot synthesize arginine, but mammals can synthesize enough arginine (in the kidney) to meet roughly 50% of the growth requirement but 100% of the maintenance requirement. Therefore, arginine is considered a non-essential amino acid for healthy adult mammalian species. (DHB)

See also: Essential amino acids

Non-protein amino acids Amino acids found in feedstuffs or in the body that are not components of protein. (DHB)

Non-protein nitrogen Although this is not a strictly defined term, it usually refers to nitrogenous compounds other than proteins and polypeptides. These include ammonia, amides, nitrogenous glucosides, urea, amino acids, and the amino acid derivatives creatine, creatinine and uric acid. These compounds can provide nitrogen which can be incorporated into amino acids and thus become part of a protein. Peptides such as glutathione (γ-glutamylcysteinylglycine) are not considered as non-protein nitrogen even though they are not proteins. (NJB)

Non-shivering thermogenesis The normal response to a **cold environment** is to increase metabolic heat production, either voluntarily by exercising or by eating more, or reflexly by shivering or increasing muscular tension. Non-shivering thermogenesis is the name given to increased heat production observable in some species, especially in the very young of those species, when there is no obvious cause for its occurrence. It tends to be seen in species that have a particular form of fat deposit, called **brown adipose tissue**. (JAMcL)

Non-starch polysaccharides The polymeric fraction of dietary fibre that includes all polysaccharides except lignin and starch. It is typically a mixture of cellulose, hemicelluloses, pectins and gums. (JAM)
See also: Carbohydrates; Cellulose; Dietary fibre; Hemicelluloses; Pectin substances

Norepinephrine A hormone, also called noradrenaline, synthesized by the chromaffin cells of the adrenal medulla. It is derived from L-tyrosine, which is hydroxylated to become DOPA, then decarboxylated to become dopamine and finally hydroxylated to become norepinephrine. It is classified as a catecholamine and is part of the sympathoadrenal system. The preganglionic nerve fibres of the splanchnic nerve terminate in the adrenal medulla where they innervate the chromaffin cells that produce the catecholamines. This system is required for adaptation to acute and chronic stress. (NJB)

Nuclear magnetic resonance (NMR) NMR spectroscopy is used to characterize the structure of organic and inorganic compounds. Certain atomic nuclei produce a magnetic moment that can be aligned by an external magnetic field producing energy levels that provide the basis for the NRM spectrum. The spectrum of a nucleus in a molecule is made up of radio frequencies that are characteristic of the position of that nucleus in the molecule. There are over 100 nuclei that give observable NMR spectra, the more common ones being ^{1}H, ^{13}C, ^{19}F, ^{31}P and ^{15}N.

Nuclear magnetic resonance imaging (MRI) uses the same principle to produce images of body organs and tissues. It is widely used in medical diagnosis and can also be used to assess body composition. (JEM)

Nucleic acids Ribonucleic acid, RNA, and deoxyribonucleic acid, DNA, are made up of three components: a purine (adenine or guanine) base or pyrimidine (cytosine, uracil or thymine) base, a 5-carbon sugar (D-2-deoxyribose or D-ribose) and phosphoric acid. DNA contains only deoxyribose and RNA contains only ribose. Both DNA and RNA contain adenine, guanine and cytosine; thymine is found only in DNA while uracil is found only in RNA. (DMS)

Nucleotides Nucleotides are derived from nucleosides, which are the combination of a purine or pyrimidine base with a pentose sugar. The nucleic acid adenine linked to ribose is called adenosine, and cytosine linked to ribose is called cytidine. Nucleotides are called ribonucleotides or deoxyribonucleotides based on whether the sugar is ribose or 2-deoxyribose. When the ribose or deoxyribose sugars of the nucleosides are phosphorylated in the 5′ position, they are designated as nucleotides. The five nucleotides are adenosine monophosphate (AMP), guanosine monophosphate (GMP), cytidine monophosphate (CMP), uridine monophosphate (UMP) and thymidine monophosphate (TMP). (NJB)

Nutraceutical A substance, contained in a food, that benefits health in addition to any role it may have in meeting established nutrient requirements. Nutraceuticals may include isolated nutrients, dietary supplements, diets, foodstuffs and herbal products. (MFF)
See also: Functional food; Pharmafood

Nutrient A substance in the diet that is physiologically useful in cellular, animal and plant metabolism. Essential nutrients (e.g. indispensable amino acids, minerals, vitamins) are those that can only be acquired from the diet or medium. Many nutrients (e.g. dispensable amino acids, glucose, most fatty acids) can also be derived from other nutrients or synthesized *de novo* from simpler substances by the organism. Nutrients are usually considered to be simple components of food, such as amino acids, rather than the more complex proteins, because it is the indispensable amino acids that are required rather than protein per se. Nutrients participate in metabolism by providing substrates and precursors but do not control metabolism, which is the role of the more complex substances made from them (e.g. DNA, enzymes, co-factors, coenzymes and hormones). Nutrients include amino acids, carbohydrates, fats, vitamins, macrominerals, trace minerals and ultra-trace minerals. Energy is also sometimes considered as a nutrient, although it is really the summation of the heats of combustion of all the components (mainly the fats, proteins and carbohydrates) in the diet. (NJB)

Nutrient balance The difference between the supply (intake + endogenous production) of a nutrient and its loss from the body. 'Balance' sometimes means equilibrium but sometimes gain (positive balance) or loss (negative balance). The concept can most easily be applied to nutrients that are not produced or destroyed in metabolism. Thus, one can measure the balance of elements such as sodium, carbon or nitrogen by deducting from intake the sum of the losses in faeces, urine, sweat, expired air, etc. For nutrients such as glucose or water, some estimate has to be made of the amounts produced or broken down in metabolism of the animal. The concept can be extended to non-nutrient balances such as energy balance, which encompasses the energy content of fat, protein and carbohydrate energy stored. (NJB)

Nutrient deficiency The supply of a nutrient at a rate below an animal's requirement, leading to clinical symptoms of deficiency. These symptoms vary widely between nutrients and between species. Primary nutrient deficiencies derive from a restricted intake of a nutrient. Secondary nutrient deficiencies may occur as result of an excess of another nutrient; for example, excess iron in the diet may sometimes cause a deficiency of copper and vice versa. A deficiency of even one essential nutrient in the diet can result in inappetence, and thence to general undernutrition. (JMF)
See also: Mineral deficiencies; Protein deficiency; Starvation; Vitamin deficiencies; individual nutrients

Nutrient requirement The amount of a nutrient needed for a specified purpose which, in farm animals, may be maximum weight gain, milk yield, etc. Because an animal's requirement for a nutrient is conditioned by many factors, nutrient requirements are no longer regarded as fixed quantities that must be supplied in all circumstances; instead, changes in animal performance with alterations in nutrient intake are now seen as dynamic responses that can be used to derive estimates of requirements that are appropriate to the particular animal and circumstances. (MFF)
See also: Response to dietary energy and nutrients

Nutrient uptake: *see* Absorption

Nutritional disorder Any malfunction of the body caused by deficiency or excess of one or more nutrients, or imbalance between nutrients. In severe disturbances, the disorder will be accompanied by clinical symptoms, in which case there is a state of disease. (JMF)

Nutritive value A non-specific term for the value of the feed as a source of energy or specific nutrients for a class of livestock. In forage evaluation, it has a special meaning related to characteristics that influence nutrition *independent of intake* – for example, chemical composition and digestibility of the forage and the nature of the digested products. (IM)

Nuts A fruit that consists of a hard or leathery (indehiscent) shell enclosing an edible kernel; or the kernel itself. Many types of nut are made into oil cakes and meals, which can be fed to all livestock classes. Groundnut is one of the most common cakes. All may contain **aflatoxins** and legally require detoxification prior to use in feeds. (JKM)

See also: Groundnut

Nylon bags: *see In sacco*.

O

Oat unit (OU) The oat unit system is very similar to the **starch equivalent**, and expresses the efficiency of feed for lipid deposition relative to the value of 1 kg of oats. The system has mainly been employed in Eastern European countries. (JvanM)
See also: Energy systems

Oats Several members of the *Gramineae* (grass) family. The best known are *Avena sativa*, *A. sterilis* and *A. strigosa*. Generally 'oats' refers to *A. sativa*, which has long been established as a feed for ruminants and horses. It is mainly cultivated in the cool, moist regions of North America and Northern Europe and the leading oat-producing countries include the USA, Russia, Kazakhstan, Canada, France, Poland, Finland, Germany and Australia. More recently, the demand for oats has been somewhat reduced due to competition from hybrid maize varieties and lucerne (also known as alfalfa). Among cereals, oats are second only to rye in their ability to survive in poor soils. With sufficient moisture, oats will grow in sandy soils or in soils of poor fertility or highly acidic soils, but the crop is particularly prone to drought.

Oat grains (kernel) comprise the seed, the pericarp (or seed coat) and the hull (or husk), the latter consisting of the palea and lemma and collectively referred to as 'glumes'. As the oat grain develops, the glumes adhere to the grain – unlike barley, in which the glumes fuse with the outer surface of the developing grain. In oats, the hull and the endosperm account for approximately 25% and 63% of the total seed weight, respectively.

Oats are cultivated mainly as a livestock feed and may be harvested unripe and fed either fresh or as silage. Oat grains are most commonly fed to livestock and may be physically processed by crushing or rolling. Relatively small quantities are used for human food purposes, since the hull is not easily removed from the grain. The contribution of the hull to the overall seed weight is affected by variety, environment and season and can vary from 23% to 35% of the seed weight. An increase in the proportion of hull results in an increased fibre content and a concomitant decrease in overall energy value. A variant called naked oats (*Avena nuda*) has a hull that can be easily removed during threshing, leaving the kernel.

The crude protein (CP) content of oat grains, at 79–149 g kg^{-1} dry matter (DM), is influenced by the level of nitrogen fertilizer

Oats will grow in soils of poor fertility.

Chemical composition of oat grains and oat by-products (as g kg^{-1} DM unless specified). (Source: MAFF, 1990, UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs.)

Feed type	DM (g kg^{-1})	CP	EE	Starch	NDF	GE (MJ kg^{-1} DM)
Oat grain (all seasons)	858	108	41.1	471	310	19.6
Naked oats (all seasons)	860	123	91.7	581	123	20.1
Oat husks[a]		14.4	4.4	10.0		
Oat dust[a]		111	50.0	111		
Oat feed meal[a]		37.8	16.7	63.3		

[a] Assuming an average DM content of 900 g kg^{-1}. Source: Givens, D.I., Clarke, P., Jacklin, D., Moss, A.R. and Savery, C.R. (1993) *Nutritional Aspects of Cereals, Cereal Grain By-products and Cereal Straws for Ruminants*. HGCA Research Review No. 24. HGCA, London, 180 pp.

CP, crude protein; DM, dry matter; EE, ether extract; GE, gross energy; NDF, neutral-detergent fibre.

application, a higher protein content resulting from increased nitrogen use (see table). However, oat proteins are generally of poor quality since they are low in the essential amino acids lysine, methionine, histidine and tryptophan (4.9, 2.7, 3.1 and 2.0 g kg^{-1} DM, respectively). Glutamic acid is the most abundant amino acid in oat protein, with a mean content of 23.4 g kg^{-1} DM (19.5–30.0 g kg^{-1} DM). The oil content of oats, at 29–80 g acid ether extract (AEE) kg^{-1} DM, is higher than in other cereal seeds and is predominantly (60%) concentrated in the endosperm. The oil fraction comprises mainly unsaturated fatty acids, particularly oleic and linoleic acids (39% and 42% of total acids, respectively). Starch is in the range 420–530 g kg^{-1} DM. Oats are rich in phosphorus, micromineral elements, thiamine, nicotinamide and pantothenic acid. In naked oats the contents of CP (range 103–164 g kg^{-1} DM), oil (range 65–113 g AEE kg^{-1} DM) and starch (range 537–637 g kg^{-1} DM) are higher and these levels largely reflect the lower fibre content of the grains, at 310 and 123 g neutral-detergent fibre (NDF) kg^{-1} DM for oats and naked oats, respectively.

While oats are largely cultivated for livestock feeding, they are also used in the manufacture of oatmeal for human consumption. Dehulled kernels are also used in breakfast cereal manufacture. Although oat flour is not generally considered suitable for bread making, it is used to make biscuits.

The processing of oats for human food gives rise to a number of by-products, which are available for livestock feeding. These include oat hulls, oat dust and meal seeds, with oat hulls representing the main by-product (about 0.7 of total). Oat hulls (or husks), comprising the hull and variable quantities (maximum of 10% of total) of oat kernels from the processing of screened oats into oat groats, consist mainly of oat bran and endosperm. The hulls contain high levels of fibre (350–380 g kg^{-1} DM) and are of very low energy value. Protein content is also extremely low (about 30 g kg^{-1} DM) and is poorly digested. Oat hulls are generally unsuitable for feeding to pigs and poultry and are mainly fed to ruminants. Oat dust comprises mainly fractions of the kernel, particularly the fine hairs, which are removed from the hulls in the final stages of processing the oat grain. This product contains modest amounts of protein (about 100 g kg^{-1} DM). A product known as oat feed is sold commercially for livestock feeding and comprises a mixture of oat dust and oat hulls (approximate ratio of 1:4) and also quantities of oat flour. It contains high levels of fibre (790 g NDF kg^{-1} DM) and the overall composition of the by-product is affected by the proportions of oat dust, hulls and flour used, especially of oat hulls. Although generally of low nutritive value, it is suited to ruminant feeding.

The de-hulled kernels (also called groats) are of high nutritive value. They are mainly used for human consumption but small quantities are used in the diets of early-weaned pigs.

During further processing the tips of the kernels, containing a high proportion of germ, are removed and these, together with any other residues removed during processing, are combined and referred to as flowmeal. This is a high quality feed and is generally used by the compound feed industry.

A further by-product arising following the harvest of oat grain is oat straw. This makes a minor contribution to the overall amount of straw available in the UK and contains comparable protein content to barley and wheat straws. Oats may also contribute an important source of forage for ruminants. In North America and Continental Europe, oats sown in the autumn and harvested in the spring are used as a forage crop for dairy cows and beef cattle. (ED)

Further reading

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D. and Morgan, C.A. (1995) *Animal Nutrition*, 5th edn. Longman, Harlow, UK, 607 pp.

Piccioni, M. (1989) *Dizionario degli Alimenti per il Bestiame*, 5th edn. Edagricole, Bologna, Italy, 1039 pp.

Ochratoxins Ochratoxins (OAs) are a family of isocoumarin derivatives of phenylalanine. Nine OAs have been identified but only ochratoxins A and B are significant. They are nephrotoxins produced by several *Aspergillus* and *Penicillium* fungi and are produced in moist grain stored at cool temperatures. Ammonia treatment of grains eliminates ochratoxin. (PC)

Octadecanoic acid An 18-carbon saturated fatty acid with the common name stearic acid. It is found in animal and plant fats. (NJB)

Odd-chain fatty acids Fatty acids with an odd number of carbon atoms (i.e. 3, 5, 7, 9, 11, 13). They are usually saturated. In animal metabolism they are catabolized by the same system as the even-chain fatty acids and this may be an advantage, because the terminal three-carbon unit derived from β-oxidation is propionyl-CoA, from which the carbon can be converted quantitatively to glucose. Odd-chain fatty acids are found in milk fat. In fatty acid biosynthesis two carbon units are added, yielding even-chain fatty acids when a two-carbon unit is the starting point and odd-chain fatty acids when propionate is the starting point. (NJB)

Oesophageal groove: *see* Ruminoreticular groove

Oestrogens Female steroid sex hormones. Oestrogens also occur in plants such as *Trifolium* spp. and include genistein, formononetin and coumestrol. These phyto-oestrogens interfere with animal reproduction. (TA)

Oestrous cycle The hormonally controlled cycle of activity of the reproductive organs of post-pubertal, non-pregnant female animals. Most non-primate mammalian species have oestrous cycles. Ovulation occurs at regular intervals in synchrony with sexual receptivity (oestrus). Appetite tends to be depressed on the day of oestrus. (PJHB)

Offal: *see* Fish products; Meat products; Milling by-products

Oil palm (*Elaeis guineensis* Jacq.) Oil palm trees are indigenous to West Africa and are grown in plantations in Asia. Indigenous trees reach 20 m in height but cultivated varieties are shorter, allowing the bunches of fruit to be picked more easily. The fruit is reddish orange when ripe and consists of a fibrous layer covering a small nut. Palm oil is extracted from both the nut and the outer covering. The fruit itself accounts for around 45% by weight of the fruit bunch. The remaining 55% can be used as fuel in the oil extraction plant. Palm oil pressed from the fibrous layer constitutes 20% of the fresh bunch weight, while a further 12% is pressed fibre. Palm oil sludge is the waste from purification of palm oil. Nuts which can be separated from the pressed fibre are 13% by weight, of which the nut kernel accounts for 4%. The kernel provides approximately equal amounts of palm kernel oil and kernel cake. Palm pressed fibre and palm oil sludge can be safely included up to 40% in ruminant rations. A mixture of palm pressed fibre and palm oil sludge in equal proportions can constitute up

Typical composition of oil palm products (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Palm pressed fibre	86.2	4.0	36.4	9.0	21.0	29.6	0.31	0.13
Palm oil sludge		9.6	11.5	11.1	21.3	46.5	0.28	0.26
Palm kernel cake, solvent extracted	90.8	18.6	37.0	4.5	1.7	38.2	0.31	0.85
Palm kernel cake, mechanically extracted	88.2	15.8	29.7	3.7	23.0	27.8	0.21	0.47

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical digestibility (%) and ME content of palm kernel cake.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Palm kernel cake, mechanically extracted	84.9	60.0	96.1	85.3	13.87
Pigs					
Palm kernel cake mechanically extracted	60.0	36.3	25.0	76.7	9.43

to 50% of the ruminant ration. However, the palatability of mixed rations containing palm oil sludge declines rapidly, and fresh feed mixes need to be prepared each day. Palm oil residue should be limited to 10–15% for non-ruminants. Palm oil sludge has a variable nutrient level, characterized by a high ash content (up to 24%) which interferes with the mineral balance.

Palm kernel cake has a high oil content but is of poor palatability on its own. Solvent extracted meal is reported to be less palatable than meal from mechanical extraction. Palatability improves when it is included in the diet of dairy cattle, raising the butterfat content of milk. Up to 30% palm kernel meal can be included in pig rations but high levels of inclusion cause scouring. Palatability is higher for older pigs than with young animals. Rations with palm kernel meal results in the production of pork with firm fat. (LR)

Further reading

Gohl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series, No. 12. FAO, Rome.

Robards, G.E. and Packham, R.G. (1983) *Feed Information and Animal Production*. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Oilmeals: *see* Oilseed; Oilseed cake

Oils Triacylglycerols, usually of vegetable origin (the main exceptions are marine oils), that are liquid at room temperature. Oils commonly used as animal and human foodstuffs are maize oil, olive oil, rapeseed oil, soybean oil and sunflower oil. These have high concentrations of unsaturated fatty acids, mainly oleic (18:1) and linoleic (18:2) acids. Linseed oil has a high content (50–60%) of linolenic acid (18:3). Other vegetable oils, such as coconut and palm kernel oils, have high concentrations of shorter-chain saturated fatty acids (12:0 and 14:0). (JRS)

See also: Fats

Oilseed The seed of plants such as soybean, rape, palm, sunflower and groundnut which contain a relatively high concentration of lipid. (JMW)

Oilseed cake The residue remaining after the extraction or expression of oil from oilseeds. Major oilseeds are soybean, rapeseed, palm kernel, sunflower and groundnut. (JMW)

Oleic acid An 18-carbon unsaturated fatty acid, *cis*-9-octadecenoic acid, 18:1 n-9 (Δ^9). It is found in vegetable oils. (NJB)

Oligopeptide A peptide made up of no more than eight amino acids. Peptides with more than eight amino acids are called polypeptides. (NJB)

Oligosaccharides Compounds containing two to ten monosaccharides linked in a linear or branched chain. The division between oligosaccharides and polysaccharides is somewhat arbitrary, varying from seven to 15 sugar residues. Oligosaccharides may be produced during the metabolism of certain polysaccharides of plant or animal origin; they are carbohydrate components of glycoproteins and proteoglycans, in which they may have signalling and immunological functions and they are carbohydrate constituents of glycolipids. (JAM)
See also: Carbohydrates; Dietary fibre; Fructans; Galactolipids; Mucin; Peptidoglycans; Raffinose; Stachyose; Verbascose

Olive The fruit of the olive tree (*Olea europeae* L.), grown in the Mediterranean region of Europe, North Africa and parts of America. Extraction of olive oil leaves a pulp, which can be dried and pelleted to produce expressed olive cake containing over 10% oil (see table) (which can quickly become rancid), and solvent-extracted oil cake. The feeding quality of these is low, especially when the pits (stones) are not removed. Dried olive cake can be fed to cattle at < 10% of the diet and to grower and finishing pigs at < 5%. Urea-treated (50 g urea kg^{-1}) olive cake has been fed to Awassi lambs as a replacement for < 30% of dietary cereals but feed intake was reduced. Olive leaves and twigs provide cattle fodder, especially when the trees are pruned. The leaves should be fed fresh but can be left on the branches and stripped later for feeding or can be ensiled. Mature drier leaves require soaking in 2.5 volume water with 0.2% salt for 12 h prior to feeding. Sheep and cattle can be fed leaves fresh at 1–1.5 kg day^{-1} or dried at 0.8–1 kg day^{-1} 100 kg^{-1} liveweight. Olive oil is high in oleic acid and can be included in rabbit diets at < 30 g kg^{-1} and, with vitamin E, in chicken diets at < 100 g kg^{-1} to reduce muscle lipid oxidation. It can be fed to ruminants at < 30 g kg^{-1} but higher levels will reduce feed intake, due to low palatability. Solid-state fermentation has been used to increase the protein content of olive pomace from 59 to 403 g kg^{-1} for inclusion in poultry diets. (JKM)

Typical composition of olive products.

	Dry matter (g kg^{-1})	Nutrient composition (g kg^{-1} DM)					
		Crude protein	Crude fibre	Ash	Ether extract	NFE	ME (MJ kg^{-1})
Fresh leaves	579	131	177	61	73	558	–
Dry leaves	921	106	229	87	82	496	–
Twigs	868	89	289	85	61	476	–
Leaf silage	770	122	202	84	79	506	–
Olive cake	852	63–105	300–400	42–68	119–145	357–376	–
Olive pulp	600–937	84–110	200	47–88	280–330	472–592	5.1

DM, dry matter; ME, metabolizable energy; NFE, nitrogen-free extract.

Omasum The third compartment of the ruminant stomach. It communicates anteriorly with the reticulum through the reticulo-omasal orifice, and posteriorly with the abomasum through the omasoabomasal opening. Many leaves (omasal laminae) project inwards from its greater curvature, largely filling its lumen and greatly increasing the absorptive surface area. It is lined by a stratified squamous epithelium through which water, volatile fatty acids and sodium are absorbed. Digesta entering intermittently through the reticulo-omasal orifice may pass between the leaves or flow along the omasal canal into the abomasum. (RNBK)
See also: Forestomach (figure)

Onion Several species (*Allium* spp.) of bulb-bearing plants cultivated in temperate and subtropical regions. The root is of fibrous material that is fed fresh or used as a flavouring in animal feed. It has diuretic qualities and stimulates the intestines. Animals fed onions have increased water intake. For ruminants, mixing chopped or crushed onions in a total mixed ration will prevent addictive consumption. Cattle fed onions (> 25% of total diet) exhibit elevated red blood cell numbers and haemoglobin concentrations, and while the packed cell volume returns to baseline values within 30 days following discontinuation of feeding, Heinz bodies will be detected in erythrocytes for longer periods at levels proportional to the amount of onions consumed. Onions can be fed to cattle at 25% and sheep at 50% of the total dry matter intake, but they cause meat and milk taint and limits of 5–10% are recommended in dairy and finishing beef cattle. The dry matter (DM) content of onions is 113 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is crude protein 104, crude fibre 159, ether extract 14, starch and sugar 762, and ash 33. (JKM)

Ophidine: *see* Balenine

Orange Globally, oranges (*Citrus sinensis*) are the largest citrus crop. They are grown mainly in the tropics and subtropics. Grass in citrus orchards can be grazed by sheep and calves. Cattle can eat approximately 40 kg day^{-1} of fresh oranges but the fruit should be fed after milking to avoid milk discoloration. Sliced oranges can be fed to pigs. Citrus pulp and meal, peel, rag (internal tissue) and seeds are palatable to cattle. Fresh pulp can be ensiled to feed all year round and fermentation is improved when the pulp is ensiled with tropical grass. Citrus molasses, a thick, bitter liquid condensed from liquor discarded from the pulp, can be fed to cattle and used to substitute 10–40% of maize in pig rations. Dry citrus pulp is very palatable and keeps well when lime is added to remove the pectin. The oil from citrus seeds can be extracted but the oil cake can be fed only to ruminants, due to its limonin content. The dry matter (DM) content of oranges is 150–250 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is crude protein 70–113, crude fibre 50–94, ash 39–66, ether extract 24–75 and NFE 400–780. (JKM)
See also: Citrus products

Organic acids Acids (R·COOH) that contain carbon. Note, however, that carbonic acid (H_2CO_3) is not considered to be an organic acid. All have a dissociable hydrogen ion ($R{\cdot}COOH \rightleftharpoons R{\cdot}COO^- + H^+$). Common examples in nutrition are acetic ($CH_3{\cdot}COOH$) and the longer straight-chain fatty acids. Other organic acids can be more complex, such as benzoic acid ($C_5H_5{\cdot}COOH$) or the bile acid, cholic acid ($C_{24}H_{40}O_5$). (NJB)

Organic compounds Compounds that contains the element carbon but excluding carbon dioxide (CO_2), bicarbonate (HCO_3^-), carbonic acid (H_2CO_3) and related compounds. Compounds can be: aliphatic (straight-chained) including alcohols and esters; or carbohydrates, simple sugars and complex carbohydrate compounds found in plant cell walls; or cyclic (closed-ring) compounds such as naphthalene, benzene and combinations of these two in fat soluble vitamins; or amino acids and products derived from them. (NJB)

Key reference

The Condensed Chemical Dictionary, 8th edn (revised by Hawley, G.G., 1971). Van Nostrand Reinhold, New York.

Organic matter Any material of which the carbon can be recovered as carbon dioxide as the result of an oxidation process. In regard to a diet, organic matter is equal to the weight lost from a dry sample due to combustion (dry matter – ash). In an animal, organic matter is the source of heat (energy) during the combustion process whereby H_2O and CO_2 and other water-soluble end-products are produced. (NJB)

Ornithine A non-protein amino acid ($C_5H_{12}N_2O_2$, molecular weight 132.2). It is a component of the urea cycle and is synthesized in the body primarily from arginine. Some ornithine synthesis occurs also from either glutamic acid or proline. (DHB)
See also: Arginine; Non-protein amino acids; Urea cycle

Orotic acid Uracil-6-carboxylic acid, $C_4N_2H_3(O_2){\cdot}COOH$. The initial step in the production of orotic acid is the production of carbamoylphosphate ($NH_2{\cdot}CO{\cdot}OPO_3^{2-}$). Carbamoylphosphate can be produced by two enzymes: carbamoylphosphate synthase I (a liver mitochondrial enzyme related to urea synthesis) and carbamoylphosphate synthase II (a cytosolic enzyme related to pyrimidine synthesis). If the **urea cycle** is compromised, carbamoylphosphate produced from carbamoylphosphate synthase II combines with aspartate to produce carbamoylaspartate which, after two steps, gives rise to orotic acid which can be excreted in urine. The amount of nitrogen excreted in the form of orotic acid is in the milligram range whereas that excreted as urea-N is in the gram range. The significance of elevated excretion of orotic acid is that it is an indication of a limitation of the urea cycle. (NJB)

Key reference

Visek, W.J. (1979) Ammonia metabolism, urea cycle capacity and their biochemical assessment. *Nutrition Review* 37, 273–282.

Osteoblast Bone-forming cell. These plump-looking cells originate in the embryonic mesenchyme, differentiating from fibroblasts in the formation of bone tissue. They synthesize collagen and glycoproteins, forming the osteoid matrix before developing into osteocytes. Calcification occurs in areas furthest from the osteoblast location. (MMax)

Osteoclast Bone-destroying cell, also known as osteophage. These large, multinucleated bone cells are involved in the breakdown and resorption of osseous tissue. Osteoclasts become activated in the presence of parathyroid hormone and are normally found lying in a cavity or groove of the underlying bone. (MMax)

Ostrich The ostrich (*Struthio camelus*) is the world's largest living bird, standing around 2 m tall and weighing 100–150 kg. It is native to Africa and four subspecies, generally geographically separated, have been recognized largely on the basis of the colour of the skin and wing and tail feathers. Generally males have black body feathers, unlike the brown-grey body feathers of the female; both genders have white (or brown) primary wing and tail feathers. In sexually active males the skin on the face, abdomen and legs flushes red. Young chicks are mottled brown, white and black, moulting out to brown-grey plumage in juveniles. The feathers are symmetrical and lack the interlocking barbules typical of other birds. Now considered to be a neotenous bird, the adult ostrich has retained chick-like characteristics (e.g. large eyes, soft downy feathers) whilst becoming sexually mature.

The ostrich is ratite, exhibiting a flightless, cursorial lifestyle in open savannah, scrub and desert areas. Although capable of running at speeds of 40 km h^{-1}, this is usually only a response to a threat. Vegetation forms the main diet of the bird, which has a relatively broad palate. This is reflected in the alimentary tract, which is characterized by a large expandable proventriculus, a large muscular gizzard (which relies on swallowed stones to assist in grinding food) and a relatively small intestine compared with the very long colon. Digestion is assisted by microbial fermentation in the large paired caeca and proximal colon and the short-chain fatty acids produced are absorbed in the distal colon. Micturition and defaecation are separate events in the ostrich.

In wild situations, breeding is relatively opportunistic and generally reliant on environmental conditions (especially rainfall). Male ostriches establish and defend territories around which the females wander before choosing one male with which to establish a nest. Courtship involves an elaborate display by the male, including a booming call and showing the female potential nest sites. Mating can occur outside of established pairs and many females will lay some of their eggs in other nests. Egg laying takes place every 48 h and the clutch of about ten eggs can take 3 weeks to complete. The number of eggs in a nest can be much higher because of egg dumping by other females but once incubation is established many of these eggs are pushed out (although it is unclear how the incubating female recognizes its own eggs). The egg is the largest laid by any living bird (average of 1500 g, measuring 15 cm × 12 cm) and has a gross composition similar to that of the domestic fowl egg. Incubation takes 42 days and is carried out continuously, with the male sitting at night and the female sitting by day. Hatched chicks are about 30 cm tall and fully precocial, leaving the nest after 24–48 h to follow their parents to look for food and water. Typically, groups of chicks amalgamate to form crèches looked after by one pair of birds until they are well-grown juveniles. Adult height is reached by 12 months of age and sexual maturity is at 2–3 years.

For many centuries ostriches were persecuted for their feathers, which were used as human adornment. Aboriginal Africans also used empty eggshells as water carriers. During the 19th century it became apparent that slaughter of wild ostriches was not sustainable and in South Africa some birds were brought into captivity. Nevertheless, the ostrich remains threatened in much of its natural range. Captive breeding was fully established by development of an artificial incubator, though foster adult birds were used to rear most chicks. Farming was largely based around providing grazing on irrigated lucerne (alfalfa) supplemented by maize. Breeding stock were either kept in large 'free-range' groups or as pairs in small enclosures. Captive breeding programmes were also established to develop a bird more suited to a farming environment and for the regular plucking of feathers (once mature) from living birds. To a large extent this farming system still applies in South Africa.

The result was a rapid expansion of the worldwide market for feathers and vast fortunes were made in the feather trade, particularly around Oudtshoorn, South Africa, which became (and remains) a major centre for ostrich farming. At this time ostriches were also exported to North America, Europe and Australia, where farming operations were established. The onset of the First World War and increasing popularity of the motor car meant that the demand for ostrich feathers in fashion fell dramatically. By the 1930s only remnant farming operations remained in South Africa and had disappeared from other parts of the world.

After the Second World War, a marketing cooperative was established in South Africa that developed the market for leather tanned from the skin of ostrich slaughtered at around 12–14 months. Characterized by patches of raised quills, ostrich leather became a high-quality luxury product. Although dominated by the cooperative, the leather market led to a second expansion of ostrich farming in South Africa. In more recent times the leather market was also supplemented by sale of the high-quality leg meat.

International sanctions against South Africa during the 1980s produced a shortage of ostrich hides and ostrich farming became more attractive for other parts of the world. Aggressive marketing caused an extremely rapid spread of ostrich farming in the USA which led to an increasing awareness around the world, with other African countries and Israel, Australia and Europe establishing ostrich farming operations.

Outside Africa, ostrich farming has been attempted in a wide range of climates and geographical conditions but the farms are usually small in size. Often breeding birds are kept in 'trios' (one male with two females) in small enclosures. Eggs are artificially incubated and the chicks are intensively reared. Common problems have involved maintaining the health of birds, getting good egg production, fertility, hatchability, and poor survivability and growth rates of chicks. Commercial production and marketing of the products has also been a major restriction to development of an ostrich industry to match that of South Africa.

During the 1990s ostrich farming spread to almost all parts of the globe. Unfortunately, many factors, including climate, lack of experience, lack of capital investment and lack of marketing, have meant that many prospective ostrich farmers failed to secure a living. This was despite the increased interest in the low-fat red meat, which is produced entirely from the legs and hips (the breast muscles are very poor in this flightless bird). The market was further complicated by fraudulent marketing operations in several countries. De-regulation of the South African market in 1993 caused a rapid expansion in the availability of ostrich hides on the world market and the price plummeted. At the start of the 21st century the market recovered to a large extent and ostrich farming remains strong within South Africa. Elsewhere, though more widespread geographically, it is practised by relatively few people.

In its native habitat the ostrich is a herbivore feeding almost exclusively on vegetation. A wide variety of plants is consumed according to the prevailing flora in the local area. Green annual forbs and grasses are preferred but leaves, flowers and fruit from succulent plants will also be consumed. Selection of food items is by sight and the beak is used to strip the leaves. Plant species known to be toxic are avoided. Stones are a critical aspect of the ostrich's diet because, employed in the muscular gizzard, they help to grind plant material before it passes into the intestines. Up to one-third of the bird's time is spent feeding, a behaviour that occurs in bouts, often whilst walking, interspersed with periods of vigilance. This pattern is maintained under captive conditions.

To digest plant fibre, ostriches rely on post-gastric microbial fermentation in the large caeca and very long colon. The passage rate for food is therefore slow (about 48 h in a juvenile bird) ensuring efficient fermentation of fibre to form volatile fatty acids (VFAs). VFA levels of 171–195 mM have been recorded in the proximal colon and VFA production accounts for up to 76% of the daily metabolizable energy in a 50 kg ostrich.

The rise in interest in ostrich farming around the world during the 1990s stimulated interest in the nutrition of the ostrich in captivity. Traditionally in South Africa, the diet was based on lucerne (alfalfa), served freshly chopped, and maize. The young birds are typically allowed to graze on lucerne pasture but, as the birds grow, the ground is stripped bare and food has to be supplied on a daily basis. Feedstuffs for captive ostriches in other parts of the world are mainly pelleted formulated rations derived from a variety of vegetation and cereals. Pasture and silage prove effective as alternative husbandry techniques so long as the birds receive a concentrate supplement. In order to reduce feed costs alternative sources of vegetation for rations, including *Phragmites* reeds, have recently been tested in South Africa with varying degrees of success.

There has been considerable research into the exact ingredients of ostrich rations, with the domestic chicken typically used as a comparison. Young ostrich chicks exhibit poor digestibility of both fat and neutral-detergent fibre (NDF) but these steadily improve as the birds grow to maturity. In some respects ostriches resemble poultry (e.g. amino acid metabolism), but in others their vegetarian ancestry is clear. Post-gastric fermentation means that fibre utilization is very high. One study showed that, because NDF digestibility in an adult ostrich was over 60%, the apparent metabolizable energy of the test diet was 11.6 MJ kg^{-1}. This compares with a value of 8.3 MJ kg^{-1} for the same diet based on values derived from poultry.

One side effect of captivity is the habit of ostriches to consume items, including barbed wire and nails, that have no nutritional value. This behaviour is almost certainly a response to stress, induced by poor environmental conditions, and access to such material. Under good captive conditions ostriches will be too busy eating their normal rations to indulge in other less beneficial items. (DCD)

Outflow, rumen: *see* Rumen

Ova: *see* Ovum

Ovalbumin Also known as egg albumin or the 'white of the egg', one of a number of simple, soluble proteins present in the clear, viscous substance of the egg and having a slight yellowish tint. It can be divided into three parts, depending on its location and density. (MMax)

Overfeeding Overfeeding can be either spontaneous or imposed. Spontaneous overeating (**hyperphagia**) is when voluntary food intake is more than required to meet nutrient requirements, resulting in excessive fat deposition. It is difficult to identify with certainty, because some apparent overeating may result from a mild deficiency in one or more nutrients causing a compensatory increase in food intake to meet the requirement for the limiting nutrient. In meeting the need for the limiting nutrient, excess energy is consumed. Such apparent overfeeding may be evident in populations of animals in which individuals vary in their requirements for particular nutrients, because of intrinsic variation in growth, rate of lay, etc.

The term overfeeding is also applicable when animals are subjected to chronic food restriction, as, for example, with growing animals destined for breeding (e.g. growing gilts, broiler breeders) when it is desirable to reduce growth rates to limit body weight at sexual maturity. Increasing daily rations much above recommended levels, or 'overfeeding', leads to heavier breeding animals which may have impaired health and reproductive performance.

Imposed overfeeding is the same as force feeding. (JSav)

Ovulation rate In birds, the number of ova released from the single functional ovary during a given period. In laying birds, at peak production, this is one per day. However, ovulation rate does not always equate to rate of oviposition, as some ova miss the oviduct and are subsequently resorbed. Also, sometimes two ova develop within a single egg shell. In mammals, ovulation rate is the number of ova shed in one oestrous cycle from either one ovary in the case of single-ovulating species, or both ovaries in the case of multiple ovulators. (PDL, JJR)

Ovum Unfertilized female gamete or egg cell (plural: ova). The ovum is a haploid cell containing the single set of chromosomes (forming a pronucleus), which the mother will contribute to the new individual at fertilization, when the haploid spermatozoon fuses with the ovum, creating a new diploid individual.

In mammals, the ovum consists of a pronucleus surrounded by cytoplasm and two small polar bodies, containing 'spare sets' of chromosomes resulting from the meiotic divisions that produced the pronucleus. The ovum is surrounded by a tough, clear, spherical shell – the zona pellucida. The ovum always contains an X chromosome, the sex of the new individual being determined when the ovum is fertilized by sperm containing either an X or a Y chromosome.

In birds, the ovum is much larger in relation to body size (up to about 20 g in the domestic fowl, for example). It is characterized by a large yolk, made up largely of lipids, which account for about one-third of the egg's weight and which will nourish the chick during incubation. A protective calcareous shell is formed around the egg after fertilization and before it is laid. Sex is determined by the ovum, which contains either a Z or a W chromosome. (PJHB)

Oxalates Salts of oxalic acid (HOOC·COOH). One of the most prominent oxalate salts in urine is calcium oxalate. Oxalic acid is produced in the catabolism of glycine and ascorbic acid. It is found in asparagus, spinach, rhubarb and other vegetables and fruits. Dietary oxalates may cause primary oxaluria in which calcium oxalate accumulates in the kidneys and other tissues (oxalosis). This may lead to kidney failure and uraemia. (NJB)

Oxaloacetate A dicarboxylic acid, $HOOC·CO·CH_2·COOH$, derived either from the transamination of aspartic acid ($HOOC·CHNH_2·CH_2·COOH$) or from the oxidation of malic acid molecules ($HOOC·CHOH·CH_2·COOH$) in the **tricarboxylic acid (TCA) cycle**. It is essential for the oxidative catabolism of acetyl-CoA derived from carbohydrates, fatty acids and amino acids. It is a critical intermediate in the TCA cycle in regard to conversion of acetyl-CoA carbon to carbon dioxide because it combines with acetyl-CoA to form citrate. It is also critical to gluconeogenesis because it is the TCA cycle intermediate that provides carbon for glucose synthesis. (NJB)

Oxidation The removal of electrons (in contrast to reduction, which is the addition of electrons). In aerobic metabolism, substrates are oxidized and the energy in the electrons removed from the substrates is carried by reduced co-factors (i.e. $NAD^+ \rightarrow NADH + H^+$; $FAD \rightarrow FADH$) which interact with the mitochondrial electron transport chain to produce ATP from ADP. The final reaction in the electron transport chain is the reduction of oxygen to form water. In anaerobic metabolism, substrates are oxidized in the same way as in aerobic metabolism but a substance other than oxygen must be reduced (e.g. CO_2 reduced to methane). (NJB)

Oxidative decarboxylation The removal of the carboxyl carbon from an α-keto acid. Oxidative decarboxylation involves an α-keto acid substrate such as pyruvate ($CH_3{\cdot}CO{\cdot}COO^-$) or α-ketoglutarate ($^-OOC{\cdot}CH_2{\cdot}CH_2{\cdot}CO{\cdot}COO^-$). In the case of pyruvate, oxidized lipoic acid (RS·SR), thiamine diphosphate, coenzyme A and the appropriate enzyme all participate in the reaction. The oxidized form of lipoic acid (RS·SR) reacts with the two-carbon decarboxylation product of pyruvate (i.e. acetate) to form the reduced lipoate-SH-acetyl complex ($CH_3{\cdot}CO{\cdot}SH{\cdot}$lipoamide·SH). The acetyl group of the acetyl·SH·lipoamide·SH complex is transferred to reduced coenzyme A (CoASH) to form acetyl·S-CoA. The reduced lipoate (HS·lipoate·SH) is released and then oxidized by FAD to regenerate oxidized lipoic acid (RS·SR). A similar series of steps occur when α-ketoglutarate is the substrate. In this case succinyl·S-CoA is the product. (NJB)

Oxidized fats Fats that have undergone oxidation by molecular oxygen resulting in the production of peroxides and free radicals. The oxidation is catalysed by heat, light and metals such as copper and iron. Oxidized fats become rancid and unpalatable, with an offensive taste and smell. If absorbed, the peroxides and free radicals in the fat can result in cellular damage and tissue death. Unsaturated vegetable fats are more susceptible to oxidative damage than saturated fats. Poor growth and lowered feed efficiency are expected. To prevent this detrimental effect, fats may have antioxidants such as butylated hydroxytoluene (BHT), ethoxyquin and tocopherols added to them. (NJB)

Oxygen An element found in nature as a diatomic gas, O_2. It has an atomic number of 8 and an atomic weight of 15.9994. It makes up 20.946 ± 0.002% of the volume of dry air. The three isotopes of oxygen are ^{16}O, ^{17}O and ^{18}O. The heavy isotope ^{18}O is used as a tracer in chemical and metabolic studies. Oxygen is required for aerobic metabolism because it is the terminal electron acceptor in the mitochondrial electron transport chain. The electrons (hydrogen) removed from substrates are used to reduce oxygen to water as part of the overall respiratory process. (NJB)
See also: Energy metabolism; Oxygen consumption

Oxygen consumption Oxygen is consumed by animals at a rate of approximately 1–2 l g^{-1} food metabolized. The amount of oxygen consumed is related more closely to the quantity of heat produced, being approximately 0.47–0.55 l kJ^{-1} energy converted into heat.

The table gives the approximate oxygen consumption (l day^{-1}) of growing farm animals at different body weights. For pregnant animals these estimates should be multiplied by approximately 1.5, for laying hens by 1.75 and for lactating animals by 2, or even 3 for a champion cow. For maintenance conditions they should be reduced to about two-thirds.

Body weight	Chickens	Sheep	Pigs	Cattle
50 g	2			
100 g	5			
200 g	10			
500 g	14			
1 kg	23			
2 kg	38	60		
5 kg		90	80	
10 kg		130	150	
20 kg		220	280	250
50 kg		360	500	500
100 kg			750	800
200 kg			1000	1200
500 kg				2000

(JAMcL)

Oxytocin A peptide hormone produced by the magnocellular neurosecretory nuclei of the posterior pituitary and by gonadal tissue. It is involved in the process of parturition and in the ‘let down’ of milk by the mammary gland. Oxytocin causes the contraction of smooth muscle in the uterus during parturition and its secretion is stimulated by the suckling stimulus in mammals, facilitating the ejection of milk from the mammary gland. (JRS)

Oyster: *see* Molluscs; Mollusc culture; Shellfish culture

Oyster shell Oyster shells are almost pure calcium carbonate (95–99%) and are good sources of **calcium** for all classes of animals. Clam shells, conch shells, coral and coral sand can all be used for feeding. Shells that have been ground to coarse grit tend to be more palatable to laying hens and help grain digestion in the gizzard, as well as producing strong eggshells. For laying hens the shells should be ground to 0.5–2.0 mm and mixed 2:1 with finely ground limestone.

(JKM)

P

Pacific salmon Pacific salmon comprise seven principally anadromous, semelparous species in the genus *Oncorhynchus*, namely the sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), chinook (*O. tshawytscha*), coho (*O. kisutch*), masu (*O. masou*) and amago (*O. rhodurus*) salmon. The first five are naturally distributed around the Pacific Rim from the Bering Sea south to California and northern Japan. The last two are strictly Asian (Seas of Japan and Okhotsk). Coho and chinook salmon are commercially cultured. (RHP)
See also: Salmon culture

Pacu (*Piaractus mesopotamicus*) A commercially important freshwater fish native to the rivers of Brazil. This large migratory fish reaches 60 cm in length and is a scavenger that eats vegetation, mostly of fruit that falls into the water as well as an occasional small fish or insect. Pacu is one of the first native fish species to be successfully cultured in Brazil. A market size of 1–2 kg can be attained in 18–20 months at water temperatures of 22–28°C. (SPL)

Palatability The term 'palatable' is defined as 'being pleasant to the taste' and hence the palatability of a food may be thought of as the degree to which an animal finds its taste pleasant. In ruminants, palatability usually designates those characteristics of a food that invoke a sensory response in the animal and is considered to be the corollary of the animal's appetite for the particular food (Baumont, 1996). Taste and smell are thought to be important determinants of palatability for mammals, while poultry are more affected by visual signals. Sheep, for example, have been shown to develop a liking for the taste of monosodium glutamate and to exhibit a preference for foods containing this additive. There is also evidence that ruminants prefer the smell of butyric acid to that of acetic acid. Young pigs find sucrose particularly attractive but are less influenced by other sweetening agents. Physical characteristics of foods are also thought to contribute to the sensory responses invoked and in this regard factors such as particle size and dry matter content can be regarded as factors affecting palatability. The palatability of a single food can be evaluated by the rate of eating at the beginning of the meal, while the palatability of different foods can be assessed by preference tests. Palatability is more likely to be achieved by providing fresh well-preserved foodstuffs of a type acceptable to an animal than by the use of attractive additives. (AJFR, RFEA)

Reference

Baumont, R. (1996) Palatability and feeding behaviour in ruminants. A review. *Annales de Zootechnie* 45(5), 385–400.

Palm kernel: *see* Oil palm

Palmitic acid Hexadecanoic acid, $CH_3{\cdot}(CH_2)_{14}{\cdot}COOH$, shorthand designation 16:0, a saturated 16-carbon fatty acid found in animal fats and plant oils. (NJB)

Palmitoleic acid *cis*-9-Hexadecenoic acid, $CH_3{\cdot}(CH_2)_7{\cdot}CH{=}CH{\cdot}(CH_2)_5{\cdot}COOH$, shorthand designation 16:1 n–9 (Δ^9), a 16-carbon unsaturated fatty acid found in nearly all fats. (NJB)

Pancreas The pancreas, an accessory organ of digestion, plays an essential role in the digestive physiology of animals. It is located near the first part of the duodenum and appears as an elongated gland of loosely connected aggregated nodules. These are composed of pancreatic acini, with exocrine functions, and the islets of Langerhans, which have endocrine functions. The exocrine function is to produce and secrete fluids necessary for digestion in the small intestine. The endocrine function is to produce and secrete the important metabolic hormones insulin and glucagon.

The exocrine products are secreted into the duodenum via the pancreatic duct. Secretion is controlled in part by autonomic nerves and in part by the gastrointestinal hormones gastrin, secretin and cholecystokinin (CCK). The secretory rate per unit of body weight (ml kg^{-1} h^{-1}) is higher in chicken (about 0.7) than in mammals (e.g. about 0.1 in sheep).

The exocrine secretions of enzymes and proenzymes are increased by parasympathetic stimulation when the stomach contents enter the intestine. In omnivores and non-ruminant herbivores, e.g. the pig and horse, parasympathetic stimulation also increases the secretion of water and electrolytes, which are needed for fermentation in the large intestine. Gastrin potentiates the parasympathetic effect on the pancreas. Secretin release is stimulated by acid perfusion of the duodenum and causes the pancreas to secrete bicarbonate. CCK is secreted in the response to the presence of protein and lipid in the duodenum and causes the pancreas to secrete enzymes and proenzymes.

In the horse, the rate of enzyme secretion is low in comparison with that of other species, because most ingested food requires microbial fermentation. The composition of pancreatic juice changes during development and alterations in composition can also be induced by changes of diet.

Pancreatic fluid contains bicarbonate, which neutralizes the acid digesta from the stomach, and an array of enzymes and precursors necessary for the digestion of proteins (trypsin, chymotrypsin, elastase, carboxypeptidases), lipids (lipase, phospholipases), starch (amylase) and nucleic acids (nuclease and ribonuclease). All proteases and phospholipase A_2 are secreted as inactive proforms in order to prevent damage to the pancreatic tissue. Active trypsin plays a central role in the activation of all enzyme precursors in the duodenum and a potent trypsin inhibitor in pancreatic tissue prevents premature activation of trypsin. (SB)

See also: individual pancreatic enzymes; Pancreatic hormones

Pancreatic diseases Pancreatic conditions include inflammation, atrophy and neoplasia. Pancreatitis is potentially very painful. Pancreatic diseases may affect either the exocrine function (the production of enzymes – proteases, amylase, lipases and nucleases – for digestion) or the endocrine function (the production of glucagon and insulin from cells in the islets of Langerhans).

Loss of exocrine function is often reflected in fatty faeces, loss of weight and increased appetite. Release of these digestive enzymes within the gland causes acute pancreatitis, severe pain and hyperlipidaemia.

Insulin is the major anabolic hormone in animals and stimulates protein synthesis, polysaccharide production from monosaccharides and lipid synthesis from fatty acids. In diabetes mellitus (sugar diabetes) there is a permanent high blood glucose level, even during fasting. The kidneys will eliminate excess glucose but require water to do this, leading to excess urination and drinking (a temporary glucosuria may be due to other factors). Diabetes mellitus is usually due to a failure of the β cells in the pancreas to produce insulin but may be due to an excess of insulin antagonists. It is often seen in dogs and cats but is uncommon in large domestic animals. (EM)

Pancreatic hormones Hormones released from pancreatic islets, primarily involved in the regulation of metabolism. They include insulin and glucagon, which regulate blood glucose levels, somatostatin, a potent inhibitor of growth hormone secretion, and pancreatic polypeptide, which is believed to act by partially inhibiting exocrine pancreatic function. (GG)

Pancreatic islets The islets of the pancreas, also known as the islets of Langerhans, are the functional units of the endocrine portion of the pancreas. Islet cells make up less that 2% of the total pancreatic mass but secrete hormones that are absolutely essential to metabolism including insulin from β-cells, glucagon from α-cells, somatostatin from δ-cells, and pancreatic polypeptide. (GG)

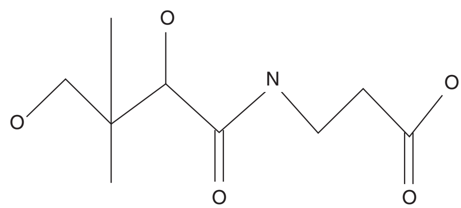
Pancreatic juice The secretion of the pancreas, an alkaline juice containing a very high content of bicarbonate and numerous digestive enzymes. The high content of bicarbonate serves primarily to neutralize the highly acid chyme produced in the stomach that passes into the duodenum. The digestive enzymes include the inactive precursors of proteases (trypsinogen, chymotrypsinogen, proelastase, procarboxypeptidase A and B), amylase, lipases (including the inactive precursor of phospholipase A_2) and nucleases. After activation in the duodenum, initiated by activation of trypsin by enterokinase and the activation of lipase from bile acids, the enzymes have a potent capacity to degrade proteins, starch, lipids and nucleic acids, respectively. (SB)

Pancreatin Freeze-dried pancreatic tissue (usually from pigs) containing the various pancreatic enzymes, including proteases (trypsin, chymotrypsin, elastase and carboxypeptidases), amylase, lipase and ribonuclease. (SB)

Pancreatitis: *see* Pancreatic diseases

Pancreozymin: *see* Zymogens

Pantothenic acid A water-soluble B vitamin, $HOCH_2{\cdot}C(CH_3)_2{\cdot}CHOH{\cdot}CO{\cdot}NH{\cdot}(CH_2)_2{\cdot}COOH$, a combination of pantoic acid and β-alanine. Only D-pantothenate is biologically active. It is a component of the enzyme co-factor coenzyme-A and part of the acyl carrier protein involved in fatty acid synthesis. Coenzyme-A is found in the cytoplasm and in the mitochondrial matrix in free form as CoASH or in bound form, for example as a acetyl-CoA. In the cytoplasm it is also found as 4′-phosphopantetheine as part of the acyl carrier protein that is involved in fatty acid chain elongation. About 80% of the pantothenic acid in tissues is found as CoA, which is widely distributed in nature because it is a participant in enzyme reactions involved in the catabolism and synthesis of carbohydrates and fatty acids (individual steps and the citric acid cycle), the catabolism of some amino acids and synthesis of cholesterol and porphyrins. CoA in food is hydrolysed by a phosphatase in the digestive tract to pantetheine (pantothenyl cysteamine) and absorbed, along with pantothenate, by a sodium-dependent transporter. In experimental animals fed pantothenic acid-deficient diets, no single set of symptoms has been observed. A unique goose-stepping has been reported in deficient pigs. A spontaneous deficiency of pantothenic acid is not expected, presumably due to its wide distribution in nature.



(NJB)

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Plesofsky-Vig, N. (1996) Pantothenic acid. In: Ziegler, K.E. and Filer, L.J. Jr (eds) *Present Knowledge in Nutrition*, 7th edn. ILSI Press, Washington, DC, pp. 236–244.

Parakeratosis A condition in which the stratum corneum of the skin is thickened, scaly and cracked: it differs from hyperkeratosis in that the keratinocytes remain nucleated. It is seen in growing pigs suffering from zinc deficiency (caused either by a diet containing less than 100 ppm of zinc or secondary to high concentrations of calcium, or of phytates). It does not cause itching (as distinct from mange mites) and does not normally occur in young pigs (as distinct from greasy pig disease). In calves, the condition is inherited (Adema disease) and may respond to treatment with zinc in the feed. Parakeratosis of the rumen has been described in cattle fed heat-treated lucerne but appears not to cause clinical illness. (WRW)

See also: Skin diseases

Parathyroid An endocrine gland responsible for regulating blood calcium concentration. Some animals (e.g. pig, rat) have one pair of parathyroid glands; others (e.g. ruminants, humans) have two pairs. The glands are located within the neck region, often with one pair residing within the thyroid gland and one pair just cranial or caudal to the thyroid gland, depending on the species. Blood is supplied to the parathyroid glands by branches of the carotid arteries. Cells of the parathyroid are capable of sensing the calcium concentration in the blood: when it falls below normal (2.25–2.5 mM in most species), the gland secretes parathyroid hormone; as the blood calcium concentration returns to normal, the secretion is reduced.

It is vital to life that calcium concentration be maintained within a fairly narrow range. When it is too low the animal will not be able to form new bone, control nervous or muscular function properly (which may result in tetany or muscle weakness; *see* **Milk fever**), form blood clots, or maintain normal intracellular calcium concentrations. If blood calcium concentration exceeds normal limits, calcium precipitates within the soft tissues of the body, disrupting their function.

Parathyroid hormone is a peptide of 84 amino acids and it has three distinct actions. Initially it increases renal tubular reabsorption of calcium from the glomerular filtrate, decreasing urinary calcium loss. This is sufficient to restore blood calcium concentration to normal levels if the perturbation in blood calcium is small. With larger decreases in blood calcium concentration, continued secretion of parathyroid hormone increases resorption of calcium from bone. Specialized bone cells known as osteoblasts have receptors for parathyroid hormone on their surface. These cells recognize the parathyroid hormone signal and initiate bone resorption activity by stimulating a second bone cell, known as an osteoclast, to begin to degrade the organic matrix of the bone to free bone minerals (primarily calcium and phosphorus) for transport to the blood to increase blood calcium concentration.

In addition, parathyroid hormone can stimulate the production of a second hormone, 1,25-dihydroxycholecalciferol, by the kidneys. The precursor for this hormone is vitamin D, which is supplied in the diet or produced in the skin. The 1,25-dihydroxycholecalciferol produced in response to parathyroid hormone stimulation of the kidney acts on the intestine to stimulate the active transport of calcium across the epithelium. Without this hormone, dietary calcium is only poorly absorbed.

A secondary effect of parathyroid hormone is on phosphorus metabolism. Parathyroid hormone increases resorption of phosphorus from bone at the same time as it increases resorption of bone calcium. To prevent a build-up of phosphorus in the blood as a result of bone phosphorus resorption, parathyroid hormone also increases phosphorus excretion by the kidneys and, in the case of ruminants, the salivary glands. (JPG)

Parathyroid diseases Diseases involving the parathyroid gland fall into two categories: those associated with excessive parathyroid hormone activity (hyperparathyroidism) and those associated with abnormally low parathyroid hormone activity. Excessive parathyroid hormone activity results in depletion of bone calcium, leading to osteoporosis and predisposing the animal to bone fracture. Excessive parathyroid hormone secretion is commonly associated with diets low in calcium. In some cases diets that are excessively high in phosphorus can interfere with calcium absorption, resulting in excessive parathyroid hormone secretion. In companion animals and humans, tumours of the parathyroid gland commonly result in uncontrolled secretion of parathyroid hormone, leading to hypercalcaemia. Low parathyroid hormone activity may also be caused by parathyroid gland tumours. Of greater significance, especially in ruminants, is the failure of the target tissues of parathyroid hormone, bone and kidney, to respond to parathyroid hormone stimulation. Dietary cation–anion balance affects blood pH, which alters tissue responsiveness to parathyroid hormone. Milk fever in dairy cows is often the result of metabolic alkalosis induced by diets high in potassium. Low blood magnesium concentration can also impair the action of parathyroid hormone on its receptors in bone and kidney, resulting in hypocalcaemia. (JPG)

Parietal cells Cells in the parietal glands, which are located in the parietal area in the stomach. Their function is to secrete HCl, which is produced by an enzymatic process using CO_2, H_2O and NaCl. The other product, $NaHCO_3$, is transferred to the blood. (SB)

Parity The number of pregnancy and lactation cycles completed by an animal. Thus, a primiparous animal (heifer, gilt, ewe lamb) is in its first pregnancy or lactation – its first parity; a multiparous animal (cow, sow, ewe) is in its second or subsequent parity.

Most farm animals enter their first parity before reaching their mature body weight. Therefore, in addition to the nutrient requirements for pregnancy and lactation, they also have nutrient requirements for continued growth. Production level (milk yield or number of offspring) also generally increases with parity. This is particularly noticeable when comparing animals in their first and second parities.

In dairy cattle, liveweight increases until the third or fourth parity and milk yield may not reach a plateau until the fifth parity. The lactation curve of a heifer (first parity) is noticeably flatter than that of a cow in its second or subsequent parity. This is because the secretory tissue of the mammary gland develops during the first lactation.

In pigs, liveweight increases until the sixth parity and litter size may increase until the third parity. Gilts are first mated at a relatively young age and light weight, compared with cattle, and so growth during the first three parities requires a higher proportion (up to 20%) of total nutrients. (PCG)

Parotid glands A pair of salivary glands located near the ears. The parotid glands are one of the three known pairs of salivary glands (parotid, submandibular, sublingual). They secrete water and the enzyme ptyalin, which is involved in starch hydrolysis. The parotid glands contribute about 20% of the 1.5 l of saliva secreted per day in humans. (NJB)

Particle size The size of food particles in gut contents depends both on the nature of the food eaten and the extent to which it is comminuted by chewing. In ruminant animals, ingested food is chewed and ensalivated until it is in a suitable state for swallowing. During periods of rumination, reticulorumen contents are regurgitated into the mouth where the more solid fraction is thoroughly re-chewed and swallowed. Long food particles in the reticulorumen tend to form a bubbly floating mat while being rapidly fermented, and avoid onward passage. Small, dense, well-fermented particles sink to lower levels and tend to be selected for onward passage through the reticulo-omasal orifice. The time for which particles are retained in the reticulorumen determines the extent of digestion of potentially degradable fibre. Grinding and pelleting roughage diets reduces particle size and so reduces retention time and the extent of fibre digestion in the reticulorumen.

A spectrum of particle size can be described by sieving rumen content (or other material), either dry or in fluid suspension, through a series of sieves of differing mesh size under standard conditions (Kennedy, 1984). (RNBK)

See also: Dilution rate

Reference and further reading

Kennedy, P.M. (ed.) (1984) *Techniques in Particle Size Analysis of Feed and Digesta in Ruminants.* Occasional Publication No. 1, Canadian Society of Animal Science, Edmonton.

Kaske, M. and Engelhardt, W. van (1990) The effect of size and density on mean retention time of particles in the digestive tract of sheep. *British Journal of Nutrition* 63, 457–465.

Parturient paresis This hypocalcaemic disorder affects dairy cows at the onset of lactation, when the mammary gland suddenly imposes a large demand for calcium. The disease occurs because the calcium homeostatic mechanisms of the body fail as a result of diet and advancing age of the cow. (JPG)

See also: Milk fever

Passage rate: *see* Transit time

Passive immunity: *see* Immunity

Pea High levels of sugar, starch and undegradable protein make peas (*Pisum* spp.) a valuable raw material in high-nutrient-density beef and dairy feeds. They are typically steamed, flaked or micronized to increase their digestibility. Some varieties may contain trypsin inhibitors and lectins, which limit their inclusion in pig and poultry diets. Heating (e.g. by extrusion) can destroy most of these. Other varieties, low in trypsin inhibitors, can be used without extrusion in diets for growing and finishing pigs. Peas can be included in diets for dairy and beef cattle, ewes, growing and finishing pigs, sows, calves and lambs, and breeder and layer chickens. Peas are usually ground and pelleted before inclusion in poultry diets. They are not typically included in diets for young pigs or chickens. (JKM)

Peanut: *see* Groundnut

Pectic substances Polysaccharides in plant tissue, gums and mucilages. Their primary structural component is a chain of (1→6)-linked residues of α-D-galacturonic acid. This main chain may be modified extensively, e.g. by methyl esterification of carboxyl groups, acetylation of hydroxyl groups, inclusion of rhamnose residues or addition of neutral sugar side-chains. Pectic substances are common in certain fruits, seeds, leaves, bark and roots. The main commercial sources are citrus peel and apple pomace. (JAM)

See also: Carbohydrates; Dietary fibre; Galactouronans; Rhamnogalactouronans; Storage polysaccharides; Structural polysaccharides; Uronans; Uronic acids

Pectins: *see* Pectic substances

Pellagra A condition caused by deficiency of **niacin** (nicotinic acid) or its precursor **tryptophan**. It is occasionally seen in pigs fed a diet high in unsupplemented maize. Signs include diarrhoea, dermatitis and loss of hair. (WRW)

See also: Maize; Skin diseases; Vitamin deficiencies

Pelleted feed A blend of raw materials that has been ground, conditioned and pressed into uniform pellets. The pellets may have a diameter of 1.5–19 mm and an average length of approximately 2.5 times their diameter, depending on their intended use. Smaller pellets are used for young animals and smaller species, larger ones for animals fed directly on the ground.

Pelleting increases the bulk density of feed, making it cheaper to store and transport. Pellets also flow more easily and quantities are measured more accurately through on-farm automated feeding systems. The raw materials will not separate once pelleted, thus ensuring that the animals receive exactly what is intended. This is particularly important when the feed contains micro-ingredients such as vitamins and medicines. Less feed is spilled and wasted by animals given pellets than by those given meal. In addition, the conditioning process required in order to pellet feed improves its digestibility and therefore its value to the animal.

Pelleted feed can be a complete balanced feed or part of a complete diet; for example, protein concentrates are specially designed to be mixed with cereals. To supply a balanced diet for the particular species, the concentrate would contain materials rich in protein supplemented with minerals and vitamins. (MG)

The nutrient composition of peas.

		Nutrient composition (g kg^{-1} DM)					Energy (MJ kg^{-1})	
	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ether extract	Ash	NDF	MER	MEP
Dried peas	860	260	70	16	35	190	13.6	13.0
Field peas	130	210	60	15	25	110	11.7	–

MER, metabolizable energy for ruminants; MEP, metabolizable energy for poultry; NDF, neutral-detergent fibre.

See also: Coating; Compound feed; Feed mixing; Quality control in feed mills

Pelleting The process of forming feed into pellets. Mixing and pressing ground raw materials has a number of advantages. It increases bulk density, which facilitates bulk storage, transport and the metering of automated feeding systems. It reduces the risk of the constituent ingredients separating over time, which is particularly important if the feed is medicated. It allows for a degree of formulation change to accommodate fluctuations in the supply of raw materials without any noticeable difference to feed intake. Finally, it decreases waste on the farm.

Pellets must be uniform, dust-free and hard enough to withstand handling and storage between manufacture and feeding. To achieve these aims the meal must be suitably prepared by grinding and conditioning. Materials need to be ground to a grist with a good particle distribution and then conditioned. Conditioning is usually carried out by passing the meal along a horizontal barrel with steam and molasses (if used) injected along its length. Revolving paddles along a central spindle blend the steam and molasses with the meal, making it more pliable and compressible. The steam injection raises the temperature of the meal, which aids the absorption of the liquids. Ruminant feeds may also be held for 20–30 min, immediately after conditioning, in a vessel called a ripener, where stirring arms aid conditioning.

Once the meal has been conditioned it is forced through a die under pressure to form the pellet. Most pelleting machines use a ring die, developed *c*. 1910. Meal drops into the centre of a rotating die, which is a metallic ring of variable diameter and thickness, depending on the equipment being used and the final product required. The die normally rotates around two or three fixed rollers that compress the conditioned meal through holes, forming the pellets. The friction further heats the pellet, aiding the ensuing chemical reactions between the starch, protein and sugars present in the raw materials and any artificial binder added. Finally, to avoid condensation and the risk of moulding, the pellets must be cooled to within a few degrees of ambient temperature before the product is stored. (MG)

Pentosans Polysaccharides comprising a large number of pentose residues joined by *O*-glycosidic linkages. Pentosans are widely distributed in plants; they are found in woody tissue, leaves, fruits and seeds. (JAM)
See also: Arabinoxylans; Carbohydrates; Dietary fibre; Hemicelluloses; Pentose; Xylan

Pentose A monosaccharide containing five carbons. Major naturally occurring pentoses include the aldoses L-arabinose and D-xylose, both of which are widely distributed in plants as constituents of polysaccharides, and D-ribose, the only sugar in ribonucleic acid (RNA) which is found in all plant and animal cells. The pentose derivative 2-deoxyribose is the only sugar in deoxyribonucleic acid (DNA). The ketopentose L-xylulose is an abnormal constituent of urine in idiopathic pentosuria. (JAM)

Pentose phosphate pathway A metabolic pathway in the cytoplasm of cells by which glucose is converted via glucose-6-phosphate to one of two pentose (5-carbon) sugars, ribose 5-phosphate or xylulose 5-phosphate. This pathway produces NADPH, which provides reducing equivalents for fatty acid biosynthesis.

Ribose is the pentose sugar found in nucleosides (adenosine, guanosine, cytidine, uridine and thymidine) and in enzyme co-substrates such as NAD, NADP, FAD, CoA and vitamin B_{12}. (NJB)

Pepsin A proteolytic enzyme (EC 3.4.23.1) in the stomach, secreted as the inactive precursor pepsinogen. The activation of pepsinogen is an autocatalytic process involving the removal of a peptide from the NH_2-terminal of pepsinogen by active pepsin in the presence of hydrogen chloride, HCl. Pepsin has optimal activity at pH 1.8–3.5 and initiates the hydrolysis of dietary proteins in the stomach by cleaving peptide linkages that involve aromatic and acidic amino acids. (SB)
See also: Digestion

Pepsinogen: *see* Pepsin

Peptidase A hydrolytic enzyme secreted by the pancreas or the brush border of the small intestinal mucosa. The pancreatic enzymes include the endopeptidases trypsin, chymotrypsin and elastase, as well as carboxypeptidase A and B, which are exopeptidases. The pancreatic peptidases are secreted as inactive zymogens that must be activated to become functional. Those in the brush border are active without activation. They include enteropeptidase, aminopeptidase, carboxypeptidase and endopeptidases. Dipeptidases are brush-border peptidases that cleave a dipeptide to yield the two free amino acids. (NJB)

Peptide A molecule formed of two or more amino acids linked by peptide bonds R·CHNH·CO·R. A dipeptide has one peptide bond, a tripeptide has two, and so on. The term peptide is not well defined: a peptide may contain two to ten amino acids whereas a polypeptide may contain 10–100 amino acids. Some dipeptides of note are carnosine (β-alanylhistidine), anserine (β-alanyl-1-methylhistidine) and balenine (β-alanyl-3-methylhistidine). Glutathione (γ-glutamylcysteinylglycine) is a tripeptide that is involved in protection against oxidative damage and in oxidation–reduction reactions in the cell. Polypeptide hormones of note in animal metabolism are shown in the table. (NJB)

Peptidoglycans Polysaccharide-peptide molecules in which parallel polysaccharide chains are covalently cross-linked through peptide bridges consisting of four, or occasionally five, amino acids, many of which are in their uncommon D-forms. Peptidoglycans are cell wall components of algae and major supporting structures of bacterial cell walls. In bacteria, the peptide portion of the molecule varies with the bacterial strain, but the disaccharide repeating unit in the polysaccharide chain always appears to consist of *N*-acetylglucosamine and an acidic sugar, *N*-acetylmuramic acid. In Gram-negative bacteria, the cross-linking usually involves the formation of amide linkages between the carboxyl groups of D-alanine residues in one chain and the ω-amino groups of the diamino acids in another chain. Cross-linking is more extensive in Gram-positive bacteria. (JAM)
See also: Carbohydrates

Pericarp The part of a fruit that develops from the ovary wall of a flower and which may be dry and hard or soft and fleshy, depending on the type of fruit. The pericarp can be made up of three layers: the outer skin (epicarp or exocarp), the middle layer (mesocarp) and the inner layer (endocarp). (ED)

Periodontal disease Disease primarily affecting the teeth, gums or jaws. The teeth of older sheep fed on roots (turnips, fodder beet) over several winters may become loose and eventually lost, making it difficult for the animal to eat sufficient roots to survive. (JMF)

Polypeptide hormones active in animal metabolism.

Source	Polypeptide hormone
Endocrine pancreas	Insulin, glucagon, somatostatin
Gastrointestinal tract	Gastrin, cholecystokinin, secretin, gastrin inhibitory peptide
Posterior pituitary	Antidiuretic hormone (arginine vasopressin), oxytocin
Hypothalamus	Thyrotropin-releasing hormone (TRH), gonadotropin-releasing hormone (GnRH), corticotropin-releasing hormone (CRH), growth hormone-releasing hormone (GHRH), somatostatin
Anterior pituitary	Adrenocorticotropic hormone (ACTH), thyroid-stimulating hormone (TSH, also called thyrotropic hormone), luteinizing hormone (LH), follicle-stimulating hormone (FSH), growth hormone (GH), prolactin
Other	Insulin-like growth factors I (IGF-I) and II (IGF-II), epidermal growth factor (EGF), fibroblast growth factor (FGF), transforming growth factors (TGF-α and TGF-β), nerve growth factor (NGF), hepatocyte growth factor (HGF), interleukins (IL-1, IL-2, IL-6, etc.), colony-stimulating factor, erythropoietin, atrial natriuretic peptide (ANP), angiotensin II, endothelin

Peristalsis Propulsive movements of the gut by which the food is propelled. Peristalsis consists of a moving ring of constriction in the wall of a tubular organ. The rings reduce the lumen diameter, pushing the bolus of food ahead of them along the gut. Peristalsis is a universal type of propulsive motility, occurring in all parts of the gastrointestinal tract, beginning in the oesophagus. (SB)

Perosis A condition seen in young birds, caused by manganese deficiency. The hock joint is greatly swollen, and the birds are severely lame. (WRW)

Peroxide Any compound with a bivalent O·O group. Because one of the oxygen atoms is not tightly bound, oxygen can be released which results in peroxides being strong oxidizing agents. In metabolism of aerobic organisms, superoxide anions (O_2^-) are produced and can be involved in the production of hydrogen peroxide (HO·OH). Under conditions where free ferrous iron is available, it can be oxidized to ferric iron with the production of a hydroxyl radical (OH·) which may also lead to the production of lipoperoxides, RO·OH. (NJB)

Pesticides Natural or synthetic chemicals or biological agents used to control a variety of pests (weeds, insects, pathogens, molluscs and vertebrate pests) that injure or compete with crops, animals or humans. They include herbicides and insecticides. Most pesticides are very specific to the target organism but some may accumulate to levels that may be harmful to crops, animals or humans. Strict regulatory requirements are placed on the use of pesticides in most countries, and tolerance limits are set and monitored to avoid harmful residues.

Herbicides are generally applied early in the season to control undesirable plants in crops and thus are generally dissipated by the time an animal consumes the crop. When applied properly, currently licensed herbicides seldom develop residues that are toxic to animals. Dinitro compounds (dinoseb) are the only highly toxic class of herbicides. Moderately toxic herbicides include bipryidyl (paraquat), carbamate (EPTC) and triazine (artizine) compounds. Low- to non-toxic herbicides include chlorobenzoic acid (dicambba), chlorophenoxy acids (2,4-D), glyphosate, substituted urea (diuron) and sulphonylureas (metsulfuron).

Insecticides are generally applied to crops later in the season, or applied directly to grains to prevent insect damage. Many insecticides are applied directly to livestock to reduce pest problems. Thus, their concentrations may be higher, and they are generally more toxic than herbicides. Classes of common insecticides include chlorinated hydrocarbons (DDT), organophosphorus compounds (parathion), carbamates (carbaryl) and pyrethrins. (MHR)

Peyer's patches Aggregated lymphatic nodules in the mucosa of the small intestine, especially in the ileum. Together with the tonsils and the lymphoid structures of the appendix, they are the initial site of many of the interactions between food antigens and the animal's immune system. (SB)

pH The negative logarithm_{10} of the concentration of H^+. Thus, pH 7 corresponds to a concentration of 10^{-7} M H^+, which is neutral. Values below pH 7 correspond to acidic and those above pH 7 to alkaline conditions, respectively. In the stomach, pH values can be as low as 1.5 (in rabbits) and 2–3 in pigs. In the duodenum, the pH value is generally about 7 in most farm animals but changes slightly along the tract according to the microbial production of short-chain fatty acids and the secretion of bicarbonate. In the faeces of cattle and horses, the pH value is generally below 7, but in those of pigs, sheep and hens it is normally above 7. (SB)

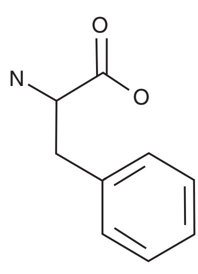
Pharmafood A food or nutrient for which claims of medical or health benefits are made. (MFF)
See also: Functional food; Nutraceutical

Phenolic compounds Compounds that have one or more hydroxyl groups (·OH) attached directly to a benzene ring (C_6H_6) replacing one of the hydrogens. Phenol ($HO{\cdot}H_5C_6$) is the simplest. Other variations are cresols (methyl phenol, $HO{\cdot}H_4C_6{\cdot}CH_3$), xylenols (dimethylphenol,

$(CH_3)_2H_3C_6{\cdot}OH$), resorcinols (*meta*dihydroxybenzene, $(HO)_2{\cdot}H_4C_6$) and naphthols ($C_{10}H_7{\cdot}OH$). The amino acid tyrosine is a phenol. The catecholamines and related compounds, dopa, dopamine, epinephrine and norepinephrine are all phenolic compounds. (NJB)

Phenylalanine An essential aromatic amino acid ($C_6H_5{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 165.2) found in protein. Phenylalanine can be irreversibly hydroxylated to tyrosine and can therefore satisfy the physiological requirement for both of these amino acids, with about half the requirement being satisfied by phenylalanine and the other half by tyrosine. Phenylalanine + tyrosine are seldom if ever deficient in practical diets for animals, because most feed ingredients are rich in these amino acids.

After being metabolized to tyrosine, the main degradative pathway consists of oxidation of tyrosine to homogentisic acid and then to furmarate and acetoacetate, and ultimately to CO_2. Some of the phenylalanine or tyrosine not used for protein synthesis and not catabolized to CO_2 is used for synthesis of several important body compounds. Some of the tyrosine is iodinated to the hormone thyroxine, some is metabolized through dopamine to norepinephrine and epinephrine (both vasoactive amines), and some is metabolized via the copper-containing enzyme tyrosinase to the pigments melanin (black) and dopachrome (red). The latter two compounds are synthesized primarily in dermal pigment cells known as melanocytes. Ultraviolet light, melanocyte stimulating hormone (MSH) in the pituitary gland and melatonin in the pineal gland function to regulate the synthesis of these pigments.



(DHB)

See also: Epinephrine; Essential amino acids; Melatonin; Norepinephrine; Thyroid; Tyrosine

Phosphatidylcholine Derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with choline. Also known as lecithin, phosphatidylcholine is the most abundant phospholipid of the cell membrane and is one of the major structural phospholipids in the brain, comprising approximately 15% of the total lipid. Some lecithins are very effective emulsifiers and surface-active agents that prevent adhesion. They are synthesized from fatty acyl-CoAs and glycerol by several enzymatic steps that are shared with triacylglycerol synthesis. The fatty acid in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)
See also: Phospholipids

Phosphatidylethanolamine A derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with ethanolamine. Phosphatidylethanolamines, also called cephalins, are the major structural phospholipid in the brain, comprising approximately 20–25% of the total lipid, and are also the precursor of phosphatidylserine. Phosphatidylethanolamine is synthesized from fatty acyl-CoAs and glycerol in several enzymatic steps that are shared with triacylglycerol synthesis. The fatty acid in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)
See also: Phospholipids

Phosphatidylglycerol A phospholipid consisting of glycerol esterified in the *sn*-1 and *sn*-2 positions with fatty acids, and in the *sn*-3 position with glycerol-3-phosphate. Synthesized in eukaryotes and bacteria from triacylglycerols and glycerol-3-phosphate. Constituent of most phospholipids. The fatty acid in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)
See also: Phospholipids

Phosphatidylinositol A derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with inositol. In eukaryotes it is the major phospholipid in plasma membranes, where it plays a central role in signal transduction. The fatty acid in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)
See also: Phospholipids

Phosphatidylserine A derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with serine. A slowly metabolized structural phospholipid found in most tissues, and major structural phospholipid in the brain. Derived from phosphaditylethanolamine in mammals (phosphaditylethanolamine + L-serine α-phosphatidylserine + ethanolamine) and synthesized from cytidine diphosphate-diacylglycerol in bacteria. The fatty acid in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)
See also: Phospholipids

Phospholipase One of a group of lipolytic enzymes, e.g. phospholipase A_2 (lecithinase A; phosphatidylcholine 2-acylhydrolase; EC 3.1.1.4), which is secreted as an inactive precursor from the pancreas into the duodenum, where it is activated by trypsin. The active enzyme hydrolyses phospholipids into fatty acids and lysophospholipids (SB)

Phospholipids Derivatives of phosphatidic acid (diacylglycerol-3-phosphate) in which the phosphate is esterified with the hydroxyl of a suitable alcohol. Phospholipids include phosphatidic acid and phosphatidylglycerol, phosphatidylcholine, phosphatidylethanolamine, phosphatidylinositol, phosphatidylserine, lysophospholipids, plasmalogens and sphingomyelins. All of these are phosphoacylglycerols except for the sphingomyelins, which do not contain glycerol. Phospholipids are main lipid constituents of cell membranes and contain hydrophobic (fatty acid) and hydrophilic (frequently an amino acid) polar ends. (JAM)
See also: individual phospholipids

Phosphorus Phosphorus (P) is a non-metallic element with an atomic mass of 30.97. It exists in biological systems combined primarily with four oxygen atoms to form the phosphate radical. About 70% of the phosphate in the body is in organic forms while 30% is inorganic. The large majority of the latter is in the sodium and potassium salts of $H_2PO_4^-$ and HPO_4^{2-}, and a small amount of PO_4^{3-}. Phosphorus is an essential nutrient, with a large amount in the bony structures of the body, where it combines with calcium in hydroxyapatite crystals in a 2:1 ratio of Ca:P. Phosphorus as the phosphate radical plays many roles in the metabolic machinery of the body. One of the most important is in the molecular structure of nucleic acids to form the genetic code. Phosphates as phospholipids also are important in the maintenance of cell membrane integrity. Another very important role is in the transfer of metabolic energy in the form of high-energy phosphate bonds such as phosphoenolpyruvate, 1,3-diphosphoglycerate and phosphocreatine, and nucleotides such as ATP, ADP, GTP and others.

Because phosphate is ubiquitous, its concentration in plant material can be fairly high, ranging from 0.1 to 0.3% in hays and grasses and 0.4 to 0.8% in grains and seeds. Thus, a phosphorus deficiency is seldom seen in animals; however, much of the phosphorus in grains and seeds is in the form of phytic acid and may not be as available for absorption as are the inorganic forms. This is especially true for non-ruminant animals, which do not have active phytases in the intestine that hydrolyse the phytic acid to release P. Microbial phytases are commonly added to the diets of pigs and poultry to aid in phosphorus utilization. In the presence of calcium, phytic acid can bind certain trace elements, such as zinc and iron, and reduce their absorption. If the animal is consuming low to marginal amounts of the trace elements, the reduced absorption rate can lead to signs of deficiency.

Inorganic P is readily absorbed from the small intestine, an active process that is stimulated by 1,25-dihydroxy vitamin D_3, the hormone metabolite of vitamin D. The normal concentration of free phosphorus in plasma is about 30 mg l^{-1}. The phosphorus status of an animal is most often determined by measuring this parameter. Because phosphate is involved in metabolic energy transfer, deficiency signs can be manifested in many ways, including anorexia, lethargy, joint stiffness and nervous-system disorders.

Because of its importance in metabolic regulation, the dietary requirement for P is high relative to other minerals. According to the US National Research Council, the P requirement for beef and dairy cattle is 3 g kg^{-1} diet for growing and lactating animals; for sheep it ranges from 1.6 to 3.8 g kg^{-1}; for poultry and horses it is 3–4 g kg^{-1}; and for pigs it ranges from 4 to 7 g P kg^{-1} diet, depending on age, with younger animals requiring more than older ones. The severity of high P intake is tied to the amount of calcium consumed. A low Ca:P molar ratio in the diet can lead to soft-tissue calcification, with the kidney being more affected than other organs. A dietary Ca:P molar ratio of less than 1 is not advised. (PGR)

See also: Availability; Iron; Phytate; Vitamin D; Zinc

Further reading

Berner, Y.N. (1997) Phosphorus. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements.* Marcel Dekker, New York, pp. 63–92.

Phosphorylation A process whereby an enzyme (a protein kinase) utilizes ATP to add a phosphorus atom to another molecule, most often a specific serine, threonine or tyrosine residue in a protein. Other amino acids (histidine, lysine, arginine and aspartate) can also be phosphorylated. This modification of the protein may activate (turn on) or inactivate (turn off) some function, usually enzymic, of the protein. The process is reversed by dephosphorylation, which is catalysed by enzymes called protein phosphatases. (NJB)

Photoperiod The period of **light** within a light/dark cycle that is interpreted as day; it is synonymous with day length. It is the most potent part of a lighting regime and it regulates the endocrine system through the pineal gland and its product, melatonin, which is secreted during the hours of darkness. Photoperiod can thereby influence virtually every aspect of production. Photoperiod influences the physiology of many mammalian species, resulting in seasonal cycles of reproductive activity, growth, food intake and pelage growth.

Wild animals show well-defined breeding seasons, but the nature and extent of these are more variable in domestic animals. Domesticated sheep, deer, goats and horses exhibit seasonality of breeding whereas cattle and swine do not. In sheep, deer and goats (short-day breeders), onset of sexual activity is triggered by the decreasing photoperiods of autumn. There are important breed differences in the duration of the breeding season; for example, the season is shorter for feral sheep breeds and for breeds of temperate latitudes (e.g. Scottish Blackface) than for tropical breeds or breeds of Mediterranean origin (e.g. Dorset Horn). Use of **melatonin** treatments to mimic short days is effective in advancing the breeding season in these species. Conversely, in mares (long-day breeders), reproductive activity is triggered by the increasing photoperiods of spring and the breeding season may be advanced by artificial light treatments. In cattle and pigs, oestrus occurs regularly throughout the year but both species show a period of reduced fertility in the summer period.

Photoperiod also has a profound effect on growth and appetite in seasonally breeding animals. Sheep and deer exhibit lower rates of growth and voluntary food intake in winter than in summer, triggered by the decreasing and increasing photoperiods of autumn and spring, respectively. Thus low intake and energy demand in short days coincide with the winter period of food shortage, providing an adaptive survival strategy. The amplitude of the appetite cycle is greater in males than in castrates or females, and differences between breeds reflect the differences in photoperiod sensitivity of their breeding activity. In production systems with winter housing, growth rates of lambs and deer can be enhanced in artificial lighting regimes by long (> 12 h) photoperiod. It follows that photoperiod and nutrition interact to affect age at puberty in these seasonal species. If spring-born offspring are not sufficiently well nourished and well grown by the autumn, their first breeding season is delayed until the following autumn. In cattle and pigs, growth and appetite are not significantly affected by photoperiod, although long day lengths tend to increase milk yield in dairy cows.

Photoperiod also influences pelage growth and moulting in deer, sheep and goats, the timing of the winter and summer pelage being appropriate for optimum survival. Thus, fleece and fibre growth are highest in autumn and winter, with clear impact for wool, cashmere and mohair production.

For avian species, photoperiods can be arbitrarily categorized as sexually stimulatory (> 10 h) or sexually non-stimulatory (< 10 h). Birds are generally reared on a non-stimulatory photoperiod prior to transfer to a stimulatory one when rapid gonadal development is required. Sexually sensitive birds reared on increasing photoperiods (spring hatched) mature earlier than birds held on constant photoperiods, which mature earlier than birds given decreasing photoperiods (autumn hatched). The degree of advance or delay in sexual maturity depends on the age at which the photoperiod is changed, the size of the change and the initial and final photoperiod. The earliest maturity for pullets reared on constant photoperiods occurs with a 10 h photoperiod, and the maximum advance in maturity is achieved by transferring pullets from 8 to 14 h at 9–10 weeks of age. Once in lay, birds on longer photoperiods tend to lay more eggs and produce larger eggs, but have higher feed intakes, thinner shells and higher mortality rates. Egg production increases with photoperiod by about 2% h^{-1} to reach a plateau at between 10 and 14 h, depending on genotype. Feed intake increases by about 1.3 g h^{-1} and egg weight by 0.1 g h^{-1} with increasing photoperiod. However, shell quality and mortality are both adversely affected by longer photoperiods. Photoperiods of > 12 h do not significantly affect body weight gain in broilers and sexually immature turkeys, though ultra-long photoperiods reduce feed conversion efficiency in broilers but improve it in older turkeys (as they become sexually mature). Mortality rate and the incidence of leg problems are positively linked to photoperiod in broilers and turkeys. In growing pullets, broiler chickens and male turkeys, body weight gain is positively correlated with photoperiod, principally because of the increased feeding opportunity on longer photoperiods, but severe feed restriction can prevent birds responding to a stimulatory lighting regime. When exposed to photoperiods that are interpreted as sexually stimulatory, male turkeys that have reached the age threshold for sexual development also have faster growth rates because of elevated plasma testosterone concentration. The effect of photoperiod on growth in female turkeys is equivocal. (PDL, CLA)

Phylloquinone 2-Me-3-phytyl-1,4-naphthoquinone, the form of vitamin K produced by plants. (JWS)

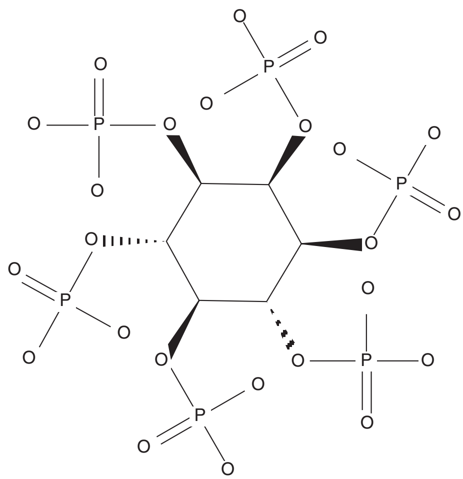
Physical activity: *see* Activity, physical

Phytase An enzyme produced by microbes (e.g. *Aspergillus niger*) that is capable of releasing the bound phosphorus from phytate, which is the major form of phosphorous in plant tissue. Phytases are produced commercially and can be added directly to diets to release phosphate from phytate while in the intestinal tract. The greatest activity of added phytase is found in the contents of the stomach and upper small intestine in pigs and in the crop and proventriculus in chickens. The addition of 500–1500 units of phytase kg^{-1} diet results in nearly complete release of phytate phosphorus. This not only increases the utilization of plant phosphorus but also reduces the need for supplemental phosphorus, resulting in lower phosphorus losses in manure. Because rumen bacteria produce phytase it is not necessary to add it to the diets of ruminant animals. (NJB)

Key reference

Anon. (1996) Phytase. In: Coelho, M.B. and Kornegay, E.T. (eds) *Animal Nutrition and Waste Management*. BSAF reference manual DC9601. BSAF, Mount Olive, New Jersey.

Phytate Phytic acid is inositolhexaphosphoric acid, $C_6H_6(OPO(OH)_2)_6$. Phytates behave as chelating agents: metals known to be chelated by phytate are calcium, cobalt, copper, iron, magnesium, manganese, nickel, selenium and zinc. Phytates are the major form in which phosphorus is found in plants and the phosphorus in cereal-based diets consequently has a low bioavailability. In maize, phytate is found mainly in the germ in a water-soluble form. In legumes, phytate is associated with protein.



(NJB)

Key reference

Harland, B.F. and Oberless, D. (1996) Phytic acid complex in feed ingredients. In: Coelho, M.B. and Kornegay, E.T. (eds) *Phytase in Animal Nutrition and Waste Management*. BSAF reference manual DC9601. BSAF, Mount Olive, New Jersey, pp. 69–75.

Phytohaemagglutinins Proteins of plant origin that possess multiple carbohydrate binding sites. They cause the clumping or agglutination of blood cells. (SEL)

See also: Lectins

Phytoplankton Phytoplankton, or microalgae, are primary producers in the aquatic food web. They use chlorophyll to convert solar energy, inorganic elements, nitrogen and carbon dioxide into carbohydrate, protein, lipid and carotenoids. Algae in marine fish culture have been used to increase the nutritional value of rotifers, as a direct source of nutrition for fish larvae, to provide background feeding for surviving prey in the rearing tanks, and to maintain light and water quality. Most of the algal species used for rotifer feeding in commercial marine fish culture belong to *Chlorophyceae*, *Prasinophyceae*, *Eustigmatophyceae*, *Prymnesiophyceae*, *Cryptophyceae* or *Bacillophyceae*. There are two predominant species: *Nannochloropsis* (*Eustigmatophyceae*, greenish yellow algae) and *Isochrysis* (*Prymnesiophyceae*, golden brown flagellate). Starter master cultures are commercially available, as are systems for containment, lighting and liquid nutrient media.

Selection of a suitable microalgal species is based on the nutritional requirements of the target fish species, the enrichment and growth of the intermediate rotifer prey, algal size and fatty acid content and, more pragmatically, the ease with which the algae can be maintained in mass culture. Algal growth is further dependent on intense illumination between 400 and 700 nm, temperature control within the species-specific optimum range, water filtration and sterilization, salinity and pH control, nutrients, aeration for suspension of cells and as a source of inorganic carbon, as well as maintaining ubiquitous stringent hygiene. Algae are generally harvested in the exponential growth phase when cells begin to divide at a constant rate. Generally, small culture volumes achieve higher cell densities due to the availability of light, but densities of < 150 million cells ml^{-1} have been reported with high-density *Nannochloropsis* systems. More common cell densities range between 2 million and 40 million cells ml^{-1}. (KP)

See also: Aquatic organisms; Fish larvae; Live fish food; Rotifer

Phytotoxins Also termed toxalbumins, phytotoxins are protein compounds produced by certain plants that provoke antibody responses. Major phytotoxins are ricin, found in castor bean (*Ricinus communis*), and robin, in black locust (*Robinia pseudo-acacia*). These highly toxic compounds produce depression, poor appetite, paralysis, abdominal pain, bloody diarrhoea, cardiac irregularities and sometimes death. (JAP)

See also: Lectins; Ricin

Pig Pigs are characterized by being hoofed (two major and two minor digits on each foot), polytocious, simple-stomached and omnivorous, having a robust but sensitive nasal disc (snout) and a sparse bristly coat. Typically the domestic pig has 38 chromosomes (2n) but the number can vary, and 36 (2n) is common in wild pigs (Bosma, 1976).

Pigs are members of the mammalian Order Artiodactyla (the even-toed ungulates) and belong to the Suborder Suina (Suiformes). At this level there are three families. Pigs are a branch of the Family Suidae and are distantly related to the peccaries (the Family Tayassuidae) and the hippopotamuses (the Family Hippopotamidae). Within the Suidae there are several genera, but wild pigs of the genus *Sus* are exclusively native to Eurasia. There are some ten species or sub-species occurring in this area of which many are very local and considered to be endangered. The domesticated pig is primarily descended from the wild boar (*Sus scrofa scrofa* L.) and some breeds may have genes from the Indian crested pig, *Sus crystatus* or *S. vittatus.*

Pigs have a poor ability to use fibrous leafy or woody materials. They compensate by being formidable excavators of roots using their specialized snout and their well-developed neck and shoulder muscles (m. brachio cephalicus). Roots are a rich source of sugars, starch and hemicelluloses which they digest easily. Pigs have virtually no ability to sweat, and cope with heat by lying in water or wallowing in mud. In hot environments, provision should be made for mist spraying or for them to wallow. Although they have only a sparse coat, adults can survive winter cold because of the thick layer of subcutaneous fat which, when vaso-constricted, provides good insulation. They are also adept at finding and using shelter if given the opportunity. In adults, there is considerable sexual dimorphism, males being larger than females, with well developed tusks and a 'shield' of collagen reinforced subcutaneous fat over the shoulders.

Pigs have been domesticated and eaten for several thousand years particularly in the Far East. Several religions regard the animal as 'unclean' and this has an historic basis. Traditionally, pigs have been kept in poor conditions and in close association with human habitation. They are opportunist omnivores and will readily consume small animals, carrion and other animal's excrement. Unfortunately, these traits can give rise to important *zoonoses.* If pigs pick up the eggs of the tapeworm *Taenia soleum* from human faeces, these develop and form cysts in the muscles and internal organs. Inadequately cooked pork from such pigs can then infect humans with tapeworm and may also cause a dangerous brain damage in a condition known as *neurocystercercosis*. Pigs can also become infected with the round worm *Trichinella* which can give rise to the painful condition in humans known as *trichinosis*. However, in developed countries, strict hygiene regulations and meat inspection ensure that human and animal health are paramount, and that the meat is perfectly safe.

The many different breeds of pig found across the world reflect past and present local needs. In earlier times, pigs were bred to produce fat meat, prized both for food energy in winter and when rendered to lard as a cooking fat. Pigs were also bred for hardiness (Duroc breed), the ability to forage (Iberian pigs and acorns), an ability to utilize poor quality and waste food products (pot-bellied pigs) and the ability to withstand extremes of heat and radiation from the sun (dark skinned and black haired breeds, e.g. the Iberian Entrepelado). The high-water mark of such diversity was probably the late 19th century. In developed countries, modern marketing methods have resulted in a dramatic loss of diversity in breed types. Selection objectives have focused on large size, feed utilization, leanness, and in terms of colour, white skin and white bristles. Many high quality markets regard dark bristles deeply embedded in the skin and fat as distasteful. Now, modern hybrids (the product of several breeds) contain a high proportion of genes from the Yorkshire (Large White) and Landrace breeds. Adult boars can weigh as much as 500 kg and adult females 400 kg. At the other end of the scale there are many breeds of miniature pig which are finding an increasing role as pets and as laboratory animals with a physiology similar to humans. An extreme type is the Mexican Cuino in which the adults do not usually exceed 15 kg.

In modern hybrids, puberty for males and females is reached between 150 and 200 days of age depending on breed, nutrition and social environment. Unbred young females are called maiden gilts, and females embarking on gestation for a second litter are usually considered as **sows**. Uncastrated males are referred to as **boars** or entires, and castrated males as hogs or barrows. The average length of the oestrus cycle is about 21 days. Gestation length is on average about 115 days (3 months, 3 weeks and 3 days) but this can range from 112 to 118 days. The number born in a single litter is between 8 and 14 with an average birthweight of about 1.3 kg. Piglets that are small at birth (< 1 kg) are very vulnerable, and neonatal mortality often runs at 15% or more. Prolific Chinese breeds such as the Meishan, can average 14 or more and may produce as many as 24 piglets in a single litter.

In nature, **piglets** become nutritionally independent of the dam after about 12 weeks, but most farmers practice a degree of early-weaning at 3–5 weeks of age. Segregated early weaning (at about 14 days) is a component of a specific health strategy in which piglets, still primed with passive immunoglobulins from the colostrum, are moved to a clean, rearing environment, so preventing the transfer of important diseases from dam to offspring. Special diets are required for early-weaned pigs incorporating easily digested proteins and preferably some dried milk products. From about 10 weeks of age (30 kg) pigs are normally fed diets based on cereal (mainly for energy) and oil-extracted soybean (high in protein) or their equivalent. Nutrient requirements and diets are given by NRC (1998) and English *et al.* (1996). Under commercial conditions, pigs growing from 30 to 100 kg have growth rates of around 600–800 g per day with a ratio of feed to live gain of about 3.3:1. However, in specialized healthy environments with low stocking densities (e.g. boar-performance testing stations), growth rates can exceed 1500 g per day with feed/gain ratios as low as 1.9:1.

Slaughter weights vary according to local market preferences. Pigs slaughtered for light pork are usually marketed at 65–70 kg live weight, for the quality bacon market at 90–100 kg and for manufacturing and detailed butchering at about 120–140 kg. Entire males have a superior feed conversion, growth rate and leanness compared with females and castrates. In many countries however, male pigs not destined for breeding, are castrated because of concerns about 'boar taint' in the meat. The odour is associated with the presence of skatole and a steroid androstenone (5α-androst-16-en-3-one), which is closely related to the male sex pheromone (Lundström *et al.*, 1994). A number of studies have shown that at weights of less than 100 kg this is not a major consideration with consumers and castration is not practised in such countries as the UK, Denmark or Australia (Willeke *et al.*, 1993). **Pig meat** is one of the most versatile of all meats and is 'manufactured', into a wide range of products including ham, bacon and sausages. High-value products include Parma and Iberian hams and fermented sausages such as salami and cherizo.

In the year 2000, on a world basis, 91 million metric tonnes of pig meat were produced. This exceeded the combined total for beef, sheep and goats by 33% and the combined total for chicken and turkey by 50% (FAO 2002), making pig meat the most popular of all meat types. (VRF)

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Pig feeding The feeding of **pigs** is typically divided into stages based on the production cycle and housing changes. Suckling piglets derive most of their nutrients from the sow's milk, but it is common practice to offer some solid feed (**creep feed**) or supplementary milk if weaning age is greater than 3 weeks. After weaning, and depending on weaning age, pigs will be fed a series of two to four different diets until reaching a weight of 20–30 kg. These diets are initially of high digestibility and nutrient density, but decrease in quality and cost as the pigs mature and achieve higher voluntary intake. Pigs are normally fed frequently to appetite or *ad libitum* at this time, although slight feed restriction in the first few days may reduce the risk of health problems. The number of different diets fed in the growing and finishing phase will depend on the size of the farm and the housing arrangements. Since the nutrient requirements of the pig change continuously as it grows, with appetite increasing and the required protein:energy ratio in the diet decreasing, greatest efficiency is achieved by making frequent changes to the diet specification. This is possible on large units with all-in all-out buildings, where all pigs in the feeding system are of similar age and weight, but it is impractical on smaller units where buildings contain a mixed-age population. In this situation the best compromise diet to meet the needs of all the different pigs must be selected, but this will inevitably either restrict the performance of the younger pigs or oversupply the older animals. Whilst this problem could be overcome by blending two different diets, this is not common practice. On most farms, therefore, two or three different diets are fed during the period from 25 kg to slaughter, depending on the logistics of housing and food supply. It is increasingly common with modern selected genotypes to feed these diets *ad libitum* throughout the life of the pigs. However, in situations where castrated males, unimproved genotypes, heavy slaughter weights or very strict carcass fat limitations are present, it is normal practice to restrict the amount of food given after 60–70 kg liveweight. This reduces fat deposition and improves carcass quality and feed utilization efficiency, but also reduces growth rate.

Within the breeding herd, the requirements of the gestating and lactating sows are very different and it is common to have two separate diets for these stages. On smaller units, a single diet can be used for all **sows** if some inefficiency is accepted. Gestating sows are normally fed a restricted amount of feed in one or two daily meals to meet their limited requirements for maintenance, growth and pregnancy but prevent obesity. In a group feeding system, this can give rise to competition between animals for food, penalizing young and low-ranking animals. To avoid this, sows may be individually housed and fed in stalls or separately tethered (now being phased out by law in the European Community), temporarily confined in individual stalls during feeding or fed individually in turn by computer-controlled feeding stations. In lactation, sows are normally housed individually in farrowing crates and must achieve a high feed intake to meet the demands for milk production. They are normally fed an increasing amount of feed from the time of farrowing until fed to appetite by 7–10 days of lactation. High feed intake is encouraged by providing fresh feed two or three times daily, or by feeding *ad libitum* with plentiful water available. A diet with high nutrient density helps to minimize body condition loss in young animals, which have limited appetites. This is especially important in countries with high environmental temperatures that reduce voluntary feed intake.

The diets fed to pigs are generally based on cereals and vegetable proteins, which provide the most cost-effective ingredients in the majority of situations. However, since the pig is an omnivore, it can efficiently utilize a very wide range of raw materials and was historically used to convert unwanted by-product materials into valuable meat. Commercial compound diets are usually formulated from the available raw materials by computer, using a least-cost formulation process, such that all essential nutrients are supplied in the correct balance at the lowest unit cost. Nutritional knowledge is used to set the appropriate nutrient targets for each production stage, and to impose constraints on the permitted inclusion levels of individual raw materials where this is necessitated by the presence of antinutritive factors, or by detrimental influences on palatability, meat quality or diet manufacturing processes.

Pigs do not produce the necessary enzymes for fibre digestion and, unlike ruminants, do not have a highly efficient gut fermentation system which enables them to perform well on high-forage diets. Adult animals can utilize fibre through microbial fermentation in the large intestine but the energy yield and efficiency of this process are low in younger animals, where gut capacity is more limited and rate of passage more rapid. Although it is possible to feed pigs on bulky vegetable material, such as root crops and fresh or ensiled herbage or cereals, this presents logistical difficulties in large intensive production units and it is normal to offer only a single compound diet. This diet can be presented in meal or pellet form, or as a liquid feed. Raw materials such as cereals are generally ground to reduce particle size and thus improve digestibility by facilitating enzyme activity. Since excessive fineness of grind can result in gastric ulceration, a 4–5 mm screen is recommended. Digestibility can be further enhanced by the pelleting process, in which heat and pressure are applied. The main benefits of pelleting lie in the enhancement of feed intake and reduction in feed wastage which occur under practical feeding conditions. Dry compound feeds can be handled in bulk from manufacture to trough using pneumatic and mechanical auger systems. Alternatively, automation can be achieved in wet feeding systems, which also permit liquid by-products to be incorporated on-farm. Ingredients are mixed in the correct proportions, often under computer control, and the final feed, with a water:meal ratio of 3:1 or 4:1, is then pumped to the destination building via a pipeline system. Timed valves regulate the amount of feed dispensed to each pen. In addition to reducing feed costs by allowing the use of by-products, liquid feed can enhance intake and growth rate. (SAE)

Pig meat The body tissue of the pig that enters the human food chain and is the main end-product of the feeding of commercial growing pigs. Typical lean muscle tissue of pork contains approximately 70% water, 20% protein, 9% lipid and 1% ash. The amino acid composition of the muscle protein is relatively invariant (see table). The ratio of lean to fat will depend on the joint selected, the genotype and nutrition of the pig and the extent of post-slaughter fat trimming. A typical loin or shoulder joint will have a fat content of approximately 40%, whilst a leg joint will typically contain only 20%. At the extreme, trimmed lean pork may have a fat level as low as 3.5%. Some breeds, such as the Duroc and Hampshire, produce meat with a higher level of intramuscular or 'marbling'

Amino acid and fatty acid composition of pig meat.

Amino acid composition	(%)	Fatty acid composition	(%)
Arginine	12.2	14:0	1.5
Cystine	2.6	14:1	0.5
Histidine	8.9	15:0	0
Isoleucine	9.2	16:0	24.0
Leucine	14.5	16:1	3.5
Lysine	19.7	17:0	0.5
Methionine	5.6	18:0	14.0
Phenylalanine	7.9	18:1	43.0
Threonine	8.9	18:2	9.5
Tryptophan	2.3	18:3	1.0
Tyrosine	7.6	20:0	0.5
Valine	9.9	20:1	1.0
Others			1.5

fat and this may improve eating quality. The fatty acid composition of pig meat (see table) typically shows a saturated:unsaturated ratio of 0.6–0.7. This ratio can be modified by the level and composition of the feed given to the pig. Pigs that are very lean at the time of slaughter tend to have less saturated fat, whilst those with higher body fat content, derived from diets based on cereals, produce more saturated fat. If the diet included ingredients high in oil, the fatty acid composition of that oil is rapidly reflected in body fat composition, with changes being apparent in 1–2 weeks. (SAE)

Pigeon pea Pigeon peas (*Cajanus cajan*) are an important grain legume in the tropics. They are grown mainly for their seed, which has an apparent metabolizable energy of 12–14 MJ kg^{-1} for sheep and poultry. The forage material can be fed to ruminants. (TA)

Piglets The nutritional management of young piglets is critical for both growth and health. In the first weeks of life, piglets can exist solely on their mother's milk. Immediately after birth, the colostrum (first milk) provides not only a source of nutrients but also immunoglobulins, which can be absorbed intact from the gut to provide systemic immune protection. This absorptive ability is lost within the first day after birth and, whilst immunoglobulins in milk still provide local protection within the gut, the nutritional role of the milk assumes primary importance. Daily milk intake increases from about 500 g per pig in the days after farrowing to a maximum of 800–1000 g when milk yield peaks at about 3 weeks. The intake that is achieved by each individual piglet depends on the teat that it is sucking. Within the first day of life, a 'teat order' is established and each piglet always returns to the same teat. Stronger piglets tend to appropriate and defend the higher-yielding mammary glands, whilst weaker piglets are relegated to poorer glands, often in the posterior region of the udder. By about 2 weeks of age, the appetite of the piglets exceeds the available milk and piglets start to look for other food. This is usually provided in the form of **creep feed** when **weaning** occurs at more than 3 weeks of age. Piglets then progressively increase their solid food intake as their own nutrient requirements continue to increase while the milk yield of the sow declines.

Commercial production impairs the natural evolution of feeding behaviour by imposing abrupt early weaning. This imposes a major nutritional challenge, since the composition of the sow's milk to which the pigs are accustomed (see table) is very different to that which can be supplied by a compound diet.

Composition of sow's milk.

	% Fresh milk	% Milk energy
Crude protein	6	21
Fat	10	65
Lactose	5	14
Water	79	

Sow's milk provides a diet with concentrated energy in the form of highly digestible, emulsified fat. It also provides sugar (lactose) and easily digestible protein (casein). Thus the digestive enzymes of the suckling piglet are adapted to dealing with these substrates, whilst the ability to digest more complex carbohydrates, proteins and fats is very limited. As the piglet starts to consume solid food, the activity of the enzymes such as amylase, maltase and sucrase, necessary to digest more complex diets, is induced. However, when weaning occurs abruptly at 3 weeks of age or less, the piglet will have little experience of solid food and an immature enzyme system. It also has a poorly developed acid secretion and difficulty in providing the optimal pH for gastric digestion and neutralization of ingested pathogens. This, together with the removal of protective milk immunoglobulins, makes the piglet very vulnerable to pathogenic bacteria in the environment.

During the **suckling** phase, the surface of the small intestine is covered by finger-like villi which project into the lumen of the gut and maximize surface area for absorption. Immediately following weaning, these villi can often become stunted, resulting in poor absorptive capacity. This is a consequence of inadequate feed intake during the weaning transition. To minimize the problems experienced at weaning, the nutritional strategy must be to maximize consumption and digestion of solid feed. Palatability of the diet is therefore of great importance. Both palatability and digestibility can be enhanced by inclusion of milk powder or related products such as casein and whey powder. Flavourings and sweeteners are also often included in diets for newly weaned piglets, although scientific evidence for their efficacy is limited.

Because voluntary feed intake is initially low, a high nutrient-density diet is desirable to minimize body tissue catabolism after weaning. Diets typically contain a high level of oil (up to 10% in specialist diets for piglets weaned very early) but it is important that this is of good quality with adequate antioxidant and vitamin E also present in the diet. Since amylase activity is initially poorly developed, precooking the cereal component of the diet to rupture the starch grains is also beneficial. Flaking, micronizing or extruding are common commercial methods. A high level of fibre in the diet is undesirable, since the greater dietary bulk and dilution of energy are deleterious when appetite is limiting and the small gut capacity of the young piglet leaves little scope for fermentation. However, some readily fermentable fibre such as that derived from oats or sugarbeet can be beneficial in promoting a favourable gut microflora and reducing colonization by pathogenic bacteria.

The nature of the protein component of the diet is just as important as the energy source, since poorly digested protein can cause diarrhoea. The most digestible proteins are those in milk products. Other animal proteins such as fish meal and meat meal (provided they are dried at low temperature) are the best substitute, though the use of meat meals is now prohibited in some countries due to concern about possible transmission of disease agents. Vegetable proteins are less digestible and are often associated with antinutritive factors with which the young piglet is poorly equipped to cope. For this reason, the inclusion rate of ingredients such as soybean meal, which may contain protease inhibitors and lectins, should be limited whilst products such as rapeseed meal, with unpalatable glucosinolates, should be completely omitted. However, vegetable protein isolates, from which antinutritive and antigenic factors have been removed by previous thermal, chemical and enzymatic treatment, can provide an acceptable alternative to animal proteins. In order to optimize amino acid balance and reduce the total amount of crude protein that must be digested, the use of synthetic amino acids can be very beneficial.

Although not directly nutritional, other aspects of raw material selection for piglet diets must also be considered. Because of the difficulty that the piglet initially experiences in secreting adequate hydrochloric acid, a lower buffering capacity of the diet assists in achieving an optimal gastric pH for enzyme activity. Selection of ingredients with a low acid-binding capacity and minimizing inclusion of powerful buffers such as limestone (calcium carbonate) will facilitate digestion and mimimize risk of diarrhoea.

It is usual to feed newly weaned piglets *ad libitum* to maximize feed intake. Since feed freshness is an important factor in palatability, the frequent feeding of small meals to appetite may be practised as an alternative in the first week after weaning. However, with poorer quality diets it may be necessary to restrict feed intake in the first week to prevent overtaxing of the immature digestive system and resultant diarrhoea. This approach requires that adequate trough space be provided to enable all piglets to eat simultaneously. The appetite of the young piglet increases rapidly in the post-weaning period. As intake and digestive maturity improve, the cost of the diet can be reduced by lowering nutrient density and increasing inclusion of less sophisticated raw materials. It is therefore common to feed two, or even three, different diets in the period between weaning and 20 kg liveweight. (SAE)

See also: Creep feeding; Early weaning; Runt

Pigments: *see* Carotenoids; Yolk pigment

Pine needle poisoning Typically associated with late-term abortion in cattle induced by the labdane resin acid, isocupressic acid, found in ponderosa and other pines and some juniper species. Occasional toxicoses occur, resulting in nephrosis and neurological dysfunction. The associated toxins are the abietane-type resin acids (abietic and dehydroabietic acid), present in high concentrations in the new growth tips of pine branches. (KEP)

Pineapple (*Ananas comosus* (L.) Merr.) A perennial stemless plant with narrow fibrous leaves. Chopped leaves can be fed fresh, dried or ensiled to ruminants. Up to 20 kg fresh leaves day^{-1} can be fed to cattle without harmful effects. Leaves are not used for non-ruminants. The main product is the fruit, from which the outer peel and central core are discarded as waste. Waste, also called pineapple bran, accounts for half of the total fruit weight, equivalent to about 10 t ha^{-1}. Waste can be fed fresh or dried. It is also sometimes fed with molasses. Waste, mixed with grass, is a good roughage feed for ruminants, having high nitrogen-free extract and fibre contents, but it is low in protein. Pineapple waste can be used in feed for older pigs but adversely affects growth and feed conversion efficiency in chicks, even at low levels of inclusion. (LR)

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Pining Pining (or pine) is the term used to describe the symptoms of a deficiency of cobalt in sheep and cattle. In ruminants, cobalt is used by rumen bacteria to synthesize vitamin B_{12} and other cobalt-containing analogues, whereas in non-ruminants a source of vitamin B_{12} is required in the diet rather than cobalt. The disease causes loss of appetite, stunted growth, matting of the coat (which is usually in poor condition), sunken eyes, anaemia and eventually death. It can be most effectively remedied by an intra-ruminal cobalt bullet. (CJCP)

Pinocytosis A method of absorption in which cells of the small intestine engulf large molecules or ions in a manner similar to that in which an amoeba engulfs its food. Pinocytosis occurs in newborn mammals and allows the large immunoglobulins from colostrum to be absorbed intact. (SB)

Plaice A common name applied primarily to two species of right-eyed North Atlantic flatfishes (Pleuronectidae). The American plaice (*Hippoglossoides platessoides*, called the long rough dab in England), a cold-water species of commercial importance in Canada, is distributed on both sides of the North Atlantic. The European plaice (*Pleuronectes platessa*), an important commercial flatfish in Europe, ranges from the Mediterranean Sea to the White Sea. (RHP)

Nutrient composition of pineapple (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh leaves	20.6	9.1	23.6	4.9	1.6	60.8		
Dried waste (bran)	87.6	3.5	16.2	5.2	0.5	74.6	0.29	0.11

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical digestibility (%) and ME content of pineapple leaves and bran.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminants					
Leaves	77.1	81.8	60.2	76.0	11.52
Waste (bran)	0	76.7	0	79.2	10.85

ME, metabolizable energy.

Plane of nutrition A description of the nutritional regimen relative to some reference value such as the **maintenance** requirement or the intake when food is offered *ad libitum* (e.g. 1.50 × maintenance; 0.90 of *ad libitum*). It is not a precise term and is variously used to refer to food intake by weight, energy intake or the intake of particular nutrients. (MMacL)
See also: Energy intake; Energy requirements

Plankton: *see* Phytoplankton

Plant oestrogens Many plants contain substances which, when consumed by animals, act like the female hormone oestrogen. These substances, termed phyto-oestrogens, are found in lucerne (alfalfa), clovers, peas, beans and other feeds. In some cases the chemical structure of the phyto-oestrogens is similar to that of mammalian oestrogens. Phyto-oestrogens bind oestrogen receptors in the brain and reproductive tract, which can cause premature growth of the uterus in young animals. Because phyto-oestrogens may have a negative feedback effect on the hypothalamus, they can also decrease the amount of natural oestrogen produced by the animal's ovaries. Without the natural ovarian oestrogens, the subsequent fertility of the animal consuming these plants may be affected. Oestrogenic compounds can also be found in plant material as a result of fungal contamination. Zearalenone is a mycotoxin found in mouldy maize, wheat, barley and other grains. It can cause severe reproductive problems in animals, especially pigs. In controlled amounts, zearalenone has been incorporated into implants and used as a growth promoter in beef animals. (JPG)

Plant oils: *see* Cottonseed; Groundnut; Linseed; Oilseed; Rape; Soybean

Plantain: *see* Banana

Plasma: *see* Blood plasma

Poisoning Farm animals are susceptible to a wide range of poisons or toxins derived from plants, microorganisms or chemicals. Many feeds contain naturally occurring toxic substances such as gossypol in cottonseed and haemagglutinins in legume seeds; grazing animals may be accidentally exposed to the poisons of bracken and ragwort. Feeds may be contaminated with fungal toxins such as ergot and aflatoxin. A number of infectious microorganisms produce toxins that lead to gastrointestinal disorders. Animals may also be exposed to herbicide and pesticide residues. (MFF)
See also: Aflatoxins; Algal toxins; Alkaloids; Aspergillosis; Botulism; Bracken fern; Carcinogens; Castor bean; Cyanide; Cyclopropenoic fatty acids; Deoxynivalenol; Dioxin; Endotoxins; Ergot; Fumonisins; Gizzerosine; Glucosinolates; Gossypol; Heavy metals; Herbicide residues; Insecticide residues; Kale; Lathyrism; Lead; Lectins; Leucaena; Lupinosis; Marine toxins; Mercury; Mimosine; Mustard; Mycotoxins; N-nitroso compounds; Nitrosamines; Ochratoxins; Pesticides; Phytotoxins; Pine needle poisoning; Poisonous plants; Polychlorinated biphenyls; Polycyclic aromatic hydrocarbons; Ragwort poisoning; Ricin; Saponins; Solanin; Thiocyanates; Trichothecenes; Vicine; Vomitoxin (MHR)

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Pollards: *see* Milling by-products

Polyamines The polyamines spermidine ($NH_2{\cdot}(CH_2)_4{\cdot}NH{\cdot}(CH_2)_3{\cdot}NH_2$) and spermine ($H_2N{\cdot}(CH_2)_3{\cdot}NH{\cdot}(CH_2)_4{\cdot}NH{\cdot}(CH_2)_3{\cdot}NH_2$) are derived from the amino acid ornithine which is decarboxylated to provide the four-carbon diamino compound, putrescine

Poisonous plants

Scientific name	Toxin	Disease
North America		
Hymenoxys odorata	Hymenoxin	Gastroenteritis
Zigadenus spp.	Steroidal alkaloids	Convulsions
Conium maculatum	Piperidine alkaloids	Birth defects, respiratory arrest
Delphinium spp.	Norditerpene alkaloids	Paralysis, bloat, respiratory failure
Astragalus, *Oxytropis* spp.	Swainsonine	Wasting disease, neurological dysfunction
Astragalus spp.	Nitropropanol	Emphysema, locomotor dysfunction
Lupinus spp.	Quinolizidine alkaloids	Respiratory paralysis
	Piperidine alkaloids	Crooked calf disease
Senecio spp.	Pyrrolizidine alkaloids	Liver disease
Cassia spp.	Unknown	Myopathy
Eupatorium rugosum	Tremetol	Trembles
Pinus ponderosa	Isocupressic acid	Abortions in cattle
South America		
Palicourea marcgravii	Monofluoracetic acid	Heart failure
Arrabidaea spp.	Unknown	Sudden death
Mascagnia spp.	Unknown	Sudden death
Ateleia glazioviana	Unknown	Heart fibrosis, abortion
Baccharis coridifolia	Trichothecenes	Gastroenteritis
Cestrum spp.	Parquin	Liver necrosis
Senecio spp.	Pyrrolizidine alkaloids	Liver disease
Pteridium aquilinum	Ptaquiloside	Enzootic haematuria, anaemia, neurological disease
Solanum malacoxylon	Vitamin D_3-like glycoside	Metastatic calcification
Nierembergia veitchi	Vitamin D_3-like glycoside	Metastatic calcification
Australia and New Zealand		
Coriaria spp.	Tutin	CNS lesions
Acacia georginae	Fluoroacetate	Heart failure
Gastrolobium, *Oxylobium*	Fluoroacetate	Heart failure
Erythrophloeun chlorostachys	Cassaine	Cardiotoxin
Crotalaria spp.	Pyrrolizidine alkaloids	Liver, lung and kidney lesions
Cycas, *Macrozamia* spp.	Methyo-azoxymethanol	Liver necrosis, gastroenteritis
Indigofera spp.	Indospicine, nitrotoxin	Birdsville disease
Homeria spp.	Bufadienolides	Gastroenteritis
Lantana camara	Lantanin	Liver damage
Pimelea spp.	Unknown	Gastroenteritis
Pteridium esculentum	Ptaquiloside	Enzootic haematuria, anaemia, neurological disease
Swainsona spp.	Swainsonine	Wasting disease
Neobassia proceriflora	Oxalates	Kidney damage
Tribulus terrestris	Unknown	Liver disease, secondary photosensitivity
Heliotropium spp.	Pyrrolizidine alkaloids	Liver disease
Echium plantaginium	Pyrrolizidine alkaloids	Liver disease
South Africa		
Dichapetalum cymosum	Monofluoroacetate	Heart damage
Pachystigma spp.	Unknown	Heart failure
Tribulus terrestris	Unknown	Secondary photosensitivity
Lantana cannara	Lantanin	Liver damage

Continued

Continued

Scientific name	Toxin	Disease
Lasiospermum bipinnatum	Furanosesquiterpene	Liver damage, secondary photosensitivity
Asaemia axillaris	Furanosesquiterpene	Liver damage, secondary photosensitivity
Senecio spp.	Pyrrolizidine alkaloids	Liver disease
Geigera spp.	Sesquiterpene lactones	Gastroenteritis
Pennisetum clandestinum	Oxalates, nitrates	Respiratory failure
Ornithogalum spp.	Unknown	Diarrhoea
Gnidia spp.	Daphentoxin	Diarrhoea
Salsola tuberculatiformis	Unknown	Distocia
Crotalaria spp.	Pyrrolizidine alkaloids	Lung lesion
Europe		
Colchicum autumnale	Colchicin	Gastroenteritis
Solanum dulcamara	Solasodin	Birth defects
Ranunculus acer	Protoanemonin	Gastroenteritis
Brassica spp.	Isothiocyanates	Gastroenteritis
Taxus baccata	Taxines	Cardiac arrest
Quercus spp.	Tannins	Gastroenteritis
Senecio jacobeae	Pyrrolizidine alkaloids	Liver disease

($NH_2 \cdot (CH_2)_4 \cdot NH_2$) and methionine, which provides its amino-N and 2, 3 and 4 carbons via *S*-adenosylmethionine. Spermidine is converted to spermine by a second addition of the methionine amino-N and 2, 3 and 4 carbons obtained from *S*-adenosylmethionine. Polyamines are required for cellular proliferation and growth. Since they have multiple positive charges, they are found associated with the polyanions DNA and RNA. (NJB)

Polychlorinated biphenyls Polychlorinated biphenyls (PCBs) consist of two chlorinated benzene rings joined together. They are structurally similar to the insecticide DDT. PCBs were used as non-flammable oils in transformers, condensers and paints, as well as other industrial applications. Because they are persistent environmental contaminants, their industrial use has been greatly restricted. They are toxic to wildlife, especially birds, and cause impaired egg hatchability, tissue damage and mortality. 'Aroclor' is a common PCB. (PC)

Polycyclic aromatic hydrocarbons (PAH) Compounds composed of carbon and hydrogen that contain two or more fused aromatic rings. There are approximately 163 PAHs, many of which are known for their carcinogenic and mutagenic properties. PAHs containing four or more rings that are not co-linear are carcinogenic, e.g. 1,2-benzathracene. PAHs are formed both naturally, from biosynthesis, natural combustion and long-term degradation followed by synthesis from biological material, and from anthropogenic sources through incomplete combustion of organic material. Their occurrence in complex environmental mixtures makes their detection, identification and quantification challenging. (JEM)

Polyenoic fatty acids: *see* Polyunsaturated fatty acids

Polyglutamates Tetrahydrofolate substrates ($PteGlu_n$) found in foods and cell extracts. The form absorbed from food in the intestine is tetrahydrofolatemonoglutamate ($PteGlu_1$). In cells, polyglutamates ($PteGlu_{1-7}$) are formed by successive additions of γ-glutamate, the most abundant form being the pentaglutamate. Addition of γ-glutamates lowers the K_m for these substrates. (NJB)

Key reference

Shane, B. (1982) High performance liquid chromatography of folates: identification of poly-τ-glutamate chain lengths of labeled and unlabeled folates. *American Journal of Clinical Nutrition* 35, 599–608.

Polyphenols Compounds that contain more than one hydroxylated phenyl group. Although the term polyphenol is more correctly limited to lignans, lignin and tannins, which are polymers, it is also used to refer to other phenolic compounds such as hydroxy cinnamic acids, monolignols and flavonoids. Plant polyphenols have several nutritional effects. Tannins inhibit the digestion and absorption of protein. Lignin prevents the fermentation of cell wall polysaccharides by anaerobic gut microorganisms. Many flavonoids have antioxidant properties that are similar to vitamin E. (NJB)

Polysaccharides Carbohydrate polymers that contain periodically repeating structures in which the dominant, but not necessarily exclusive, interunit linkages are of the *O*-glycosidic type. This classification includes polymers consisting entirely of monosaccharide monomers as well as proteoglycans, peptidoglycans, lipopolysaccharides and teichoic acids. Homopolysaccharides are polymers of a single monosaccharide (e.g. glucose in starch and cellulose). Heteropolysaccharides have more than one monosaccharide in the polymeric structure (e.g. arabinose and xylose in arabinoxylans). (JAM, JDR)
See also: Carbohydrates; Cellulose; Dietary fibre; Hemicelluloses; Pectic substances; Starch

Polyunsaturated fatty acids (PUFAs) Long-chain fatty acids (C-18 to C-22) that contain more than one unsaturated (·HC=CH·) carbon–carbon linkage. They are classified into two groups: n-3 and n-6. In the n-3 group the first double bond is between carbons 3 and 4, counting from the terminal methyl (CH_3·) carbon, and in the n-6 group the first double bond is between carbons 6 and 7 from the methyl end. For example, linolenic acid (all-*cis*-9,12,15-octadecatrienoic acid) is designated 18:3 n-3 and arachidonic acid (all-*cis*-5,8,11,14-eicosatetraenoic acid) is designated 20:4 n-6. (NJB)

Ponds: *see* Fish pond

Pork The unprocessed meat of **pigs**. Pig meat is also cured, and may additionally be smoked, to produce ham and bacon. (MFF)

Postabsorptive state The state of an animal after it has digested and absorbed the nutrients consumed in a meal. (JMW)

Potassium Potassium (K) is an alkali metal with an atomic mass of 39.098. Potassium is absolutely essential in the diet of animals. In mammalian systems, it is usually associated with the intracellular fluid. The intestinal absorption of K is not regulated per se, but is facilitated by a number of pumps, co-transporters and conductance channels. These include (located in cell membranes and involving K exchange) the Na,K-ATPase pump, the H,K-ATPase pump and the Na-Cl-K co-transporter. The body maintains a fairly constant amount of K. The kidneys eliminate about 95% of K absorbed beyond the body's needs and the other 5% is excreted through the gastrointestinal tract.

One of the key roles of K, along with sodium, is in the maintenance of an electrical potential across the membranes of all cells. This is accomplished to a great degree by the Na^+/K^+ pump in the membrane that exchanges three Na ions inside the cell for two K ions outside the cell. The Na/K pump is an ATPase and is especially important in the propagation of impulses in muscle and nerve cells.

The US National Research Council recommends from 6 g K kg^{-1} diet for growth to 7 g kg^{-1} for early lactation in beef cattle, and 9–10 g kg^{-1} diet for lactating dairy cows, depending on the milk yield, but only 6 g K kg^{-1} diet for growing heifers and bulls. The K requirement for pigs ranges from 1.7 to 3 g kg^{-1} diet, depending on the age of the animal: young growing pigs require more than adults. The K requirement for poultry is 2.5 g kg^{-1} diet across all age groups of the birds. For growth and maintenance of horses the requirement is 3 g kg^{-1} of diet, but it increases to 3.5 to 4.2 g kg^{-1} diet for lactating mares and working horses. The requirement for sheep ranges from 5 to 8 g kg^{-1} diet. Almost all farm animal feedstuffs are reasonably high in K concentration, but grains have less than forages. Thus, under normal feeding practices, animal diets may require supplements of K salts.

Potassium deficiency can depress plasma K concentrations, which can result in muscle paralysis and cardiac dysfunction in animals. Ingestion of high amounts of K can reduce magnesium absorption and enhance the onset of tetany, especially in ruminant animals. (PGR)
See also: Chloride; Magnesium; Sodium

Further reading

Peterson, L.N. (1997) Potassium in nutrition. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements.* Marcel Dekker, New York, pp. 153–183.

Potato Potatoes (*Solanum tuberosum*) may be fed to ruminants either raw or cooked. They can be fed whole to adult cattle but to avoid the risk of them becoming stuck in the gullet they can be fed from low troughs or they can be mashed or chopped. Dairy cattle can be given potatoes at 15 kg day^{-1} and beef cattle at 20 kg day^{-1}, or < 12% of the diet, and ewes at 3% of diet. However, as potatoes have a laxative effect they should be introduced gradually. Due to the structure of the starch granules, non-ruminants poorly digest raw potato starch: most is digested by hindgut fermentation. Raw potatoes also contain a protease inhibitor. Cooking renders the starch highly digestible and also inactivates the protease inhibitor. For these reasons potatoes should be cooked before being fed to young pigs and poultry. Sows can adapt to eating raw potatoes at < 6 kg day^{-1} or 15% of the diet, while weaners can be fed at 10%. Heavily soiled, rotten, green and sprouted potatoes should not be fed to livestock, or the sprouts should be removed before they are fed to pigs or poultry as they contain toxic alkaloids. Ensiled potato haulm can be fed to cattle at < 20 kg day^{-1} but may have a high ash content due to soil inclusion. Potato processing wastes include sludge, peelings and potato chip scraps. (JKM)

Poult A young turkey. (CN)

Poultry A general term applied to domesticated avian species but frequently used in the narrower context of domestic fowl. (KJMcC)
See also: Duck; Goose; Guineafowl; Ostrich; Turkey

Poultry by-products: *see* Feather meal; Hatchery waste; Poultry offal meal

Poultry droppings Poultry droppings are shed from the cloaca via the anus and are a mixture of faecal material from the intestine and urine. The large intestine empties into the coprodaeum and the urinary (and reproductive) tract into the urodaeum. These in turn empty into the proctodaeum which opens externally through the anus. Mixture of the faecal and urinary material can take place in the coprodaeum and the recto-colon by rhythmic contractions of the intestine, including physiological reverse peristalsis. Conservation of water and electrolytes and absorption of some nutrients may occur in the coprodaeum, recto-colon and the caeca as a consequence of the retrograde flow of the faecal–urine admixture. Re-entry of the colonic contents into the small intestine is prevented by the ileocaecal-colonic junction, which behaves as a functional sphincter. Chickens may produce > 250 g of droppings per day but this may vary markedly with total urine output.

The nutrient composition of potato.

		Nutrient composition (g kg^{-1} DM)				
	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE
Haulm	230	109	270	135	43	443
Haulm silage	250	128	176	224	108	364
Fresh tubers	200–241	103–121	20–40	50–55	2–5	781–818
Fresh peelings	212	99	33	61	5	802

DM, dry matter; NFE, nitrogen-free extract.

The majority of the droppings produced each day are coprodeal in origin; when first shed they appear normally as a rounded brown to green mass with a characteristic white cap of uric acid. This is due to the presence of the main bile pigment, biliverdin. Droppings are also shed from the caeca by powerful evacuatory contractions. Caecal droppings are more glutinous than coprodeal material and tend to be light brown at the point of defecation, turning dark brown on exposure to air probably as a consequence of the conversion of biliverdin to bilirubin by bacterial action and subsequent dehydrogenation. The ratio of caecal to coprodeal evacuation is between 1:5 and 1:12.

Dependent upon dietary composition, poultry droppings may have a high nutritive value and recycling of the material in the form of used poultry litter as the basis for ruminant diets has frequently been employed. (MMit)
See also: Large intestine; Litter; Urine

Poultry feeding This general term applies to the feeding of any domestic avian species at any stage of production. (KJMcC)
See also: Duck; Goose; Hen feeding; Ostrich; Poultry

Poultry litter: *see* Litter

Poultry manure This can be almost pure poultry excreta, if collected under cages, or a mixture of excreta and bedding (litter) if obtained from a broiler house or a deep litter system for laying hens. Therefore the moisture and nutrient contents can vary widely. Poultry manure is usually spread on land, where it provides useful amounts of nitrogen and phosphorus thus reducing the need for artificial fertilizer. (KJMcC)
See also: Litter; Poultry droppings

Poultry meat The four main species of domesticated poultry used for meat production are **domestic fowl**, **turkey**, **goose** and **duck**. The carcass yields of poultry (as a percentage of the liveweight) are around 71–74%. The edible meat yield (also as a percentage of liveweight) ranges from around 29% in ducks to 34% in geese, 44% in meat-line strains of domestic fowl and 51% in turkeys. Both the carcass yield and the edible meat yield depend on the slaughter weight and the figures quoted should only be used as guidelines. In general, breast meat of poultry has a greater economic value than leg meat. Of the edible meat approximately 35% is breast meat, 38% leg and thigh meat and 27% wing and other meat. Although the breast meat in turkey (38%) is a greater proportion of the edible meat than in domestic fowl (34%), there is a greater proportion of wing and leg meat in turkeys (39%) than in domestic fowl (29%). These figures represent average ranges and will depend on the genetic strain of the poultry.

One of the main differences between breast and leg meat is the appearance, breast meat being generally lighter in colour due to its having less myoglobin than the leg muscles. There are biochemical differences between the breast and leg muscles that reflect their original use for flight. The breast muscles predominantly contain ‘fast glycolytic’ (type IIB) muscle fibres, i.e. those that can contract fast and have an enzyme profile for a glycolytic-type metabolism. For example, the pectoralis major, the main muscle in breast meat, has 100% fast glycolytic-type fibres. The leg muscles, on the other hand, have a predominantly oxidative metabolism. For example, the illiotibialis, one of the leg muscles in domestic fowl, has 40% oxidative fibres at 20 weeks of age. The proportion of oxidative fibres increases with age in this muscle.

Although the water contents of the breast and leg muscles are similar, the dark leg meat has a higher fat content (5.5%) and less protein (19%) than breast meat (3.2% and 22%, respectively). The collagen content is higher in the thigh muscle (17 mg g^{-1} dry matter) than in the breast muscle (8 mg g^{-1} dry matter). In the thigh muscle the amount of collagen increases with age and its solubility deceases with age.

The fatty acid profile of the meat reflects the fatty acid profile of the diet. For example, increasing the proportion of fish meal in the diet results in increased concentrations of 22:6 n-3 fatty acids in both the white and dark meat of broilers. Increasing the proportion of n-3 polyunsaturated fatty acid (PUFA) content can lead to reduced oxidative stability and increased rancidity during refrigerated storage. Feeding vitamin E (α-tocopherol) results in increased incorporation of this into the muscle and this can act as an antioxidant. (BMM)

See also: Meat composition; Meat quality; Meat yield

Poultry offal meal The viscera, feathers, etc., obtained during slaughter and processing account for up to 30% of poultry meat production. Spent hen meal, arising from complete rendering of laying hens at the end of the productive cycle, is a recent variant. These by-products are potentially good sources of nutrients (particularly **protein** and amino acids) if properly processed. Typically, poultry offal meal contains around 600 g protein kg^{-1} and is a good source of amino acids. The protein contents of spent hen meal and feather meal are around 670 and 820 g kg^{-1}, respectively. However, the amino acid content and availability of the latter are relatively poor. (KJMcC)

See also: Blood meal; Fish products; Meat products

Prawn A freshwater crustacean, the Malaysian giant prawn, farmed primarily in Asia but experimentally cultured in other areas of the world. 'Prawn' is sometimes used to distinguish larger shrimp. (DEC)

See also: Crustacean feeding; Shrimp

Key reference

New, M.B. and Valenti, W.C. (2000) *Freshwater Prawn Culture: the Farming of* Macrobrachium rosenbergii. Blackwell Science, Oxford, UK, 443 pp.

Prebiotic A non-digestible food ingredient that beneficially affects the host by selectively stimulating the growth or activity of one or a limited number of bacteria in the digestive tract that have the potential to improve host health. Examples include oligosaccharides, resistant starch and specific non-starch polysaccharides. (SB)

See also: Probiotics

Pregnancy: *see* Cow pregnancy; Ewe pregnancy

Preservation The process of storing food in a state designed to control or prevent the development of undesirable bacteria and moulds, and which ensures minimal losses of nutrients during storage. Common methods of preservation are drying and ensiling. (JMW)

Preservative Material used to control or prevent the development of undesirable bacteria or moulds in animal feeds. Preservatives include ammonia, propionic acid, formic acid, lactic acid bacteria (in inoculants for silage) and antioxidants. (JMW)

Pressing The act of squeezing a feed mechanically to remove a liquid component, which may be water or oil (*see* **Extraction, oil**; **Fractionation, green-crop**). (JMW)

Prey size The mouth size of the predator dictates the size of prey that can be ingested. Optimal prey size for fish larvae is often presented as a proportion of mouth diameter. Prey organisms that are too large may take an inordinate amount of time to consume. Prey that is too small may require a high energy investment for capture or handling with little reward. (DN)

Probiotics Feed supplements that are added to the diet of farm animals to improve intestinal microbial balance. They were first used in the 1970s. In ruminants, they are more effective in controlling the diseases of the gastrointestinal tract of young animals, as there is no complication of the rumen microflora. They must be able to pass the stomach–duodenum barrier and multiply at the desired site. Colonization of the intestine by benign bacteria may confer protection against pathogenic bacteria. This is not only by competitive exclusion; they can also limit the adhesion of some bacteria to the intestinal wall and most improve the immunocompetence of the host animal. Some probiotics, particularly the lactobacilli, can neutralize *Escherichia coli* enterotoxins; others, notably *Lactobacillus acidophilus*, produce large quantities of lactic acid that reduce pH and prevent the growth of some pH-sensitive bacterial strains.

The initial colonization of the small intestine is from the dam's microflora and the immediate surroundings, and usually includes streptococci, *E. coli* and *Clostridium welchii.* When milk feeding commences, the lactobacilli become the predominant bacteria present. Calf probiotics contain benign lactobacilli or streptococci and are likely to be valuable only when given to calves that have suffered stress or have been treated with antibiotics that have destroyed the natural microflora. Addition of probiotics to the diet produces variable benefit, depending on whether the animals are in poor health. It is also difficult to determine which bacterial species would be beneficial in any given circumstance.

Probiotics have sometimes been found to be beneficial in protecting pigs from infectious diseases. Lactic acid bacteria isolated from the gastrointestinal tract of pigs, such as *Enterococcus faecium* and *L. acidophilus*, can inhibit enteric indicator strains, such as *Salmonella enteritidis*, *S. cholera suis*, *S. typhimurium* and *Yersinia enterocolitica*. Dry yeast (*Saccharomyces cerevisiae*) has the advantage over bacterial probiotics that it is more tolerant of extreme pH and environmental conditions. Probiotic use is subject to extensive legislation designed to protect farm animals and consumers. In adult ruminants yeasts may be used as probiotics to improve rumen fermentation. (CJCP)

Procarboxypeptidase: *see* Carboxypeptidase

Processing: *see* Coating; Crushing; Extraction, oil; Extrusion; Grinders; Heat treatment; Pelletting; Toasting; Wafering

Production efficiency factor Production efficiency factors have been devised to calculate the efficiency of broiler chicken enterprises. They generally incorporate measures of feed conversion efficiency with measures of the survivability of birds within a flock. The European Poultry efficiency factor (EPEF) calculation is shown at the bottom of the page. (SPR)

Proelastase: *see* Elastase

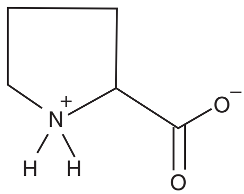
Progesterone A steroid hormone produced by the corpus luteum, the placenta or both. Progesterone production peaks during the luteal phase of the oestrous cycle and its production is maintained throughout pregnancy until just prior to parturition. Progesterone-releasing intravaginal devices (PRIDs) can be used in animals as a means of synchronizing the oestrous cycle to facilitate natural and artificial insemination programmes. (JRS)

Prolactin A peptide hormone produced by the anterior pituitary and involved in mammogenesis and the stimulation of milk synthesis. Inhibition of prolactin secretion results in a decrease in milk yield. (JRS)

Proline An amino acid ($C_4H_8N{\cdot}COOH$, molecular weight 115.1) found in protein. It is synthesized in the body from either glutamic acid or ornithine. Proline, together with its hydroxylated product hydroxyproline, accounts for about one-third of the amino acid residues in collagen. Although some of the proline contained in protein can be hydroxylated directly to hydroxyproline, this pathway is not reversible. Thus, whereas proline catabolism gives rise to glutamate, hydroxyproline catabolism gives rise to pyruvate and glyoxylate. Both proline and hydroxyproline are therefore gluconeogenic amino acids. Consumption of diets with a high collagen content, such as those with significant quantities of meat and bone meal, result in large quantities of proline and hydroxyproline being consumed. If digested and absorbed,

$$\text{EPEF} = \frac{\text{Mean bird slaughter weight (kg)} \times \dfrac{\text{Total weight of birds sold (kg)}}{\text{Number of chicks housed}}}{\text{Age of birds at slaughter (days)} \times \dfrac{\text{Total feed used by flock (kg)}}{\text{Number of birds sold at slaughter}}} \times 10{,}000$$

most of these two compounds are catabolized and used for either energy or glucose production.

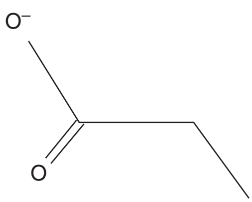


(DHB)

See also: Hydroxyproline

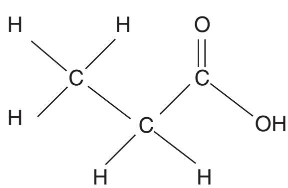
Pronase A proprietary name for a bacterial non-specific protease (EC 3.4.24.31) from *Streptomyces griseus*. (SB)

Propionate A three-carbon fatty acid, $CH_3{\cdot}CH_2{\cdot}COO^-$, one of the steam-volatile fatty acids. It is produced in anaerobic fermentation, together with two other volatile fatty acids, acetate ($CH_3{\cdot}COO^-$) and butyrate ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$). In the liver, propionate is converted to succinyl-CoA and is thus a source of carbon for gluconeogenesis.



(NJB)

Propionic acid Propanoic acid. In common with most of the short-chain carboxylic acids its use as a preservative in animal feeding stuffs rests with its antimicrobial properties. It is listed in EU legislation as 'E280, Propionic acid, $C_3H_6O_2$, suitable for use in all feeding stuffs'.



Propionic acid is a colourless, slightly oily, corrosive liquid with a slightly sweet odour. It is a weak acid and so does not have a dramatic effect on pH but it has good antimicrobial properties in respect of clostridia, fungi and yeasts. Its main use is in the preservation of moist grain (typically 18–25% moisture). Evenly distributed throughout the grain at an appropriate concentration (0.8–1.2%, depending on moisture) it will kill around 90% of common spoilage organisms and restrict the growth of others. Propionic acid has also been used alone and in mixtures with other acids or substances such as formaldehyde as an aid to silage making and as a hay preservative. It is a natural product of rumen fermentation and so is absorbed and used as an energy source when present in feeding stuffs given to ruminants. (CRL)

Prostacyclin: *see* Prostaglandins

Prostaglandins Members of a large group of lipid-derived signalling molecules known as eicosanoids. These molecules are synthesized in the plasma membrane and released to the cell exterior, where they act in an autocrine or paracrine mechanism to alter the function of the same cell or surrounding cells. Synthesis begins with the hydrolysis and release of (mainly) arachidonic acid, a 20-carbon ω-6 polyunsaturated fatty acid, from membrane phospholipid via the activation of phospholipase A_2. Arachidonic acid is acted on by either a cyclooxygenase or a lipooxygenase enzyme. The cyclooxygenase-dependent pathway leads to the production of prostaglandins, prostacyclins and thromboxanes. Alternatively the lipooxygenase-dependent pathway produces leukotrienes. Collectively these molecules, including arachadonic acid itself, regulate a variety of physiological processes, including uterine contraction, blood flow, gastric acid secretion, platelet aggregation and much of the inflammatory response that accompanies cell injury. These pathways are the targets of a number of therapeutic agents, including the non-steroidal anti-inflammatory drugs aspirin and ibuprofen, which inhibit the cyclooxygenase enzyme. Corticosteroid hormones inhibit phospholipase A_2 in the first step of the pathway and are effective in treating non-infectious inflammatory disorders. Prostaglandins as a group are composed of a 20-carbon fatty acid that contains a five-membered carbon ring. The diverse number of molecular forms comprising each eicosanoid species underscores the wide range of cellular effects elicited by these agents. (GG)

Prosthetic group A chemical complex, such as the metal-porphyrin in haemoglobin, with a protein, allowing the protein to function. It can also be a coenzyme (such as NAD, NADP or FAD) which, when associated with an enzyme protein, allows the enzyme to catalyse a specific reaction. (NJB)

Protease inhibitors Chemical compounds that inhibit the activity of proteases by forming a strong complex with their active proteolytic site. Protease inhibitors in the seeds and storage organs of plants specifically inhibit the activity of one or more of the digestive enzymes in non-ruminant animals; for example, the Kunitz and Bowman-Birk inhibitors in soybeans inhibit both trypsin and chymotrypsin and may seriously affect digestion if the soybeans are not effectively heat-treated by toasting. A potent trypsin inhibitor in the pancreas protects the pancreatic tissue from autodigestion by spontaneously activated trypsin. (SB)

Proteases Enzymes that degrade proteins by hydrolysing peptide bonds (R·CHNH·CO·R), yielding smaller amino acid chains called peptides. In digestion, peptides produced by intestinal proteases are further degraded by endopeptidases, aminopeptidases and carboxypeptidases to yield di- and tripeptides that may in turn be further hydrolysed to free amino acids. (NJB)

Protected fat Fat treated for use in ruminant feed either to minimize biohydrogenation of unsaturated fatty acids in the rumen or to permit addition of fat to ruminant diets without adversely affecting fibre degradation in the rumen. Protection can be achieved in a number of ways, e.g. encapsulation of small fat droplets in casein which is then sprayed with formaldehyde to cross-link the proteins, making it undegradable in the rumen. Alternatively, non-esterified fatty acids can be converted to their calcium salts, which are insoluble in rumen fluid. (JRS)

Protected protein Proteins may be protected from digestion in the rumen by heating or by reaction with chemicals such as formaldehyde. Total digestibility is reduced by overheating, which denatures the proteins. (JMW)

Protein A polymer of amino acids joined together by peptide bonds and containing the elements carbon, hydrogen, oxygen, nitrogen and sulphur. Some proteins contain selenium in the form of selenocysteine or selenomethionine. Crude protein, generally used to describe the protein content of diets, is defined as nitrogen $\times$ 6.25. (DHB)

Protein absorption Absorption of intact proteins, e.g. immunoglobulins from colostrum, can occur up to 24 h after birth by specialized intestinal epithelium capable of **pinocytosis**, i.e. engulfing soluble proteins intact, transferring them from the intestinal lumen into the cell, from whence they are transferred to the blood. (SB)

Protein concentrate A feed material that is relatively high in protein, often used in the production of compound feeds. Protein concentrates include oilseed meals and cakes and, where permitted, animal by-products such as fish meal. (JMW)

Protein deficiency A lack of protein may be due to underfeeding, with a shortage of all nutrients, or to a diet of low protein content. In growing animals, protein deficiency causes slow growth; in mature animals it results in mobilization of body protein. Initially this has little impact on body functions but eventually it threatens essential pathways and structures, resulting in muscular weakness, thin and easily damaged skin and impairment of the immune system, with reduced ability to respond to disease.

Ruminants can obtain much of their protein supply from rumen microbes, which synthesize it from non-protein sources of nitrogen (NPN), but non-ruminants require all the indispensable amino acids as well as either dispensable amino acids or other sources of nitrogen from which the dispensable amino acids can be synthesized.

Protein supply is most likely to be deficient in rapidly growing animals, where the appetite is not fully developed, or highly lactating cows or goats. Such ruminants will require supplementary protein that is not degraded in the rumen but is digested by the host's enzymes post-ruminally. The requirements of dairy cows are particularly high in early lactation. Preparing the cow by feeding rumen-undegraded protein before she calves will help to ensure adequate protein in early lactation. (JMF)

Protein degradation Protein degradation in living cells can be both part of normal protein turnover and a response to tissue damage. It can be by digestion in lysosomes or by a targeted system involving a small 8.5 kDa protein called ubiquitin. Protein catabolism (breakdown) is difficult to measure because of isotope reincorporation. To measure degradation, the protein or tissue is labelled and the rate at which the specific activity of the protein or tissue declines is used to estimate a half-life ($t_{1/2}$) which is the time it takes for the specific activity tracer/non-tracer atom (e.g.^3H or $^2H/H$, or ^{14}C or $^{13}C/^{12}C$) to decrease by half. The specific activity of the protein can only change when both synthesis and degradation are occurring simultaneously. The labelled amino acids released from protein degradation make up ~ 80% of the amino supply for protein synthesis, thus reincorporation of tracer decreases the decline in specific activity and increases the half-life. Rate constants for the degradation of single proteins can be estimated by isolating them and measuring the rate at which the specific activity of the labelled amino declines. The semilog plot of specific activity vs. time is linear, but still has the problem of tracer reincorporation. The decline in specific activity is curved with tissue proteins because of the different half-lives and amounts of the many proteins in a bulk (e.g. liver) sample.

Another approach to estimate the rate constant for protein breakdown (K_d) has been to use the difference between the rate constants for synthesis (K_s) and growth (K_g). The basis for this approach is that growth is the difference between synthesis and degradation (i.e. $K_g = K_s - K_d$). Again this can be difficult to measure because the measurement of interest is the difference between two independent estimates, each with its own inherent error. If the interval between the two estimates is small, the estimated value based on a difference may vary from plus infinity to minus infinity.

In general the half-lives ($t_{1/2}$) of individual proteins are thought to be a function of the structure of the protein and thus have a tendency to have a repeatable value but can be altered by substrate, coenzymes and ions. Another approach used to estimate the rate constant for protein breakdown (K_d) in animals has been to measure urinary excretion of 3-methylhistidine. This unique amino acid is the result of protein-bound histidine being methylated by *S*-adenosylmethionine. It is found in actin and myosin in muscle but significant amounts are also found in skin and intestine. When the protein is degraded to its constituent amino acids, 3-methylhistidine is released and partially or quantitatively excreted in urine. In rats and humans, 3-methylhistidine is quantitatively excreted hence estimates of protein catabolism can be made. This method has not been uniformly productive in its use in food animals (pig, sheep and chicken) because of incomplete recovery of known amounts of injected 3-methylhistidine. (NJB)

Protein digestibility A measure of the extent to which ingested protein is digested and absorbed from the intestine. It commonly refers to crude protein, i.e. N × 6.25. Protein digestibility is indicative of the digestibility of individual amino acids in the protein but, for a correct evaluation, individual values for all essential amino acids are needed.

Crude protein digestibility by the whole digestive tract in non-ruminants may be determined by analysis of faeces but, because of extensive microbial activity in the large intestine, faecal amino acid analysis does not accurately reflect the extent to which dietary amino acids have been absorbed. For this reason amino acid digestibility is commonly estimated from analysis of digesta collected at the terminal ileum. Ileal digesta can be obtained from cannulated animals or by a slaughter technique in which the animal is anaesthetized whilst the digesta are sampled, in order to avoid the shedding of mucosal cells into the lumen that may occur at death. Digestibility may be estimated by measurement of the total flow of digesta (or the total excretion of faeces). It may also be estimated from the increase in concentration of an indigestible **marker**, added to the diet, in relation to the concentration of N (or amino acid). Among a large number of possible markers, chromium oxide is commonly used.

Values of protein digestibility are most often higher at the faecal level than at the ileal level. This is mainly due to absorption of ammonia occurring from the microbial activity in the large intestine by which undigested dietary protein and non-reabsorbed endogenous protein are also converted to microbial protein. The presence of easily fermentable dietary carbohydrates, i.e. water-soluble dietary fibre and, in adult non-ruminants, also lactose, may considerably increase the microbial utilization of ammonia for protein synthesis and, consequently, reduce the intestinal absorption. Protein digestibility measured at the ileal level is therefore a better indicator of the proportion of the dietary amino acids that is available to the animal.

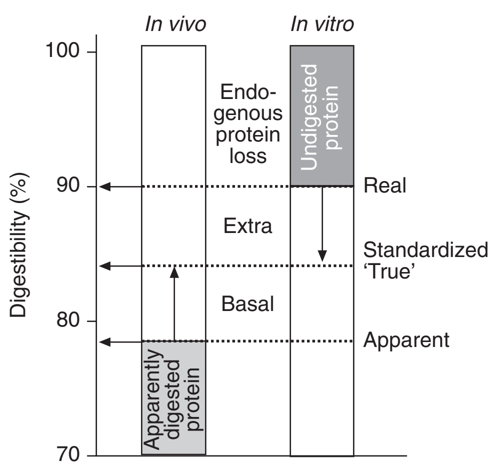
Apparent digestibility is so called because it is a simple measure of the difference between dietary protein intake and protein in the analysed digesta, which also includes endogenous protein secreted into the gut during digestion. Apparent digestibility can be measured directly in low-protein feeds fed alone, or in protein-rich foodstuffs diluted with a semi-synthetic N-free mixture. In the latter case, endogenous ileal protein flow is induced by both the protein source and the N-free mixture. Apparent digestibility does not include a correction for the endogenous contribution.

Net digestibility is a measure of apparent protein digestibility relating directly to the foodstuff itself rather than to a test diet. Thus, for low-protein foodstuffs which can be analysed directly, net digestibility may be identical to apparent digestibility. For protein-rich foodstuffs, which need to be diluted with a protein-free mixture to obtain a suitable protein level in the test diet, net digestibility must be determined by extrapolation to the pure foodstuff according to a theoretical 100% level of inclusion.

True digestibility is a measure of protein digestibility in which a correction is made for the flow of undigested protein by using an estimate of the basal **endogenous protein** flow determined by feeding either an easily digestible nitrogen-free diet or a diet containing a 100% digestible protein. This endogenous loss is considered to correspond to the minimal (basal) protein loss for the digestive processes.

Standardized digestibility refers to tabulated values of true digestibility calculated from estimates of basal endogenous losses determined at well-defined and standardized conditions (see figure and table).

Real digestibility is a measure of protein digestibility relating directly to the foodstuff itself. This can be performed by a ^{15}N isotope-dilution technique after labelling the experimental animal with ^{15}N and measuring the dilution of $^{15}N/^{14}N$ in the digesta compared with the $^{15}N/^{14}N$ in the blood. In this value, a correction is made for all components of the endogenous ileal protein flow, i.e. nonspecific basal losses and extra losses specifically induced by the particular diet. The extra losses are primarily related to dietary fibre and



Standardized (or true) digestibility of protein calculated from either *in vivo* or *in vitro* measurements.

Ileal standardized digestibility of crude protein (CP) and essential amino acids in common foodstuffs for pigs.[1]

	Obs.[2]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Barley	13	10.9	80	75	75	84	84	79	81	83	80	81	84	83	83
Barley brewers' grains	1	20.9	53	50	31	61	22	41	59	59	42	61	52	53	58
Barley distillers' grains[3]	1	21.5	83	73	84	89	87	86	90	90	86	87	92	93	93
Beet pulp, dehydrated	1	11.1	53	50	31	61	22	41	59	59	42	61	52	53	58
Blood meal	8	85.4	82	86	85	85	77	88	86	84	84	82	86	86	86
Bone meal	2	38.4	81	86	85	89	66	–	85	86	84	86	86	85	84
Cottonseed meal, decorticated	8	40.4	77	63	71	73	76	68	74	76	76	76	83	81	90
Cottonseed meal, part. decorticated	1	31.3	74	70	75	79	69	–	77	80	79	80	86	82	90
Faba bean	6	27.6	84	88	82	83	77	81	85	87	82	87	87	84	91
Feather meal	3	80.5	77	65	78	71	70	72	86	83	83	71	86	76	84
Fish meal	15	65.5	89	93	92	93	86	89	93	94	92	89	92	92	94
Fish solubles	1	80.2	93	96	96	96	84	–	97	98	96	95	99	98	99
Greaves	1	82.9	82	84	80	85	79	79	88	88	88	85	90	88	92
Groundnut meal, detoxified	1	50.3	77	61	71	74	75	72	83	86	81	–	90	90	91
Groundnut meal, not detoxified	2	47.3	90	88	89	92	88	–	92	94	92	90	95	95	97
Lucerne, dehydrated	2	17.6	60	59	65	76	35	46	70	73	68	60	72	69	77
Lupin	3	31.1	85	86	81	83	83	–	88	87	80	90	89	88	93
Maize	15	8.9	86	80	83	91	89	80	88	93	87	89	91	90	91
distillers	1	23.6	62	58	62	76	59	28	72	78	66	59	79	76	76
Maize germ meal, starch by-product	1	27.5	68	61	71	81	67	71	74	76	72	84	81	78	84
gluten feed	12	20.2	69	66	70	84	69	66	78	84	75	70	84	83	86
gluten meal	5	60.4	92	89	92	95	92	87	92	95	91	92	94	94	95
Maize hominy feed	1	15.3	72	65	65	86	67	60	75	83	73	74	84	88	86
Meat and bone meal	17	51.1	81	84	82	86	67	80	84	85	83	79	85	82	86
Meat and bone meal, low digestibility	5	54.7	66	72	64	76	46	78	72	70	68	71	72	70	75
Milk powder, skimmed	1	33.8	89	97	91	97	84	–	88	96	89	95	98	97	96
Milk powder, whole	1	33.8	90	89	94	96	95	97	89	97	92	97	98	98	88
Milk protein concentrate	1	48.7	90	94	86	89	86	90	91	93	90	95	92	89	94
Oats	10	10.5	76	73	69	84	75	78	79	81	77	83	84	80	88
Oats, decorticated	1	14.7	79	79	80	85	85	82	83	83	81	83	83	85	86
Palm kernel meal, expeller	5	16.0	54	37	52	68	47	52	66	70	66	61	75	67	78
Pea	39	21.4	80	83	76	80	72	73	79	80	77	84	80	81	89
Pea, extruded	2	23.3	90	93	90	86	88	89	91	92	89	94	93	94	94
Potato protein concentrate	2	78.7	87	89	90	91	78	75	89	91	89	89	91	89	92
Poultry offal meal	5	57.0	76	77	76	80	68	69	81	80	77	70	81	78	85
Rapeseed meal	18	35.2	76	75	75	87	81	80	78	82	77	84	83	80	87
Rapeseed, full-fat	2	19.9	72	78	71	81	80	73	68	71	70	73	73	74	81
Rapeseed, full-fat, treated	2	20.0	73	81	72	85	81	75	73	75	73	82	75	72	84
Rice bran	4	14.2	70	75	68	78	68	74	72	72	71	84	74	80	86
Rye	8	8.4	77	72	71	81	84	76	77	78	75	79	82	77	80
Sesame meal, solvent extracted	1	40.5	91	87	89	94	94	–	91	92	90	92	94	92	96
Sorghum	13	9.7	79	74	76	85	77	79	83	86	81	78	85	85	82
Soybean concentrate	1	65.4	94	95	94	93	94	94	94	95	94	97	96	96	99
Soybean hulls	1	11.6	57	60	61	71	63	63	68	70	61	58	72	64	84
Soybean meal, crude fibre < 5%	13	47.1	89	92	88	93	89	92	91	90	90	92	91	92	95

Continued

Table *continued*

	Obs.[2]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Soybean meal, crude fibre > 5%	11	44.6	87	89	86	91	84	88	88	88	87	90	89	90	93
Soybean meal, extruded	3	47.4	87	89	86	88	85	86	87	88	87	90	89	88	95
Soybean, full-fat, treated	5	35.8	78	82	79	81	77	80	78	79	78	84	81	82	86
Sunflower meal, not decorticated	2	27.2	81	80	82	92	81	85	86	87	84	86	90	92	95
Sunflower meal, partially decorticated	9	33.4	82	82	81	92	82	84	85	85	83	84	87	89	93
Triticale	12	10.3	87	83	82	90	91	88	87	88	86	89	90	90	91
Wheat	17	12.3	88	81	83	89	91	88	89	90	86	90	91	90	88
Wheat bran	10	15.4	72	72	69	79	76	78	77	79	75	80	82	81	86
Wheat distillers' grains[3]	1	27.4	82	66	80	86	82	81	83	85	80	80	90	88	88
Wheat feed flour	4	13.7	93	90	90	94	94	92	93	95	91	96	96	95	96
Wheat germ meal	2	27.0	85	89	82	90	81	81	86	88	85	90	88	87	94
Wheat gluten	1	81.0	89	64	78	89	95	79	91	93	89	–	95	94	87
Wheat gluten feed	3	14.0	68	57	67	72	72	66	70	73	66	73	78	78	80
Wheat middlings	15	15.7	84	84	80	88	83	86	86	87	84	89	89	88	91
Whey, acid, dehydrated	2	10.5	70	83	70	74	66	79	80	77	69	80	82	78	51
Yeast, brewers'	1	47.4	69	74	66	69	49	55	72	73	66	77	66	64	78
Yeast, brewers', high protein	1	69.0	59	52	58	51	32	40	54	55	64	52	53	54	61

[1]Adapted from AmiPig (2000).
[2]Number of observations.
[3]Ethanol by-product.

various antinutritional factors and they may be considerably higher than the basal losses.

Protein and amino acid digestibility in foodstuffs and diets can be predicted from *in vitro* incubations of the diet with suitable enzyme preparations that simulate the digestion in the stomach and small intestine. Values of *in vitro* digestibility are not influenced by endogenous losses and thus correspond to real digestibility. The prediction of protein digestibility from *in vitro* analyses is therefore dependent on proper correction for the endogenous losses. (SB)

See also: Digestibility; Endogenous protein; Protein digestion

Further reading

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Protein digestion Protein digestion is a complex process, because proteins consist of some 20 different amino acids and thus contain over 400 different peptide bonds. This means that a large number of proteolytic enzymes (proteases and peptidases) with different specificities are needed to complete the hydrolysis of proteins to amino acids.

Protein digestion begins in the stomach, where hydrochloric acid denatures the proteins, i.e. destroys their three-dimensional structure, which make the peptide bonds susceptible to enzymatic hydrolysis. Pepsins secreted from the gastric mucosal cells initiate protein digestion by cleaving some of the peptide linkages. Pepsins are secreted in the form of inactive precursors, called pepsinogens, which are activated by gastric hydrochloric acid and previously activated pepsin. Pepsins are most active from pH 1.5 to 3 and hydrolyse the peptide bonds between aromatic amino acids such as phenylalanine or tyrosine and a second amino acid. Chymosin, a milk-clotting enzyme, also called rennin, is found in the stomach of young animals.

In avian species, pepsin is ready for secretion at the time of hatching and is at a high level from the first meal, which can be of the same composition as that eaten by adults and is digested efficiently. The site of gastric secretory glands (HCl and pepsin) in birds is the proventriculus; peptic hydrolysis occurs in the gizzard, which is also responsible for grinding food particles.

In ruminants, most of the dietary protein is utilized by the microbial flora in the rumen; consequently the proteins of the rumen flora are the major source of protein for ruminants. Processing can render some proteins indigestible in the rumen (by-pass protein) but the protein can be digested better postruminally. This is particularly important in fast-growing animals and high-yielding dairy cows, in which essential amino acids may be limiting for growth or milk synthesis.

In the small intestine of ruminants and non-ruminants alike, the polypeptides resulting from digestion in the stomach are further degraded by the proteolytic enzymes of the pancreas and intestinal mucosa. The pH is about 6.5.

Enterokinase is found only in enterocytes and is released from the apical membrane by the detergent action of bile salts secreted from the liver. The activity of enterokinase is stimulated by trypsinogen which is its only substrate. Enterokinase is responsible for initiating the luminal phase of pancreatic protein digestion by cleaving a peptide from the amino terminus of trypsinogen, producing trypsin. The activated trypsin then activates the other pancreatic proenzymes.

Trypsin, chymotrypsin and elastase are closely related in their molecular structure, in particular in their active catalytic site around the hydroxy group of serine; they are therefore called serine proteases. Because they all cleave interior peptide bonds in the peptide molecules, they are called endopeptidases. Trypsin cleaves the bonds on the carboxyl side of the basic amino acids lysine and arginine; chymotrypsin those on the carboxyl side of the aromatic amino acids (tyrosine, phenylalanine, tryptophan); and elastase on the carboxyl side of aliphatic amino acids (e.g. alanine, glycine, leucine, isoleucine, valine).

Carboxypeptidases act on peptide bonds at the carboxyl end of polypeptides, releasing free amino acids or oligopeptides of two to six residues. Carboxypeptidase A cleaves all peptide bonds except at the basic amino acids, lysine and arginine, whereas carboxypeptidase B cleaves only peptide bonds at these amino acids.

The proteolytic actions of gastric and pancreatic enzymes result in a mixture of free amino acids (40%) and peptides (60%) in the intestinal lumen. Some of the di- and tripeptides are absorbed intact by active transport systems but the completion of digestion of the major fraction of peptides requires a large number of specific peptidases. These are mostly metalloenzymes found in the apical membrane or within the enterocytes.

Most **brush border** peptidases belong to one of four classes: endopeptidases, aminopeptidases, carboxypeptidases and dipeptidases. The carboxypeptidases of the pancreas and the aminopeptidases of the brush border are exopeptidases that hydrolyse the amino acids at the carboxy and amino ends of the polypeptides. Some amino acids are liberated in the intestinal lumen; others are liberated at the surface by the aminopeptidases and dipeptidases in the brush border of the mucosal cells. Some di- and tripeptides are actively transported into the intestinal cells and hydrolysed by intracellular peptidases, with the amino acids entering the bloodstream. Thus, the final digestion to amino acids occurs in three locations: the intestinal lumen, the brush border, and the cytoplasm of the mucosal cells.

Dipeptides containing the secondary amino acid proline cannot be hydrolysed by pancreatic carboxypeptidases and may not have sufficient residence time to be hydrolysed by brush border peptidases. However, such peptides may be absorbed intact.

Most dietary protein digestion and amino acid absorption occur in the first 60% of the small intestine. Protein in the distal segment of the small intestine is to a large extent of endogenous origin.

In most animals amino acids cannot be absorbed in the large intestine and bacterial proteases in the large intestine have generally little influence on amino acid utilization. However, liberated ammonia can be absorbed and utilized by the host animal for synthesis of non-essential amino acids. In some herbivorous animals with a sacculated caecum or colon, e.g. the horse, amino acids may be absorbed in the large intestine; in coprophagous or caecotrophic animals, such as the rabbit, bacterial protein can also be utilized. Finally, back-flow of digesta from the large intestine to the small intestine may provide non-ruminants with microbial protein.

(SB)

See also: individual enzymes; Intestinal absorption

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Protein efficiency ratio (PER) A system used to evaluate the quality of dietary proteins. Groups of animals (usually laboratory rats or chicks) are fed diets containing 10% crude protein from the source to be evaluated. PER is calculated as the weight gain in grams divided by the grams of protein consumed over 4 weeks. In theory, the more closely the pattern of amino acids in the protein matches the pattern of amino acids the animal requires, the higher the quality. A high quality protein has a high PER because a smaller quantity can meet an animal's needs.

(NJB)

Key reference

Derse, P.H. (1962) Evaluation of protein quality (biological method). *Journal of the Association of Official Analytical Chemists* 45, 418–422.

Protein:energy ratio The ratio of protein to energy in a feed or diet. It may be expressed as the ratio of digestible protein to digestible energy, as the ratio of metabolizable protein to metabolizable energy, or as the ratio of effective rumen degradable protein to fermentable metabolizable energy. (JMW)

Protein extraction The process of extracting a pure protein from a mixture of other components, e.g. the extraction of casein from milk to produce casein isolate.

(JMW)

Protein isolate A feed ingredient that is very high in protein, or which is pure protein, produced by extracting the protein component from the feed. (JMW)

Protein metabolism Protein metabolism in animals involves ingestion and digestion of dietary protein with the absorption of the resulting peptides and amino acids. It involves cellular-based synthesis of protein to meet the cells' own needs for maintenance of cellular membrane and subcellular organelle structure and function and for changes in the amount of specific proteins such as enzymes, transporters or hormones that are required to support and alter the functional capacity of the cells and tissues. It also involves excretion of proteins from liver cells into blood for maintenance of osmoregulation, the proteins involved in blood coagulation, or proteins from the pancreas for extracellular digestion of foodstuffs in the intestinal lumen. Within cells, in addition to synthesis there is breakdown of proteins in a process called turnover. The continuous synthesis and breakdown of proteins provides animals with the potential for repair and the potential for altering capacity to carry out a function. The processes discussed above aid in maintenance of homeostasis at a cellular and animal level.

The enzymes involved in the digestion of protein are pepsinogen, secreted by the chief cells of the stomach, and the pro-enzymes trypsinogen, chymotrypsinogen, procarboxypeptidase, elastase and collagenase, secreted by the pancreas. The peptides produced by these enzymes are attacked by the brush-border enzyme, aminopeptidase, followed by the cytosolic dipeptidase. Digestion of protein in the stomach is less than 2% and approximately 85% of the digestion of protein occurs in the upper one-half of the small intestine. Both di- and tripeptides are absorbed by the enterocyte and hydrolysed prior to being transferred to the bloodstream as amino acids. In some cases peptides are taken up at rates that exceed those of the amino acids. The amino acids leaving the small intestine must pass through the liver, where the pattern of free amino acids obtained from the diet is modified. The liver is the main contributor of dispensable amino acids to the mixture of indispensable and dispensable amino acids available to support tissue needs. It can use blood ammonium and carbon skeletons produced in the metabolism of carbohydrates and amino acids to produce the dispensable amino acids. In addition to modifying the pattern of amino acids available to the other tissues, the liver utilizes amino acids in the production of amino acids that are critical to metabolism and essential non-amino acid factors also required by the animal. These amino acids provide co-factors, which are essential portions of hormones, as well as intermediates and crucial compounds. A partial list is shown in the table.

The free amino acids in the animal provide the essential intermediates and co-substrates (arginine, ornithine, citrulline and aspartate) for operation of the urea cycle, which is involved in converting ammonium (which is toxic) to urea (which is not). These amino acids (glycine, aspartate-N and glutamine-N) are also critical to the production of uric acid, which is an important system for the conversion of toxic ammonium to a non-toxic excretion product in animals that cannot produce urea. Another aspect of protein metabolism is that of protein synthesis and protein degradation, both of which are involved in growth and restructuring tissue architecture. The restructuring of tissue is due to the two processes, synthesis and degradation, which contribute to protein turnover. This process occurs in all cells and can vary with diet and time of day. Half-lives of proteins can vary from times of less than 30 seconds to months. (NJB)

See also: Protein degradation; Protein synthesis; Protein turnover

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'Essential' products derived from amino acids.

Amino acid[a]	Product(s)
Arginine	Nitric oxide, citrulline, ornithine, creatine
Cyst(e)ine	Taurine, glutathione, SO_4
Glutamic A	γ-Aminobutyric acid
Glycine	Creatine, glutathione, purine(s)
Histidine	Histamine, carnosine, anserine, balenine, 3-methylhistidine
Isoleucine	None known
Leucine	None known
Lysine	Cadaverine (polyamine), carnitine, trimethyllysine
Methionine	Cysteine, (Ado-Met) *S*-adenosyl-methionine (the source of methyl groups for methylations), choline, creatine, polyamines (spermine and spermidine), via decarboxylated Ado-Met
Ornithine	Citrulline (essential in urea cycle), putrescine (polyamine)
Phenylalanine	Tyrosine, melatonin
Threonine	None known
Tyrosine	Dopa (3,4 dihydroxyphenylalanine), dopamine, norepinephrine, epinephrine, melanin, triiodothyronine (T_3), thyroxine (tetraiodothyronine, T_4)
Serine	Phosphatidyl-serine, phosphatidyl-ethanolamine
Tryptophan	Niacin, serotonin, tryptamine
Valine	None known

[a]Essential amino acids shown in **bold**.

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Protein quality A term used to describe the relative values of dietary proteins. In concept it is an estimate of how well the amino acid (AA) pattern of a dietary protein or combination of dietary proteins matches the pattern of the amino acids an animal requires. In application, less of a high quality protein (or a mixture of proteins with a high quality) will be needed to meet an animal's requirement than when proteins of lower quality are used. Estimates of protein quality can be made by calculation of the chemical score (mg AA g^{-1} N) of the protein relative to the calculated pattern (mg AA g^{-1} N) from the requirement of the animal. Chemical scores have percentage values such as 70%, etc. The chemical score is estimated from the amino acid content of the protein: it does not involve an animal assay. These estimates are the least accurate because they do not involve consumption, digestion and absorption of the dietary amino acids by the animal in question.

The simplest animal experiment to estimate the quality of dietary protein is protein efficiency ratio (PER), which is the animal's weight gain (in grams) per gram of protein consumed. To remove variation in different laboratory estimates, PER values can be corrected by using a standard casein PER value determined at the same time. A problem with this estimate is that no value is given for meeting the maintenance requirement for protein. If an animal does not grow, PER is zero, even though the protein has provided its maintenance needs.

Two other similar animal growth assays have been used to estimate protein quality. Net protein ratio (NPR) takes into account the value of the protein in meeting the animal's maintenance requirement by adding to the weight gain of the test group the weight loss of a similar group of animals given a protein-free diet. Net protein utilization (NPU) is a similar assay based on the gain of body N, rather than weight. In principle, both these methods give value to the dietary protein for providing for maintenance. These estimates also take account of protein intake and digestibility, which is appropriate as animals have to eat, digest and absorb the amino acids released from the protein in order for it to be of value to them.

Another assay of protein quality is biological value (BV). This method also requires an animal feeding experiment. A diet is fed containing the protein or protein mixture in question and measurement is taken of total faecal N corrected for endogenous N loss and total urinary N corrected for endogenous loss, i.e. BV is the percentage of absorbed N retained. While the equation suggests a linear response, the amount of protein in the diet affects the BV (Bressani, 1974).

Another estimate of protein quality is the slope ratio assay (Hegsted, 1974). In this approach animals are fed diets with graded amounts of the proteins to be compared and the slope of the response over the linear portion of the response curve is compared with that of the response to a standard high quality purified protein such as lactalbumin, which is given a value of 100. These values are dependent on the animal's response to lactalbumin. In this test proteins are always compared against a standard protein. The response can be the gain of weight gain, of N or of an amino acid over a specific time. Values are generally < 100 because lactalbumin is a very high quality protein for growing animals. Others (Finke *et al.*, 1987) have used the slope ratio assay to estimate protein quality but did not compare values in the linear portion of the response curve because of strong evidence of curvature at responses that were < 50% of the maximum response. Because a continuous curve could be generated, the relative value of proteins could be estimated at maintenance (zero growth) or at various fractions of the maximum response. These studies revealed that the relative values of proteins vary over the response curve such that no protein or mixture of proteins has a constant predictable value. Thus, while the idea of assessing the relative values of proteins is an important one from a nutritionist's point of view one must recognize that the relative values of proteins vary with level in the diet and for the purpose for which they are used. (NJB)

See also: Protein utilization

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Protein requirement of ruminants

The protein requirement of the ruminant animal is generally considered in terms of the main activities of the body – the maintenance of essential functions (Table 1), lactation (Table 2), pregnancy (Table 3) and weight change (Table 4). The requirement is calculated as net protein and is converted from net protein to metabolizable protein (MP), which takes account of the variable efficiency with which metabolizable protein is utilized.

The requirement for MP for lactation is quantitatively the most important, varying with milk yield and, to a lesser extent, with the protein concentration in the milk (Table 2).

Table 1. Requirements for metabolizable protein (MP; g day^{-1}) for maintenance.

Cattle		Sheep	
Liveweight	MP required (g day^{-1})	Liveweight	MP required (g day^{-1})
100	105	20	23
200	140	30	31
300	178	40	39
400	216	50	46
500	256	60	52
600	293	70	59
700	329	80	65

Table 2. Requirements for metabolizable protein (MP) for lactation.

Cattle		Sheep	
Milk yield (kg day^{-1}) at 32 g protein kg^{-1}	MP (g day^{-1})	Milk yield (kg day^{-1}) at 82 g protein l^{-1}	MP (g day^{-1})
10	456	1	106
15	684	2	212
20	912	3	317
25	1140	4	423
30	1382	5	529
35	1660	6	635
40	1967		
45	2339		
50	2780		

Table 3. Requirements for metabolizable protein (MP) for pregnancy.

Cattle		Sheep	
Month of gestation	MP required (g day^{-1})	Month of gestation	MP required (g day^{-1})
1	1	1	0.2
3	7	2	1
5	22	3	3
7	63	4	10
8	114	5	22
9	160		

Table 4. Requirements for metabolizable protein (MP) for weight change.

Dairy cattle		Sheep		
Weight change (kg day^{-1})	MP (g day^{-1})	Weight (kg)	MP for 200 g day^{-1} weight gain	MP for 400 g day^{-1} weight gain
–1.5	–197	20	48	95
–1.0	–131	30	46	86
–0.5	–66	40	42	83
0	0	50	40	81
0.5	122			
1.0	245			
1.5	367			

The requirement for metabolizable protein to support fetal growth in pregnancy is very low in the early stages and only becomes significant in cattle in the final 2 months of gestation, and in the final month in sheep (Table 3).

The total requirement for metabolizable protein is calculated as the sum of the requirements for the appropriate bodily functions. Thus, for a dairy cow weighing 600 kg liveweight, yielding 25 l milk, in her third month of pregnancy and gaining 0.5 kg liveweight day^{-1}, the total requirement is 293 g (maintenance) + 1140 g (lactation) + 7 g (pregnancy) + 122 (weight gain) = 1562 g MP day^{-1}.

In some situations the protein requirement is expressed as a recommended crude protein concentration in the total diet dry matter. This may appear to be an oversimplification, but if the degradability characteristics of the protein in some dietary ingredients are not known, and if there is uncertainty about the actual animal production level, diets should be formulated as crude protein, according to Table 5.

The metabolizable protein system for dairy cows works reasonably well at low and medium levels of milk yield (20–30 l day^{-1}), but at higher levels of production the MP required is underestimated. This implies that the efficiency of utilization of MP for milk production is not constant at 0.68 (*see* **Metabolizable protein**), but that it decreases at increased levels of output. The values given in Table 2 for MP requirement for lactation have been adjusted upwards to take account of the decrease in efficiency of utilization of MP for milk production above a milk yield of 25 l day^{-1}. Other systems of assessing protein supply and requirements, e.g. the French PDI system, also take account of the relatively greater requirement for MP of the high-yielding cow. (JMW)

See also: Microbial protein

Table 5. Recommended concentrations of crude protein (CP; g kg^{-1} dry matter) in diets for ruminants.

Dairy cows		Beef suckler cows		Growing beef cattle			Lactating sheep		Growing sheep	
					CP (g kg^{-1}DM)					
Milk yield (kg day^{-1})	CP (g kg^{-1} DM)	Milk yield (kg day^{-1})	CP (g kg^{-1} DM)	Liveweight (kg)	ME total diet (MJ kg^{-1} DM)		Milk yield (kg day^{-1})	CP (g kg^{-1} DM)	Liveweight (kg)	CP (g kg^{-1} DM)
				< 100	11	12	5	180	20	180
> 40	180			100	180	210	4	170	30	160
30–40	170			200	140	150	3	160	40	150
20–30	160	10	150	> 200	130	140	2	150	50	140
< 20	150	5	150				1	150	60	130
Dry	150	Dry	120				Dry	140	> 60	130

Protein retention A value derived from nitrogen balance experiments in which the amount of N retained in the body is estimated. Crude protein retention is calculated by multiplying the N retained by 6.25. (NJB)

Protein source A feed included in diets primarily for the protein it supplies (in contrast to energy sources). The major sources of protein in animal feeds are pasture grasses, forage legumes, legume seeds, oilseed meals and cakes, and fish meal. (JMW)

Protein supplement A feed, which may be a mixture of ingredients, used to add protein to a diet. The major protein supplements in animal feeds are legume seeds, oilseed meals and cakes, and fish meal. (JMW)

Protein synthesis Proteins are formed by a directed condensation of a sequence of 20 amino acids. The information for the sequence of amino acids in a protein is in the nucleotide sequence of DNA in a single gene. DNA is transcribed to produce an RNA message (messenger RNA, mRNA) which directs the protein synthesis machinery of cells to produce a specific peptide or protein. Synthesis of proteins involves five stages: (i) activation of amino acids; (ii) initiation; (iii) elongation; (iv) termination and release; and (v) folding and post-translational processing.

To become a substrate for protein synthesis, each amino acid must first be *activated* by its specific aminoacyl-tRNA synthetase to form aminoacyl-AMP at the expense of two ATP equivalents. The amino acid is then transferred from the aminoacyl-AMP to its specific tRNA to form the specific aminoacyl-tRNA. The tRNA is now said to be 'charged'. There are 20 amino acids, and 20 aminoacyl-tRNA synthetases and 20 or more tRNAs. The overall reaction for the production of an aminoacyl-tRNA is given at the bottom of the page.

Thus three components of the system lead to a specific amino acid being placed in the correct place in the sequence of amino acids making up the protein. These are the amino acid-specific aminoacyl-tRNA synthetase, tRNA and the triplet code in the mRNA.

Protein synthesis begins with the formation of an *initiation* complex, an association of a specific aminoacyl-tRNA, the mRNA message, small (30S) and large (50S) ribosomal subunits, initiation factors, energy (GTP), Mg^{2+} and other factors. The process of *elongation* now follows, in which amino acids are added one by one to the growing peptide chain. Each of these last processes requires use of GTP, making a total of 4 ATP equivalents of energy required for each peptide bond formed. Termination is signalled by another triplet code.

After leaving the ribosome, a protein undergoes post-translational processing, which begins with a unique pattern of folding so that the protein takes up the specific three-dimensional structure essential to its function. Further post-translational modifications may include the modification of specific amino acid residues (lysine to hydroxylysine or methyl lysine; proline to hydroxyproline; histidine to 3-methyl histidine), cross-linking through oxidation of two cysteine residues (to form cystine); glycosylation (addition of sugars and amino sugars, linked by either *N*-glycosidic bonds to asparagine or by *O*-glycosidic bonds to serine or threonine). In addition, certain parts of the peptide chain may be removed, such as signal sequences, especially from proteins that are destined to be secreted from the cell.

Protein synthesis continues throughout life, accompanied by protein degradation: the two processes are together referred to as protein turnover. The difference between the two rates is the rate of protein accretion. In any growing animal, fractional rates of protein turnover are highest in early life and decline progressively as maturity is approached, at which point the rate of accretion falls to zero.

$$\text{amino acid} + \text{tRNA} + \text{ATP} \xrightarrow[\textit{aminoacyl-tRNA synthetase}]{Mg^{2+}} \text{aminoacyl-tRNA} + \text{AMP} + \text{PPi}$$

Rates of protein synthesis are usually measured by the incorporation of isotopically labelled amino acids, using either a constant infusion or a 'flooding dose'. They may be expressed either as absolute rates (e.g. g day^{-1}), which describe the total amount of a protein, or mixture of proteins, synthesized per unit time, or as fractional rates (e.g. % day^{-1}), which describe the fraction of a mass of protein that is replaced each day. Fractional rates are converted to absolute rates by multiplying by the protein mass. Fractional rates of protein synthesis vary greatly amongst different proteins in the body, from a few per cent per day in tissues such as muscle, skin and bone to many hundred per cent per day in some liver enzymes. Protein synthesis is regulated at the level of transcription of individual genes, i.e. the production of the specific mRNA, and at the level of whole tissues or organs, e.g. the hormonal stimulation of muscle growth.

In a nutritional context, rates of protein synthesis most commonly relate not to individual proteins but to total protein synthesis in an organ or in the whole animal. Organs such as gut, liver and pancreas are characterized by relatively high fractional rates of protein synthesis; bone and muscle by relatively low rates (Table 1). Rates in whole animals are intermediate (Table 2). Protein synthesis is sensitive to nutrient intake (Table 3) and alterations of diet affect growth rate by altering the rate of protein accretion, which is the result of alterations in the relative rates of protein synthesis and protein degradation (Table 3). (NJB)

See also: Protein degradation; Protein metabolism; Protein turnover

Table 1. Fractional and absolute rates of protein synthesis in various tissues of 44 kg pigs (from Simon, 1989).

Organ	Protein content of organ (g)	Fractional rate of protein synthesis (% day^{-1})	Absolute rate of protein synthesis in the organ (g day^{-1})
Liver	211	11–28	24–59
Pancreas	21	75–88	16–19
Stomach	49	13–23	6–11
Small intestine	135	22–53	30–72
Caecum	8	27–57	2–5
Colon	54	17–44	10–24
Kidney	27	10–15	3–4
Skeletal muscle	2800	2–5	71–150
Heart	23	5–6	1
Skin	400	4–9	15–34

Table 2. Rates of protein synthesis in the whole body of various species (from Simon, 1989).

Species	Body weight (kg)	Fractional rate (% day^{-1})	Absolute rate (g day^{-1})
Rainbow trout	0.12	5	1
Chick, 1 week	0.08	34	5
Chick, 2 weeks	0.14	32	8
Chick, 3 weeks	0.23	30	13
Chick, 4 weeks	0.31	26	16
Rabbit, adult	3.6	8	49
Sheep	20	7.8	240
Pig	30	9	406
Pig	60	6.7	606
Cow	250	4.1	1650
Cow	480	3.5	2690

Table 3. The effects of adding carbohydrate, fat or protein to the diets of young pigs (data of Reeds *et al.*, 1981).

Diet	ME (MJ kg $^{-0.75}$ day^{-1})	Digestible N (g kg$^{-0.75}$ day^{-1})	Protein synthesis (g kg$^{-0.75}$ day^{-1})	Protein degradation (g kg$^{-0.75}$ day^{-1})
Basal	1.18	2.17	5.47	4.15
Basal + carbohydrate	1.58	2.31	6.12	4.39
Basal + fat	1.75	2.30	6.01	4.14
Basal + protein	1.25	4.35	7.40	5.65

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Protein turnover A term used to describe the constant synthesis (K_s) and degradation (K_d) of proteins. Protein turnover is essential for organisms to grow and develop, to alter organ structure and to respond metabolically to the ever-changing physical and biochemical environment. The continuous synthesis and breakdown of protein provide a mechanism whereby the amount of each of the individual proteins involved in metabolism can be altered. For example, by varying the amount of enzyme protein, the flow of metabolites in pathways involved in both the production and destruction of cellular constituents can be controlled, as well as substrate utilization for cellular ATP production. The initial studies by Schoenheimer in the 1940s using ^{15}N-labelled amino acids led to the concept that individual cellular proteins were synthesized and degraded (i.e. turnover) at rates varying from minutes to months.

Protein synthesis and degradation in the intact animal can be estimated by infusing amino acids containing one or more of the isotopes ^{2}H, ^{3}H, ^{13}C, ^{14}C, ^{15}N, ^{18}O or ^{35}S. The rate constant for protein synthesis has been estimated in experiments using either a single bolus or a continuous infusion of the tracer over a specified time. Usually protein synthetic rates are expressed in units of percentage of the pool per day (% day^{-1}). Tissues such as intestinal mucosa and liver may have values close to 100% day^{-1} while connective tissue may have a rate < 1% day^{-1}.

Animal size and metabolic rate per unit weight have an effect on protein turnover. Smaller animals have higher rates of protein turnover (per unit of body weight per day) than larger animals. Turnover is scaled to the metabolic body size (kg$^{0.75}$). (NJB)

See also: Protein degradation; Protein metabolism; Protein synthesis

Key reference

Reeds, P.J. and Beckett, P.R. (1996) Protein and amino acids. In: Ziegler, E.E. and Filer, L.J. Jr (eds) *Present Knowledge in Nutrition*, 7th edn. ILSI Press, Washington, DC, pp. 67–86.

Protein utilization Protein utilization depends on not only the amino acid content of dietary proteins, but also the digestion and absorption of the **amino acids** in the protein. The rate of digestion of proteins in the diet can affect the pattern of amino acids available for protein synthesis (*see* **Amino acid metabolism**). This is most obvious when limiting amino acids are added in free form to a diet. The rate of growth may not be the same as when a similar amino acid pattern is provided to the animal as part of a protein. Apparently the time at which an amino acid is available for protein synthesis affects the utilization of the amino acids for protein synthesis, probably because of the concomitant destruction of amino acids that could have been used to support growth. Components of the diet that decrease the rate and extent of digestion, such as lignin and other fibrous materials or antinutritional factors such as trypsin inhibitors, decrease the nutritional value of the protein source.

The amino acid content of the proteins can have an effect on dietary protein utilization because a full spectrum of the eight to ten indispensable amino acids plus the dispensable amino acid produced by the animal is required for the animal to utilize the dietary amino acids for protein synthesis. The spectrum of amino acids available for protein synthesis is a mixture of dietary amino acids and those available from protein turnover in the animal. In general about 80% of the amino acids available for tissue protein synthesis is derived from cellular protein turnover and 20% from the diet. From the point of view of indispensable amino acids available for protein synthesis, it is common to use mixtures of plant proteins and/or animal proteins to improve overall protein utilization. The pattern of dietary amino acids is improved when soybean is added to maize (maize is low in lysine and soybean is low in sulphur amino acids) because these two proteins complement each other's amino acid pattern deficit. With respect to dispensable amino acids (e.g. alanine, serine, glycine, arginine, aspartate, glutamate, proline), the liver plays an essential role in their biosynthesis from intermediates of carbohydrate (glucose and related sugars) degradation and from intermediates (pyruvate, oxaloacetate and α-ketoglutarate) of amino acid catabolism.

The efficiency of amino acid (i.e. protein) utilization is directly dependent on the energy content of the diet. When the energy requirement of the animal is not met fully, amino acids (protein) are used as a source of energy and thus the resulting growth or N retention increments are less than expected. The efficiency of amino acid utilization is not constant, in that the response to increased equal dietary increments decreases with additional increments (a diminishing returns response). The figure opposite shows the change in N gain over a range of N intakes of Mormon cricket meal without or with supplemental L-methionine. An indication of a decrease in protein utilization is evident from a decrease in N gain per unit of N intake with higher N intakes. Relative to zero gain (i.e. maintenance) the amount of N intake required to reach 50% of maximum is 6 and 9 times more N (supplemented vs. unsupplemented) while that required for 95% of maximum is 17 and 27 times more, showing markedly less response as level of response approaches the maximum. Furthermore, the response to identical increments of N from the two N sources is different. The relative value of the unsupplemented protein changes with the level of N intake. Setting the value of the supplemented protein at 100, that of the unsupplemented protein at 0, 50 or 95% of the response maximum is at 0, 90%, 50, 74% and 95, 62%. These comparisons show that the utilization of protein varies with level and that the relative values of protein change with level of intake. (NJB)

Key references

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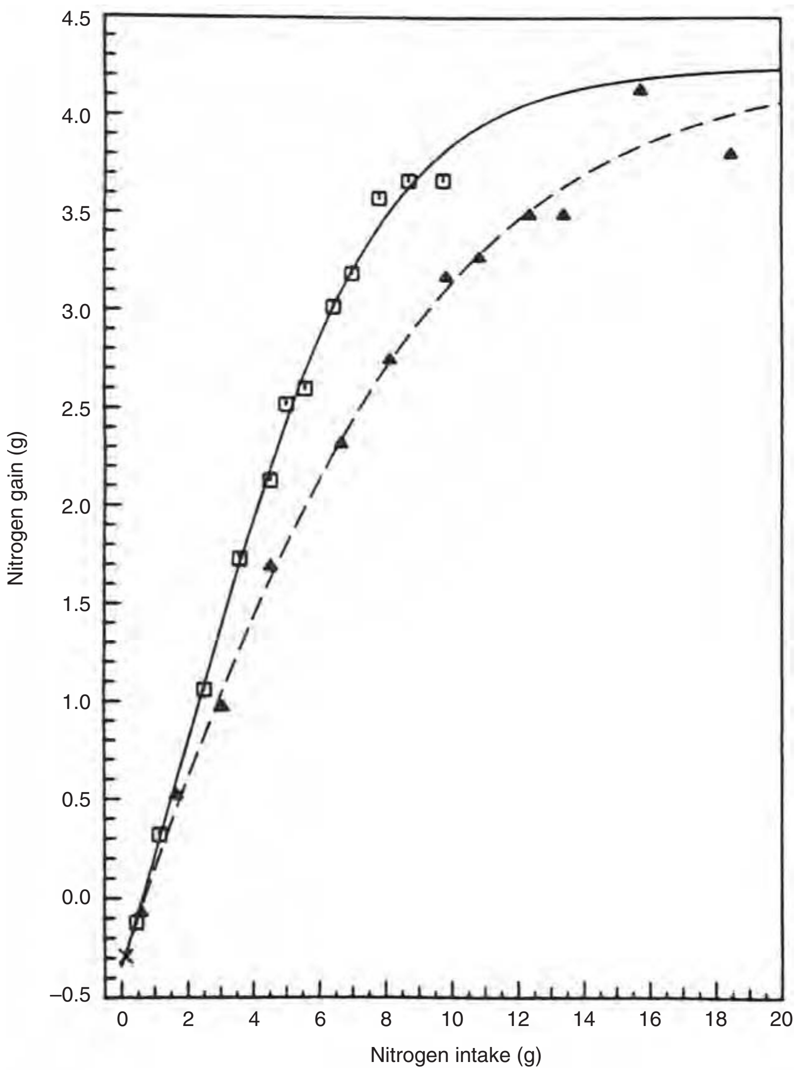
Finke, M.D., DeFoliart, G.R. and Benevenga, N.J. (1987) Use of a four-parameter logistic model to evaluate the protein quality of mixtures of Mormon cricket meal and corn gluten meal in rats. *Journal of Nutrition* 117, 1740–1750.

Proteinase: *see* Proteases

Proteinase inhibitors: *see* Protease inhibitors

Proteolysis: *see* Protein degradation

Protozoa Protozoa (mobile, asymmetrical, single-celled organisms) are important inhabitants of the gastrointestinal tract of ruminants. Although rarely exceeding 10^6 ml^{-1} rumen fluid, because of their size (50–170 μm) they comprise a substantial portion of the rumen microbial biomass. While a number of flagellate species are present, the ciliated oligotrich and holotrich protozoa pre-



Changes in N gain with N intake from Mormon cricket meal.

dominate. Their ability to take up both soluble substrates and feed particles (including bacteria) by engulfment markedly influences the rumen environment, population dynamics and the rate, site and extent of fermentation. Protozoa, unlike bacteria, are not vital for the development and survival of the ruminant host, and their elimination (defaunation), although producing a less stable rumen environment, has been found to reduce gaseous carbon and nitrogen losses. (FLM)

See also: Gastrointestinal microflora; Rumen microorganisms

Proventriculus The anterior part of the glandular stomach in birds. The proventriculus can be found above the liver and between the oesophagus and gizzard. It is a spindle-shaped, thick-walled organ with a secretory function of gastric enzyme and hydrochloric acid release in preparation for the digestion of food prior to passage to the gizzard. (MMax)

Proximate analysis of foods The basic requirement in defining the nutritive value of a food is information on its contents of the major nutrients, viz. carbohydrate, lipid and protein. 'Proximate analysis' is the term given to the separate analyses necessary to quantitate these components. From data on these components the energy content of the food may also be calculated. Besides the major nutrients, proximate analysis also includes measurements of moisture and ash levels. The ash component can be used for mineral analyses and the lipid component can be further analysed for cholesterol and fatty acids.

Proximate analysis is best initiated by determining the moisture content of the food. A sample of the food is dried to constant weight at 103°C and the loss on drying ascertained.

Proximate analysis of the carbohydrates attempted to divide them into two groups: those well digested (named nitrogen-free extract) and those less well digested (called crude fibre). The method used was designed at the Weende experimental station in Germany over 100 years ago. Crude fibre was the residue remaining after all soluble components had been removed by boiling a sample of the food successively in weak acid followed by weak alkali. Nitrogen-free extract was obtained by difference, being the value obtained when all other measured components (crude fibre, lipid, protein, ash and moisture) were subtracted from the whole. Because this scheme did not always separate carbohydrates into readily digestible and indigestible fractions, another method of partitioning food carbohydrate has since been developed. This utilizes detergents which complex with protein, rendering it soluble. Boiling the sample with a neutral detergent removes soluble carbohydrates, protein, organic acids and so on, leaving a residue (neutral detergent fraction) comprising hemicellulose, cellulose and lignin. Boiling this residue with an acid detergent hydrolyses hemicellulose, leaving cellulose and lignin as acid detergent fibre.

The lipid content of a food is normally measured gravimetrically after quantitative extraction with diethyl ether in a Soxhlet apparatus. The lipid residue is weighed after evaporation of the ether. Alternatively, an acid extraction procedure, employing a Monjonnier extraction flask, has been used. A sample of the food under test is digested with ethanolic HCl at 70–80°C for 45 min. After cooling, the digest is quantitatively transferred to a Monjonnier fat extraction apparatus and quantitatively extracted with three separate portions of diethyl ether followed by a single portion of light petroleum. The combined ether extracts are evaporated to constant weight.

Proximate analysis of protein is carried out by quantitative measurement of the nitrogen content of the food under test. Nitrogen is usually measured by a Kjeldahl procedure and the crude protein content of the food obtained by multiplying the value so obtained by the factor 6.25. This factor is based on the fact that, on average, proteins contain 16% N. Proximate analysis of protein is referred to as 'crude protein' because: (i) not all the N in foods is protein N (a variable amount occurs as free amino acids, amides, purines, pyrimidines and so on); and (ii) the protein in the food may not contain precisely 16% N.

The amount of ash in a food is measured gravimetrically after burning off the organic matter in a muffle furnace at 600°C for 18 h. During this process ('ashing'), the organic matter in the food is oxidized. (CBC)

See also: Ash; Crude fibre; Crude protein; Dry matter; Ether extract; Kjeldahl; Nitrogen-free extractives; Weende analysis

Pseudostem: *see* Banana

Pseudovitamins Compounds similar in structure to vitamins but without vitamin activity. Some pseudovitamins have the same empirical formula as the true vitamin but not the correct stearic configuration and hence have no biological activity. For example, L-biotin has none of the activity of the active form D-biotin. Pseudo-pyridoxine (pyridoxamine or pyridoxal) does not support the growth of rats. Similar structural variations have been noted with vitamin B_{12}-related compounds of which some are designated pseudovitamin B_{12}. (NJB)

Pteroylglutamic acid Folic acid, a water-soluble B vitamin. It is a compound of 2-amino-4-oxo-6-methylene pteridine, *para-*

aminobenzoic acid and L-glutamic acid. Folic acid as such is not functional in cells but must first be converted to tetrahydrofolatemonoglutamate ($PteGlu_1$). In the cell as many as seven L-glutamates are added (Pte_{1-7}) with five (Pte_5) being the most common. These polyglutamate forms of tetrahydrofolate are involved in cell metabolism as substrates in one-carbon transfer and can be found with the oxidation of carbon varying from $-CH_3$, $-CH_2-$, -CHO. (NJB)

Ptyalin α-Amylase (1,4-α-D-glucan-glucanohydrolase; EC 3.2.1.1), found in the saliva of omnivorous animals. It hydrolyses α(1→4) glucosidic bonds in starch and glycogen, producing maltose, isomaltose and limit dextrins. (SB)

Puberty The stage in the life of an animal when the sex glands become functional and ovulation or semen production is initiated (*see* **Sexual maturity**). Puberty is generally delayed by undernutrition and is only attained when a threshold weight is reached. In seasonal breeders, the month of birth may also affect age at sexual maturity. (PJHB)

Puffer fish Puffers includes two families of fish: balloonfish and the spiny burrfish or porcupine fish. These fish swallow water to enlarge their body size to discourage predation. An additional deterrent to predators is the spines of the puffers. The skin and organs of these fish contain tetrodotoxin, which is lethal when consumed by humans and other aquatic organisms. The flesh of puffer fish is considered a delicacy in Japan and is prepared after specially trained chefs remove this toxin from certain parts of the fish's body. (SPL)

Pumpkin (*Cucurbita* spp.) Pumpkins are creeping plants, often intercropped at low density with maize. As a sole crop, a yield of 30–40 t ha^{-1} is often achieved in higher rainfall areas on fertile soils. Pumpkins have a high moisture content; cattle and pigs find them succulent and highly palatable, especially during the dry season. As a result of the low dry matter content, they have a low nutritive value. Care should be taken when feeding pumpkins to pigs because the carcass may contain soft fat if the intake is too high. (LR)

Further reading

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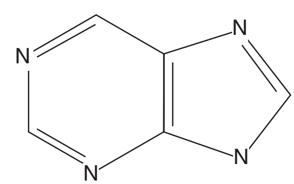
Pup (Also kit, or kitling) a young rabbit, from birth to weaning. (PC)

Purines Bicyclic nine-member heterocyclic rings with the general formula $C_5H_4N_4$.



Typical composition of pumpkins (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh pumpkins	7.6	14.5	13.2	7.9	2.6	61.8	0.39	0.26

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical digestibility (%) and ME content of pumpkins.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Fresh pumpkins	90.0	80.0	83.0	95.0	13.58

ME, metabolizable energy.

The following purines are designated as nucleic acids: adenine (A), $C_5H_5N_5$; and guanine (G), $C_5H_5N_5O$. When ribose (in ribonucleic acid, RNA) or deoxyribose (in deoxyribonucleic acid, DNA) is added to A or G, the resulting compounds are nucleosides: when the sugars are phosphorylated the compounds are designated as the nucleotides adenosine monophosphate (AMP) and guanosine monophosphate (GMP). Inosine monophosphate (IMP) is the source of both AMP and GMP. In DNA the purine adenosine (A) is always paired with the pyrimidine thymine (T), $C_5H_6N_2O_2$, and the purine guanosine (G) is always paired with the pyrimidine cytosine (C), $C_4H_5N_3O$. The A–T and G–C pairings in DNA are the basis of its three-dimensional structure and its replication, because the coding strand of DNA is the basis for the template strand. In the synthesis of RNA, G always binds to C but A, instead of binding to T, binds to uracil (U), $C_4H_4N_2O_2$. In DNA replication, A in the coding strand always results in T in the template strand. In the production of RNA from DNA, T always gives rise to A but A always gives rise to U. Other purines of importance in animal metabolism are hypoxanthine, an intermediate in the catabolism of adenosine, and precursor of xanthine, an intermediate in the catabolism of adenosine, inosine and guanosine. The excretory end-product of purine catabolism is uric acid, which is also the urinary excretion product of N metabolism in uricotelic animals. (NJB)

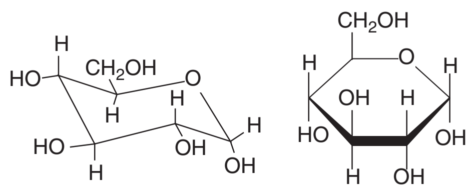
See also: Pyrimidines

Putrescine Putrescine (1,4, diaminobutane, $NH_2 \cdot (CH_2)_4 \cdot NH_2$) is a precursor of the polyamines spermidine and spermine. The initial step in polyamine synthesis is the formation of putrescine from L-ornithine by ornithine decarboxylase. Polyamines are associated with the polyanions DNA and RNA and are involved in stabilization and packaging of DNA. (NJB)

Pylloquinone Phylloquinone, 2-Me-3-phytyl-1,4-naphthoquinone is the form of vitamin K produced by plants. (JWS)

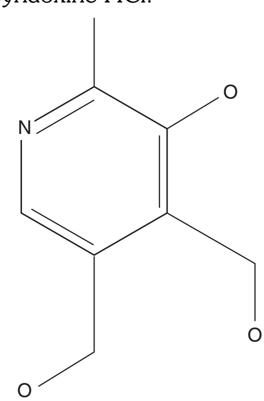
Pyranose Six-member ring structure of a monosaccharide created by the reaction of the alcoholic hydroxyl group on carbon 5 with the aldehydic group at carbon 1 or the reaction of the oxygen of the hydroxyl group on carbon 6 with the carbonyl group on carbon 2. This term is used as it indicates that the six-member ring compound is a derivative of pyran.

Structures of pyranoses and furanoses are more meaningfully depicted as hexagons and pentagons. Glucose is used in this example to depict the three-dimensional orientation of a carbohydrate molecule by the conformational (left) and Haworth formulations. With the Haworth convention, the plane of the ring is shown as perpendicular to the plane of the paper, and this is emphasized by shading those bonds that are indicated to be nearer the reader. In the alpha form, the hydroxyl group on the anomeric carbon is below the plane of the paper, which is thus indicated by placing the hydroxyl below the bond. The conformational representation of alpha-D-glucose is useful in interpreting the reactivity of the hydroxyl groups. (JAM)



See also: Carbohydrates; Furanose; Galactose; Glucose; Mannose

Pyridoxine $CH_3C_5HN(OH)(CH_2OH)_2$, vitamin B_6, one of the water-soluble B vitamins. It is synthesized commercially and available as pyridoxine HCl.

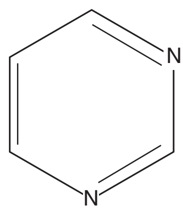


Pyridoxine is synthesized by bacteria in the rumen and is thus not required in the diets of ruminants. It is also synthesized by bacteria in the intestine of non-ruminants, but this takes place lower down the gut than the sites where the vitamin is digested and absorbed so that for these animals a dietary supply is essential. In addition to the normal forms of the vitamin, many plant sources contain variable amounts of pyridoxine as a glucoside (this maybe a storage form) in which glucose is linked to the 5′-position (5′-*O*-(β-D-glucopyranosyl) pyridoxine). Three phosphorylated forms of pyridoxine are found in animal and plant tissue. They are pyridoxine 5′-phosphate (PNP), pyridoxal 5′-phosphate (PLP) and pyridoxamine 5′-phosphate (PMP). In laboratory animals and humans the vitamin is associated with the enzyme glycogen phosphorylase in muscle: as much as 70–80% of the total body pool of vitamin B_6 may be associated with this muscle enzyme in the laboratory rat.

Because pyridoxine in coenzyme form is intimately associated with amino acid metabolism, it is widely distributed in nature and found in numerous animal and plant products. At the concentrations found in foodstuffs, PNP, PLP and PMP are digested and absorbed as the free vitamin pyridoxine and as pyridoxal and pyridoxamine. When supraphysiological levels of PNP, PLP and PMP are used, the phosphorylated forms of the vitamin are taken up. The three forms of the vitamin PN, PL and PM are phosphorylated in the 5′-position by the same enzyme, pyridoxal kinase: they can be interconverted but all must be changed to pyridoxal (PL) for the production of 4-pyridoxic acid, which is the form in which pyridoxine is excreted in the urine. In animal metabolism, PLP and PMP are the coenzyme forms associated with enzymatic transamination, decarboxylation, side-chain cleavage, dehydratase reactions, and D–L interconversion of amino acids. Some of these reactions are critical to the synthesis of dispensable amino acids from carbon sources such as α-keto acids (pyruvate, oxaloacetate, α-ketoglutarate) derived from glucose and other carbohydrates.

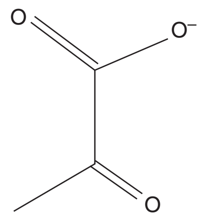
A deficiency of pyridoxine can be assessed by an oral load test of the amino acids tryptophan or methionine and measuring urinary excretion of xanthuranic acid or cystathionine, respectively. As a deficiency progresses, the urinary excretion of these products increases. Another approach to identifying a deficiency of pyridoxine is that of measuring the activity of the erythrocyte enzyme aspartate aminotransferase, which requires PLP as a co-factor. This assay is most meaningful when it is tested with and without the addition of the enzyme co-factor PLP. As a deficiency progresses, the amount of cellular co-factor available to support the activity of the enzyme decreases and the activity of the enzyme declines. In the laboratory test, direct addition of the co-factor (PLP) to the *in vitro* test results in a greater stimulation or recovery of enzyme activity. Thus, a greater stimulation of enzyme activity due to supplemental PLP is an indication of a deficiency. Requirements for this vitamin are in the range of mg kg^{-1} diet. (NJB)

Pyrimidines Six-membered heterocyclic unsaturated ring compounds with the general formula $C_4H_4N_2$. The B vitamin thiamine is a pyrimidine derivative and the pyrimidine-based compounds alloxan and thiouracil are important in medicine. The following pyrimidines are designated as nucleic acids: uracil (U), $C_4H_5N_3O$; thymine (T), $C_5H_6N_2O_2$; and cytosine (C), $C_4H_5N_3O$. Small amounts of the pyrimidine 5-methylcytosine ($C_5H_6N_3O$) are found in bacterial and human DNA while the pyrimidine 5-hydroxymethylcytosine ($C_5H_6N_3O_2$) is found in the DNA of bacteria and viruses. When ribose is added to C or U or deoxyribose is added to C or T they become nucleosides and when the sugars are phosphorylated they become the nucleotides uridine monophosphate (UMP), cytidine monophosphate (CMP) and thymidine monophosphate (TMP). RNA contains C and U but DNA contains C and T. In DNA the purine adenosine (A) is paired always with the pyrimidine thymidine (T) and the purine guanosine (G) is always paired with the pyrimidine cytosine (C). The A–T and G–C pairings in DNA are the basis of its three-dimensional structure and its replication, because the coding strand of DNA is the basis of the template strand. In the synthesis of RNA, G always binds to C but now A, instead of binding to T, binds to U. In DNA replication A in the coding strand always results in T in the template strand. In the production of RNA from DNA, T always gives rise to A but A always gives rise to U.



(NJB)

Pyruvate The anion of pyruvic acid, CH_3·CO·COOH, a key substrate in intermediary energy metabolism. Pyruvate is produced from glucose and related three-carbon compounds (triose phosphates, i.e. 3-phosphoglycerate in the process of glycolysis, Embden-Meyerhof pathway) and is in equilibrium with L-lactate, CH_3·HCOH·COO^-. It is also produced in the catabolism of three-carbon amino acids such as L-alanine, L-serine and L-cysteine. Pyruvate CH_3·CO·COO^- in muscle takes up ammonium nitrogen (NH_4^+) to become alanine CH_3·$HCNH_3^+$·COO^- for disposal of N in the liver as urea. This is referred to as the pyruvate–alanine shuttle.



(NJB)

Pyruvic acid: *see* Pyruvate

Q

Quality control in feed mills Quality control standards within the modern feed mill are set by central governments. However, mills supplying feed for livestock that are entering the supermarket retail business normally work to higher standards laid out by retail quality assurance schemes. As part of these, all raw materials entering the feed mill must come from an approved supplier or be part of a farm quality-assured production system. All materials must adhere to predetermined quality criteria. They are then mixed according to a known formula and the amount of each raw material is recorded against a batch number, so that there is full traceability of all feeds produced. To avoid any cross-contamination from one feed to another, feeds can only be manufactured in a specific order, with particular reference to the scheduling of any feed that may contain some form of medication. Mills are required to have written standard operating procedures (SOPs) for the whole process and to have a hazard analysis by critical control points (HACCP) programme in place. There is usually a legislative requirement to monitor and control production by the chemical analysis of the finished feed. (KF)
See also: Compound feed; Feed mixing

Quinolines Aromatic bicyclic unsaturated six-member ringed compounds, C_9H_7N. Quinolines are organic bases. They have a penetrating odour approaching that of pyridine. They are used to preserve tissue samples, as an anti-malarial and in the manufacture of the B vitamin niacin. (NJB)

Quinones Six-member unsaturated ring compounds, $C_6H_5O_2$. They have a penetrating odour resembling chlorine and are toxic by ingestion or inhalation and an irritant to the skin, eyes and mucous membranes. (NJB)

R

Rabbit Rabbits are small herbivores that have an enlarged hindgut (caecum and colon), facilitating their utilization of forages and other fibrous feeds. Their digestive strategy is to separate and rapidly excrete fibre and to retain non-fibre material in the caecum, where it is subjected to microbial digestion. Selective excretion of fibre and retention of non-fibre components are accomplished by muscular activities of the colon. At regular daily intervals, the caecum is evacuated and the animal consumes the caecal contents (caecotropes, soft faeces, night faeces) directly from the anus (caecotrophy). The nutritional benefits of caecotrophy are mainly that microbially synthesized water-soluble vitamins (B-complex) are obtained independently of a dietary source. A secondary benefit is the utilization of caecally synthesized microbial protein. Although there is some microbial protein synthesis in the caecum, the rabbit has a very limited ability to utilize dietary sources of non-protein nitrogen such as urea. Because of the selective and rapid excretion of fibre as a major component of the hard faeces, the digestibility of crude fibre in the rabbit is much lower than in horses and ruminants.

The microbiology of the rabbit caecum is unique. The dominant organisms are *Bacteroides* spp. *Lactobacilli* and *Escherichia coli* are generally absent from the rabbit digestive tract. The major volatile fatty acids (VFAs) produced in caecal fermentation are acetic and butyric acids.

Calcium is absorbed very efficiently in the rabbit, in contrast to other animals in which calcium absorption is regulated according to need by vitamin D. High dietary calcium levels result in elevated plasma calcium and the excretion of excess calcium in the urine. The urine often contains high levels of calcium carbonate as a white precipitate. Urolithiasis is common in older rabbits (especially pets) that are chronically exposed to high calcium intakes.

Rabbits are susceptible to both deficiencies and toxicities of vitamin A. Because most rabbit diets contain lucerne or other forages, there is generally an adequate quantity of β-carotene in the diet. Addition of synthetic vitamin A to diets rich in carotene may cause vitamin A toxicity. Levels in excess of 40,000 IU vitamin A kg^{-1} may cause severe reproductive effects, including fetal resorption, abortion, small litters, hydrocephalus and low neonatal viability. Vitamin A deficiency produces similar signs. A dietary level of 10,000 IU vitamin A kg^{-1} diet will prevent both deficiencies and toxicities. Little information is available on vitamin E requirements of the rabbit. Deficiency causes muscular dystrophy, paralysis of hindlegs and reproductive failure. Vitamin D toxicity has been observed in rabbits, due to errors in diet formulation. Signs include progressive emaciation and weakness, anorexia, diarrhoea, intense thirst, ataxia, and paralysis leading to death. Extensive soft tissue (liver, kidney, artery walls, muscle) calcification occurs.

Compared with other animals, rabbits have a high water requirement. Water intake is about 120 ml kg^{-1} body weight per day. Rabbit urine is usually alkaline, is often pigmented red or yellow, and may be turbid because of precipitates of calcium carbonate. (PC)

Rabbit feeding Appropriate feeding of rabbits necessitates appreciation of some unique features of their digestive tract physiology. Having evolved as a herbivore, the rabbit has a feeding strategy of consuming feeds high in fibre but also has ileo-caecal-colonic mechanisms for separation and rapid excretion of fibre. It requires a fibrous diet for maintaining health of the digestive tract but also ample concentrations of high-quality sources of energy and protein. The crude protein requirement for growth is lower than the requirement for optimal reproductive performance. A dietary concentration of 16% crude protein is adequate for maximum growth, while for lactating females 18–19% dietary protein is optimal. Precise values for amino acid requirements have not been established. Provisional requirements of growing rabbits are 0.75% lysine, 0.65% sulphur amino acids and 0.64% threonine.

Feeding excess dietary protein may increase caecal ammonia and pH, leading to increased incidence of enteritis. Excretion of excess nitrogen in the faeces and urine results in elevated environmental ammonia concentrations, which may provoke increased respiratory disease. The highest energy requirements of rabbits are for lactation: does in early lactation are typically in negative energy balance. High-energy diets containing added fat may be beneficial during lactation.

Dietary fibre levels are important, with optimal levels of 10–15% crude fibre for growing rabbits. Lower concentrations may result in reduced growth rate, fur chewing, with formation of gastric hairballs (trichobezoars), and an increased incidence of enteritis. With Angora rabbits, in which the occurrence of trichobezoars is a major problem, feeding long hay or straw as a supplement to a pelleted diet may be beneficial. Administration of a source of proteolytic enzymes, such as raw pineapple or papaya juice or enzyme tablets (papain, bromelain), is effective in breaking down trichobezoars and facilitating passage of hair from the stomach. The digestibility of crude fibre in rabbits is variable, being less than 15% for feeds high in lignin and cellulose (e.g. lucerne meal) but as high as 60% in non-lignified fibre sources such as beet pulp.

Major feedstuffs for rabbit production include dried forages such as lucerne meal, cereal grain by-products such as wheat bran, and plant protein supplements (e.g. soybean meal). Molasses and fats are used as energy supplements.

Ideally, a series of different diets (e.g. starter, grower, finisher and lactation diets) would be used. However, under most practical conditions of rabbit production, only one diet is used. Allowances for differences in requirements can be made to some extent by adjusting the amount of feed offered. Gestating females and the males are usually fed restricted amounts of feed, while lactating females and growing-finishing rabbits are fed *ad libitum*.

There is little information on breed differences in nutritional requirements. Dwarf breeds require higher-energy diets, while giant breeds have the greatest ability to utilize high-fibre diets. (PC)

Raffinose A trisaccharide, $C_{18}H_{32}O_{16}$, molecular weight 504, consisting of one galactose residue and one sucrose molecule. It is found in sugarbeet, legumes and cottonseed. It is converted by invertase into fructose and melibiose. Other names: melitose, melitriose, gossypose. (JAM)

See also: Carbohydrates; Fructans; Glucofructans; Lychnose; Oligosaccharides

Ragwort poisoning Ragwort is the common name for several species of *Senecio* that contain pyrrolizidine alkaloids. Although pyrrolizidine alkaloids have been identified in over 100 *Senecio* species, only about a dozen poison livestock. Most livestock poisoning is caused by the widely distributed and highly toxic tansy ragwort (*S. jacobaea*). Relatively non-toxic pyrrolizidine alkaloids are bioactivated by liver mono-oxygenase enzymes into toxic pyrroles. Pyrroles are potent electrophiles that bind and form adducts with cellular nucleic acids and proteins, resulting in liver necrosis, proliferation of bile duct epithelium and fibrosis (similar to cirrhosis). Pyrroles also alter cell growth and division, resulting in large liver cells (megalocytosis). High doses cause immediate liver failure. Low dose exposures result in prolonged disease that becomes fatal when the animal cannot compensate for the progressive liver damage. Plants containing pyrrolizidine alkaloids have worldwide distribution. Though they are generally not palatable, they often contaminate feeds and food, resulting in animal and human poisoning. As animals often do not develop clinical symptoms until months after exposure, identifying the contaminating seeds or plants is often impossible. (BLS)

Rainbow trout (*Oncorhynchus mykiss* Smith & Stearley) A salmonid endemic to western North America from southern Alaska to Mexico. It has been introduced to eastern North America, Asia, Africa, Australasia, Europe and South America. There are at least three forms recognized: the anadromous 'steelhead' form, the lake-dwelling 'Kamloops' form and the stream-dwelling rainbow. Both marine steelheads and freshwater rainbows are extensively cultured around the world, with production in 1998 totalling over 448,141 t, mostly (90%) in fresh water. (RHP)

Rainy season Many regions, including much of the tropics and subtropics, have defined rainy seasons. These are usually in the summer, as in the tropics, but occasionally in winter (e.g. Mediterranean area). In the tropics, agricultural production and food security depend on the amount and distribution of rainfall in the rainy seasons. (TS)
See also: Wet season

Ram The mature uncastrated male of any species of sheep. The term is usually applied after the animal has reached sexual maturity. The primary function of the ram is to produce spermatozoa and introduce them into the female reproductive tract at oestrus in order to fertilize any ova that are shed some hours after the end of oestrus. The ram's reproductive tract consists of primary, secondary and accessory sex organs. These are similar to those of the bull, except that the testes are much larger in relation to overall body size. Also, in the ram, the glans penis is equipped with a filiform appendage, which rotates rapidly during ejaculation and sprays semen around the outer opening of the cervix. There is no prostate body in the ram. After puberty, semen production is essentially a continuous process in the ram, but there are seasonal fluctuations in the quantity and quality of semen produced as well as in libido, and rams tend to be most fertile during the ewe's breeding season. This seasonality is more pronounced in some breeds than in others and is timed to ensure that lambs are born in the spring, when there is fresh forage to feed the lactating ewe and subsequently the weaned lambs. (PJHB)

Rancidity The occurrence of undesirable flavours (usually characterized as bitter or metallic) in lipid-containing foods. *Lipolytic* rancidity is due to unesterified fatty acids derived from endogenous lipolytic activity (a frequent occurrence in milk fat). *Oxidative* rancidity is due to the oxidation of unsaturated lipids. Oxidation is initiated by interaction of a free radical with the methylene carbon allylic to double bonds, resulting in abstraction of a proton and generation of an unstable bond which undergoes further reactions and generation of more free radicals; thus a chain reaction occurs. Peroxidized molecules are vulnerable to scission, generating a multitude of products. Some products are quite volatile; aldehydes are generated, which have low taste thresholds and contribute greatly to the rancid flavour. Methylene groups between double bonds are most susceptible to free radical attack; thus polyunsaturated fatty acids have the greatest potential for peroxidation. Antioxidants, such as lipid-soluble vitamin E, function by quenching free radicals that are generated during metabolism or oxidative insult. (NJB)

Randle cycle A control mechanism by which glucose utilization is decreased when fatty acids are available (especially to muscle). It functions through a hormone-sensitive lipase and is thought to vary the activity of the mitochondrial enzyme pyruvate dehydrogenase (PDH). Glucose oxidation is dependent on the activity of PDH. The rate of fatty acid oxidation can alter the ratios of metabolites in the mitochondria (acetyl CoA:CoA; $NADH+H^+$:NAD; ATP:ADP) and alter the proportion of PDH in the active form. A decrease in PDH can alter glucose oxidation. (NJB)

Key reference

Randle, P.J., Kerbey, A.L. and Epinal, J. (1988) Mechanisms decreasing glucose oxidation in diabetes and starvation: role of lipid fuels and hormones. *Diabetes Metabolism Reviews* 4, 623–638.

Rangeland Natural grazing used for extensive livestock production, containing many species of grasses, forbs, shrubs or bushes and trees. Best usage is from mixed livestock species, both grazers and browsers (e.g. goats and cattle, or wildlife and cattle). Amounts of land needed per livestock unit are relatively large. Rangeland also supplies thatching grass and wood for fuel and construction. (TS)

Rape A member of the genus *Brassica*, rape is in the mustard family (*Brassicaceae*). Alternative common names include rapeseed, oilseed rape, summer turnip, field mustard and canola (some cultivars specifically). Rape is grown throughout China, the Indian subcontinent, northern Europe and Canada. There is not a single species of oilseed rape: the two commonly cultivated species are *Brassica campestris*, a spring annual, and *Brassica napus*, a winter annual, though both species include varieties that are both spring and winter crops; other species are *Brassica carinata* (Ethiopian mustard) and *Brassica juncea* (Indian mustard). They are all closely related to the species *Brassica nigra* (black mustard) and *Brassica oleracea* (the cabbages).

Rape grows from 1 m to 1.5 m tall; it has a deep taproot and a bright yellow inflorescence of four-petalled flowers, producing small, spherical seeds that are brown, yellow or black. The lighter-coloured seeds, with their thinner husks and consequent reduced fibre content, are considered more valuable. Rape is tolerant of cool temperatures but can be sensitive to high temperatures.

The uses of rape are primarily the oil (the seeds containing 40–44% oil) and the meal, which is a high-protein (35–40%) feed for both ruminant and non-ruminant livestock. These include poultry and fish species, the latter principally benefitting from the provision of lipid rather than protein. The composition of rapeseed protein and oil have been much manipulated through breeding. In general rapeseed protein is high in sulphur-containing amino acids and deficient in lysine. The fatty acid composition of rapeseed oil varies with maturity but in the mature seed comprises mainly unsaturated fatty acids, with linoleate and oleate being the most significant. Saturated fatty acids present include palmitate and stearate. Feeding rapeseed oil to dairy cows has been shown to influence the fatty acid profile of milk. By thus increasing the oleate:palmitate proportion of milk, the value of milk can be increased (e.g. for producers of soft cheeses). Rape has also been used as a forage for both pigs and poultry.

Oilseed rape is the third most important source of edible vegetable oil globally, behind soybean and palm oils. Industrial uses of the oil have included soap production, lamp oil, high-temperature lubricating oils, the manufacture of plastics and a biofuel to power high-speed diesel engines.

Rape contains antinutritive substances, including erucic and eicosenoic acids, sulphur-containing glucosinolates (which are responsible for the mustard flavour), phytates, non-starch polysaccharides and aromatic choline esters. All these limit the value of rape as a feed. Canola cultivars contain low levels of glucosinolates (in the meal) and erucic acid (in the oil), improving the palatability for both human and animal feed products. Further improvements in palatability and animal production have been achieved by both heat treatment and enzyme treatment of the rapeseed meal. Most of the rape varieties other than canola are used to produce oil for industrial purposes only.

In addition to the nutritive value, the lipids in rape meal can favourably affect the composition of the fat produced by the animal, improving profitability. Subcutaneous fat in pig carcasses contains higher concentrations of polyunsaturated fatty acids (particularly linoleic and linolenic acids). Increased concentrations of *trans* fatty acids in milk fat from cows given rapeseed meal are associated with improved spreadability of the butter. However, high dietary concentrations of rapeseed meal can reduce feed intakes and growth in pigs and poultry, and impair rumen function in cows, resulting in reduced digestibility and intakes. (DA)

See also: Erucic acid; Glucosinolates

Further reading

Oplinger Hardman, L.L., Gritton, E.T., Doll, J.D. and Kelling, K.A. (1989) *Canola (Rapeseed). Alternative Field Crops Manual*. University of Wisconsin, Madison.

Rapidly digestible starch Starch that is rapidly digested *in vitro* and which is therefore expected to be effectively digested by animal enzymes in the small intestine. (SB)

Real digestibility A value of digestibility that relates solely to the dietary material, generally protein and amino acids, and is thus not directly influenced by endogenous losses or microbial metabolism. Estimates of the real digestibility of protein and amino acids can be made by the ^{15}N isotope dilution method in which dietary N in the digesta can be distinguished from endogenous N. (SB)
See also: Protein digestibility

Rearing techniques: *see* Artificial rearing of mammals

Rectum The terminal section of the large intestine, between the colon and the anus. (SB)
See also: Gastrointestinal tract

Recycling: *see* Nitrogen recycling

Red drum (*Sciaenops ocellatus*) A euryhaline marine fish of the family Sciaenidae, native to the Gulf of Mexico and Atlantic Ocean, also called redfish or channel bass. This fish supported commercial and recreational fisheries for many decades, but overfishing in the Gulf of Mexico resulted in closure of the commercial fishery in the 1980s and escalated research efforts to culture this species for stock enhancement and food production.

Red drum undergo larval development after hatching from very small (~ 0.6 mm) buoyant eggs and primarily consume zooplankton such as rotifers and copepods until reaching a size of approximately 50 mm. Red drum juveniles naturally consume small benthic invertebrates such as shrimp and crabs along with small fish. They readily adapt to artificial prepared diets under aquacultural conditions in a variety of culture systems, including earthen ponds, recirculating raceways, cages and net pens.

Dietary requirements of red drum for many of the most critical nutrients have been determined. These carnivorous fish require between 35 and 45% crude protein in the diet with a digestible energy level of approximately 15 kJ g^{-1} diet or 35–45 kJ energy g^{-1} protein for maximum weight gain and desirable body composition. Although red drum is a carnivorous fish in nature, it is not adversely affected by relatively high levels (~ 30%) of soluble carbohydrate in the diet, though at levels between 7 and 11% of diet they use lipid more efficiently than carbohydrate. Marine oils containing highly unsaturated fatty acids of the linolenic acid (n-3) family are needed to satisfy the essential fatty acid requirements of red drum because of their limited ability to elongate and desaturate short-chain fatty acids. Limited information is currently available on mineral and vitamin requirements of red drum. (DMG)
See also: Aquaculture; Fish larvae; Marine fish

Key references

Gatlin, D.M. III (1995) Review of red drum nutrition. In: Lim, C.E. and Sessa, D.J. (eds) *Nutrition and Utilization Technology in Aquaculture*. AOCS Press, Champaign, Illinois, pp. 41–49.
Gatlin, D.M. III (2000) Red drum aquaculture. In: Stickney, R.R. (ed.) *Encyclopedia of Aquaculture*. John Wiley & Sons, New York.

Reducing sugars Sugars that can reduce Fehling's solution (cupric sulphate, sodium potassium tartrate and sodium hydroxide, $NaKCuC_4H_2O_6$), which involves reduction of copper ($2CuO \rightarrow Cu_2O$) and is dependent on the presence of an aldehyde or ketone group in the sugar not attached to another atom in the form of glycoside. All the monosaccharides are reducing sugars, as are the disaccharides maltose, lactose and cellobiose, but sucrose is not. (NJB)

Rehydration The restoration of the fluid content of the body. This may involve more than merely an oral supply of water, for it may be necessary to administer sodium chloride as well so as to maintain the plasma osmotic pressure. This can be achieved by parenteral administration of isotonic saline (0.9%). However, if there has been appreciable haemorrhage, then an intravenous infusion of blood, or of a plasma substitute such

as dextran polysaccharides of high molecular weight (e.g. 70,000), may be required to maintain the plasma colloid osmotic pressure.
(ADC)

Reindeer Reindeer (*Rangifer tarandus*) inhabit a large area of northern circumpolar latitudes and have the greatest circumpolar distribution of any ungulate. Called caribou in North America and Greenland, a number of subspecies have been described based on anatomical differences that adapt them to different environments. Slight differences in the gastrointestinal system between reindeer allow them to adapt to regional variations in indigenous forage availability.

The dietary requirements of reindeer for many nutrients have not been specifically determined. Their natural diet exhibits a high degree of seasonal variation associated with their often migratory life. For example, the vegetation on which Svalbard reindeer feed ranges from rich tundra vegetation to areas with poor plant cover. New growth is selected during spring, while in summer reindeer feed selectively on a mixed diet of vascular plants, choosing plant items of high digestibility and high biomass within patches of forage. Some studies suggest that digestibility alone cannot explain diet selection; abundance of plant species and plant constituents (e.g. protein and secondary plant compounds) also seem important in determining foraging strategy. If nutritional resources are poor during early lactation, maternal fat reserves become exhausted, milk production declines and calf growth suffers as a consequence. During winter, carbohydrate-rich lichens and mosses form an important mainstay of the diet, together with fine twigs. Initial early winter weight loss appears to be primarily as a result of a decrease in gut fill, probably reflecting seasonal inappetence. Although the winter diet has a low nitrogen content, the energy content is generally adequate. Reindeer's feet are adapted to digging for food material through snow (as well as providing support on a snowy substrate). They may augment their diet with animal matter such as dead fish and dead lemmings and, like other deer, may gnaw the bones of dead animals. This is likely to be a response to a high demand for minerals during both lactation and antler growth (both male and female reindeer grow antlers). During antler growth, it may not be possible for males to meet their requirement for calcium. In addition, impaired calcium homeostasis may occur in magnesium-deficient animals.

It is common for reindeer herders to provide supplementary feed for 'managed' reindeer at critical times during the winter when animals find access to lichens difficult, and several specialized diets have been developed. There are reports of problems with the introduction of diets with a high water content (e.g. some grass silages) to reindeer in a catabolic (winter) state. A syndrome known as 'wet belly' has been described in reindeer fed during the winter and has been associated with starvation or indigestion. While the cause remains unknown, supplementary feeding seems to be one of the factors involved (possibly related to kidney dysfunction) since the condition has not been observed in grazing reindeer. In addition, reindeer may be limited in their ability to digest rough, fibrous silage. Supplementary food offered to reindeer in an emergency situation must therefore be highly acceptable and not lead to digestive disturbances; if silage is fed it must be of high quality. (AJFR)

Renal failure: *see* Kidney disease

Rennin A proteolytic enzyme (chymosin; EC 3.4.23.4) occurring in the gastric juice of newborn ruminants. When activated by HCl in the presence of Ca^{2+} it coagulates milk protein, which delays its passage, resulting in increased digestion in the stomach. (SB)
See also: Protein digestion

Reproduction The production of a new generation by the fusion of the male sex cell, the spermatozoan, with its female counterpart, the oocyte. In mammals, the resulting zygote develops into an embryo and also contributes to the placenta. Placental invasion of the uterine wall accesses maternal nutrients for fetal growth and the birth of a new generation. In avian and also some fish species, the embryo is nourished by the lipids and proteins within the egg until hatching.

In seasonal breeders such as sheep, young are born in time for the spring flush of grass.

Cattle

Puberty occurs around 10–12 months and 11–15 months of age in the main dairy and beef breeds, respectively. Nutrition, season of birth and genotype each influence the timing of puberty. For example, in zebus these factors interact to delay puberty until 18–24 months of age. The optimum calving intervals for all cattle genotypes is 1 year but this is seldom achieved on a herd basis, due to post-calving delays in the resumption of regular 21-day oestrous cycles. Singleton calves are the norm, with surveys indicating a 2–3% incidence of twins though this is environment and breed dependent and can be as high as 10% in some herds. On average the numbers of parities are four and seven for dairy and beef breeds, respectively, but in very high-yielding dairy herds the number is now closer to three.

Sheep and goats

For lambs and kids born in the spring and well nourished, puberty usually occurs in the autumn, i.e. at 5–7 months of age. Those whose growth is restricted and those born during the summer months usually do not achieve puberty until the autumn of the year following their birth, i.e. 15–20 months of age. Ewes and does of most breeds are seasonally polyoestrous short-day breeders, with oestrous cycle lengths of 17 and 21 days, respectively. Following gestation lengths of approximately 150 days, both species normally produce one to three offspring (but occasionally four) at a single annual parturition. Some breeds (e.g. those kept in equatorial environments and non-equatorial breeds such as the Dorset Horn, which tends to be non-seasonal in its breeding activity) can lamb every 8 months, provided that poor nutrition does not limit the expression of oestrus. Duration of breeding life varies with nutrition and genotype and is on average seven parities for both species.

Horses

Reproduction in mares is very variable. Some are truly polyoestrous but most are seasonally polyoestrous long-day breeders. Although puberty occurs from 12 to 24 months of age, in practice first mating is usually delayed until 3 years of age. The incidence of twin pregnancies is low (approximately 2%) and when it occurs manual intervention is used to eliminate one embryo so that only one foal is born. Mares breed once annually up to the age of 15–16 years, giving a total of 10–12 parities over their breeding life.

Pigs

Puberty in gilts occurs around 25 weeks of age. A 16-week gestation followed by abrupt weaning after 3 weeks of lactation results in oestrus about 1 week later and an average of 2.5 litters per year. The number of piglets per litter varies with genotype and nutrition, with an average of about ten. The number of parities per lifetime is about seven, with maternal oversize and a decline in reproductive performance being the main reasons for culling.

Rabbits

Commercial intensive production units achieve an average of 6.5 litters per doe per year with a mean litter size of 8.5–9.0. The reproductive lifespan of the doe is approximately 1 year.

Chickens

From a relatively short natural egg-laying period each year followed by broodiness and the hatching of the chicks after a 21-day incubation period, selective breeding, improved management and extended lighting regimens have produced strains with production approaching 300 eggs (250 chicks) in 50 weeks, followed by culling. Broiler or meat-type strains have a shorter laying period of about 40 weeks and produce about 180 eggs, followed by culling.

Ducks

Ducks reach sexual maturity at 6–7 months, i.e. approximately 1 month later than chickens, and have a 28-day incubation period. Modern layer and meat-type strains have first-year production of about 275 eggs (about 220 ducklings) in a 47-week laying period. Following an 8-week moult a second laying cycle, with 85–90% of the production of the first, is usually taken before culling.

Geese

Small and large types have 30-day and 33-day incubation periods, respectively, and reach sexual maturity at 9–10 and 10–12 months, respectively. Both types produce from 30 to 70 eggs (15–35 goslings) in their first laying year and have a breeding lifespan of 3–4 years.

Turkeys

Turkeys reach sexual maturity at 7–8 months of age, have an incubation period of 28 days, produce 110–120 eggs (about 85 chicks) in their first breeding season (duration 25–30 weeks) and are then culled.

Ostriches

Ostriches reach puberty at 2 years of age and have a breeding life which, in some individuals, can extend to 30 years. Peak egg production usually occurs around 9–10 years of age. Potential annual egg production is about 100 during a 7-month laying period. Of these, 50% should produce chicks after a 42-day incubation period. Currently many production systems fall short of these levels of egg laying and hatchability. Microbial contamination of eggs through poor nest structure is a major cause of reduced hatchability.

Fish

Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) can achieve breeding status in their second year of life. Mature salmon females weigh 3–6 kg and produce about 1500 eggs kg^{-1} body weight. Fewer than 5% spawn a second time in the wild but with re-alimentation and good management some can spawn for a further 10 years in captivity. Female rainbow trout produce 2000–12,000 eggs, with up to 10% spawning the following year in the wild. Some can spawn for up to 5 successive years when nutrition and management are good. (JJR)

Reproductive disorders Reproductive disorders are the most important veterinary causes of financial loss in farm animals and a major reason for veterinary attention. Nutrition is frequently blamed, though without good evidence. Copper deficiency or molybdenosis has been shown to reduce fertility in cattle by inhibiting release of luteinizing hormone (LH; Phillippo *et al.*, 1987). Selenium deficiency in cattle may be associated with retained fetal membranes, persistent metritis, reduced resistance to infection and reduced fertility (McClure *et al.*, 1986). Iodine deficiency is commonly associated with stillbirths in cattle, with enlargement of the thyroid. Phosphorus deficiency is widely believed to be associated with reduced fertility but evidence for this as a separate entity is not convincing. Energy deficit is a major cause of reduced fertility in cattle, and increasing milk yields in dairy cattle is associated with a progressive reduction in pregnancy rate. Overfeeding of dairy cows in late lactation and in the dry period, leading to overcondition, results in reduced appetite in early lactation, fat mobilization syndrome (fatty liver) and reduced fertility. Excess protein in the diet is associated with reduced fertility in cattle but evidence that this occurs in the absence of energy deficit is controversial. In pigs, biotin deficiency is associated with reduced fertility. Ergot poisoning can cause small litters and small piglets. (WRW)

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Requirement: *see* Nutrient requirement

Resistant starch Starch that is not degraded by enzymes during passage of the upper part of the digestive tract of non-ruminants. It has physiological effects that make it comparable to dietary fibre. Resistant starch (RS) occurs in such materials as partially milled grains and seeds and in raw and cooled cooked potatoes. RS is inaccessible to α-amylase because it is either physically entrapped or in starch granules. Amylose, but not amylopectin, may also become unavailable to α-amylase after technological treatments (heating, freezing, etc.) during which the physical structure of the starch is degraded and, with time, it recrystallizes, becoming retrograded starch. (SB)

Resorption Synonymous with reabsorption. The absorption from the gastrointestinal tract of endogenous materials originating from secretions or cells that pass into the gastrointestinal tract. (SB)

Respiration chamber The term respiration chamber is most commonly used in reference to methods of **indirect calorimetry** in which air is recirculated by a fan round a closed system that includes an animal chamber and absorbers for **carbon dioxide** and water vapour. The method was first introduced 150 years ago by the French scientists Regnault and Reiset and has since been refined for use with farm animals, especially by Blaxter and his co-workers at the Hannah and Rowett Research Institutes in Scotland.

The animal chamber is a box of sheet metal with a cooling jacket which can be maintained at a temperature in the range −10 to 40°C. The entrance door requires a good gasket as the system must be completely free of leaks. The animal, which is trained to wear a harness with devices for collection of faeces and urine, stands in an inner cage of steel mesh. Lights, air-circulating fans, food hoppers and a drinking bowl are controlled from outside the chamber.

Air is drawn by a compressor from the chamber and then returned to it via three circuits, A, B and C, each controlled by a valve. Circuit A is a simple bypass and includes a gas-sampling loop. The main absorption loop, B, consists firstly of silica gel absorbers for removal of water; these are followed by caustic potash absorbers and more silica gel absorbers, whose combined weight gain represents carbon dioxide produced by the animal, and a flowmeter. Circuit C has further silica gel absorbers. Adjustment of the valves regulating the relative flow through B and C allows some degree of humidity control. Oxygen to replenish that consumed by the animal is provided from a calibrated reservoir called a spirometer. Methane produced by the animal builds up in the chamber over the period of measurement, which is normally 24 h. Gas samples taken from loop A at the start and end of the measurement period are analysed for calculation of methane produced plus any changes in oxygen and carbon dioxide content of the chamber. These values are used as corrections to the volume of oxygen supplied by the spirometer and the weight of carbon dioxide absorbed. Further corrections are made to allow for changes in atmospheric pressure, temperature and humidity during the measurement period. Food consumed and faeces and urine excreted are all collected, weighed, sampled and analysed.

The system makes possible measurement of **oxygen consumption**, carbon dioxide and methane production and urinary nitrogen excretion. From these, heat production may be calculated and also carbon and nitrogen turnover. It has proved possible to demonstrate excellent agreement between energy retention measured from respiratory exchange and by the **carbon and nitrogen balance** technique (although the two estimations are not completely independent of one another). (JAMcL)

Further reading

McLean, J.A. and Tobin, G. (1987) Indirect calorimeters. In: *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, pp. 37–76.

Respiratory diseases Respiratory diseases occur in all species of domestic animals and birds. A common cause is infection with a bacterial agent, such as *Pasteurella multocida* or *Bordetella bronchiseptica*. Respiratory disease is usually accompanied by nasal discharge and laboured breathing. Viral infection may also be involved, especially in disorders such as bovine respiratory disease (BVD), which involves a complex interaction of environment, pathogens and host factors. Environmental stressors include crowding, inadequate ventilation and airborne particles (dust). Shipping fever of cattle is similarly a result of complex interactions among nutritional, environmental and pathogen factors. Respiratory disease may result from inhalation of foreign objects (inhalation or aspiration pneumonia) such as rumen contents, fungal spores (farmer's lung disease) and toxic gases such as silo gases (nitrous oxide). Parasites such as lungworms cause signs of bronchitis and pneumonia. Acute bovine pulmonary emphysema is caused by rumen metabolism of tryptophan to 3-methyl indole, a pneumotoxic agent. Certain plants, such as purple mint (*Perilla frutescens*) and mouldy sweet potato (*Ipomoea batatus*), contain pneumotoxic furans. (PC)

Respiratory exchange ratio The ratio (R) of the volume of carbon dioxide produced to the volume of oxygen consumed at any time whether or not equilibrium has been reached, as distinct from **respiratory quotient** (RQ), which is the ratio of carbon dioxide produced to oxygen consumed in the steady state. In the steady state, RQ is 1.0 if carbohydrate is being exclusively metabolized, because hydrogen and oxygen are present in carbohydrate in the same proportions as in water. The RQ for exclusive fat metabolism is 0.70, because extra oxygen is necessary for the formation of water. The RQ for protein metabolism is less straightforward, but it has been calculated to be 0.82. (JAM)

Respiratory quotient (RQ) The ratio of **carbon dioxide** production to **oxygen consumption**. The RQ for a food or food substance is the same gas ratio when the substance is metabolized. The RQ for carbohydrates is 1.00, that for fat is 0.70 and that for protein 0.82. The RQ of an animal can provide an indication of the type of nutrient being metabolized and how it is utilized. At maintenance on a carbohydrate diet RQ = 1; during starvation, when body reserves are being utilized, RQ drops towards 0.7; for a cow synthesizing milk fat from a mainly carbohydrate diet RQ can be as high as 1.2. (JAMcL)
See also: Indirect calorimetry

Response to dietary energy and nutrients Responses are usually measured in terms of an increase in a given output (meat, milk, eggs, wool or growth) in relation to an increase in a particular input such as energy or protein (usually expressed in relation to body weight). The gross response varies throughout the input range, depending on a number of factors. These include, at the bottom of the range, the extent to which the needs for maintenance are met and, at the top of the range, whether the animal has sufficient genetic potential to respond to a further input. Responses are also affected by the age and weight of the animal, its gender and genotype, and its health status.

A key feature of modern animal husbandry is to seek to provide nutrients in appropriate amounts so that performance and efficiency can be optimized. Although this can be done empirically, as it is in many traditional production systems, there is an increasing need to develop models that allow responses to be predicted. Modelling responses is especially relevant when feeding systems and feed mixing are semi-automated. In the future this could allow an individual animal to be offered an optimized diet and feed allocation on a daily basis.

When responses are graphically represented, it is usual to assign the input variable to the x axis and the output to the y axis. At their simplest, responses so represented may appear as two straight lines, one ascending and the other a plateau. The slope of the ascending limb can indicate the net efficiency of utilization of the nutrient and the horizontal line the limit of responsiveness. This 'broken stick' presentation has been much used in modelling and the intersection of the two lines is often taken to represent the 'requirement' for a particular nutrient. In a simple example, the nutrient input might be ideal protein and the output might be nitrogen retention or muscle growth. The point of intersection gives the requirement for ideal protein. The same principle, with an appropriate measure of response, can be applied to any nutrient. Although such simply defined responses work well for individual animals, a more complex response curve is required for populations of animals. This is because, as the input increases, individuals run out of responsiveness at different points along the input axis. Some evaluations of energy and protein sources are determined by slope ratio assays. It is important that the slopes are compared well within the responsive range.

Responses to dietary protein can be considered either as a response to the limiting amino acid in the diet, which for pigs and poultry is usually lysine, or as a response to an increment of ideal protein. An ideal protein is one in which the balance of the essential amino acids required for a productive purpose cannot be improved by the addition or subtraction of any one of them. Responses to supplements of individual amino acids usually reflect the extent to which the available protein is moved towards the ideal balance by the addition. Provided that the supplementary amino acid remains limiting, additional increments will have the effect of increasing the available ideal protein. Eventually further additions will have no further benefit because either some other amino acid becomes limiting or the total ideal protein is adequate.

The strategy for modelling and defining responses is affected by whether the species is a ruminant or a non-ruminant. Predicting the responses to nutrients that must pass through a functioning rumen requires an understanding of what controls the fermentation process. Different dietary substrates may change the ratio of volatile fatty acids produced in the rumen and this can have a profound influence on voluntary intake and, for example, the yield of butter fat in milk. A further factor is the extent to which the protein supplied can pass through the rumen undegraded by the bacteria and still be digested in the abomasum and small intestine.

A major consideration in defining responses is to take proper account of the effect of change of input on appetite or daily feed intake. Ruminants can increase their daily intake of energy in response to an improvement in the quality of the roughage in the diet. Pigs and poultry may modify their intake to balance changes in energy concentration of the diet so that the daily intake of metabolizable energy remains more or less constant. It is also possible that pigs and poultry compensate, on being offered a diet marginally deficient in a given nutrient, by increasing intake. Major deficiencies and excesses, however, reduce intake.

Because the daily intake of feed can vary, it is usual to fix one component of the diet, metabolizable energy for example, and express all other constituents as ratios to that. In the case of poultry nutrition, it is considered better to examine responses to changes in energy:protein ratio (E:P) rather than consider the two nutrients separately. In most normal circumstances the response to increases in vitamins and minerals is a reduction in signs of deficiency and in morbidity. Provided that the net requirements are comfortably met by the dietary supply and that there are no serious excesses, 'responses' as such are not usually considered important. An exception is in the case of vitamins such as vitamin E and C and the mineral selenium which have interacting antioxidant roles. These may also promote or facilitate the activity of the immune system, particularly in young animals under stress. For these nutrients, it has proved difficult to define a precise requirement and for populations a 'response' approach may be more appropriate than an absolute requirement.

Of increasing concern is the danger that certain nutrients may be provided in excess and, consequent upon excretion, may damage the environment. These include nitrogen, phosphorus compounds and potassium. Phosphorus particularly has been implicated in the eutrophication of water courses. Excesses of dietary protein result in deamination and the wasteful excretion of the nitrogen. In addition to faecal nitrogen, this excess is excreted in urine. Unless recaptured in a growing crop, nitrogenous compounds can be a pollutant of air and water.

The use of supplementary phosphorus and calcium raises a number of controversial issues. Although both minerals have a metabolic function, they have structural roles in bone formation. The problem is that neither is used very efficiently for bone formation. Maximum bone density and mineralization may only be achieved by high inputs at which the efficiency of retention of phosphorus is as low as 20%, whereas much lower inputs are required if a lower degree of mineralization is accepted as adequate, and the efficiencies can rise to two or three times this. This highlights the difference between maximizing output and optimizing utilization. In the final analysis, optimizing responses can only be achieved when true costs can be assigned to the nutrient inputs and true values to the outputs. (VRF)

Restricted feeding Any regimen in which an animal's **feed intake** is limited to less than it would voluntarily consume. There are several contexts in which restricted feeding is, or has been, used in commercial animal production, usually when unrestricted feeding would lead to obesity. Feed restriction does, however, represent a potential welfare concern in the context of the first of the UK Farm Animal Welfare Council's 'Five Freedoms' (freedom from hunger and thirst).

Growing layer pullets

In the past, various forms of mild food restriction were used to reduce body weight at point of lay, and thereby improve egg production and efficiency of food conversion. Restricted birds showed stereotyped pecking at non-food objects characteristic of frustration of feeding motivation when their food supply was exhausted. Such practices are no longer used routinely with modern layer strains.

Adult layers

The most severe form of food restriction has been the total withdrawal of food for periods of several days imposed at the end of the first laying year, in order to induce a moult and a pause in laying in hens being taken into a second laying cycle. This practice compromises bird welfare and it has been illegal in the UK since 1987; very few flocks in the UK are now taken into a second laying cycle.

Growing broilers

A period of reduced food or energy intake is sometimes imposed for a week or so early in the life of growing broilers, in order to reduce the incidence of skeletal and metabolic disease. The restriction can be achieved with short photoperiods, and is likely to benefit broiler welfare rather than compromise it.

Growing broiler breeders

All broiler breeders are fed on restricted rations during the growing period in order to limit body weight at sexual maturity and thereby improve health and reproductive performance. Male and female birds are reared separately, and rations are usually provided once a day, or sometimes (as in the USA) on alternate days. Females fed on such (daily) rations typically eat them in < 10 min, eat only one-third as much as they would with free access to food, and are highly motivated to feed at all times. They are much more active than unrestricted birds and (unlike the latter) show abnormal pacing and oral behaviours characteristic of frustration of feeding. There is no evidence that welfare is improved, or that feeding motivational state is reduced, by using qualitative (e.g. low protein, diet dilution, appetite suppression) rather than quantitative restriction to limit growth rate.

Adult broiler breeders

Broiler breeders continue to be subjected to mild food restriction throughout the breeding period, when some form of separate-sex feeding system is normally used which allows the heavier males to receive a larger ration than females. There is a risk of injury to both sexes with some such systems, and care is needed to ensure they operate efficiently.

Growing pigs

The practice of restricting the feed intake of pigs used to be common to limit fatness, particularly of castrated males, at traditional slaughter weights. It is now less usual, for several reasons. Firstly, genetic improvement has resulted in pigs that can be fed *ad libitum* to slaughter without becoming excessively fat. Secondly, fewer male pigs are now castrated: intact males are less inclined to become over-fat. Thirdly, meat processing can more easily accommodate over-fat carcasses. Feeding of gilts being reared for breeding is restricted to prevent their becoming obese, which would compromise their lifetime reproductive performance.

Pregnant sows

Sows fed *ad libitum* on conventional foods during pregnancy become obese and suffer numerous problems, such as high piglet mortality and lactation disorders. They are usually restricted to 2.0 kg of concentrated food per day, which is approximately two-thirds of the amount they would eat voluntarily. If allowed to compete in a group for this limited amount of food, there would be considerable inequality in the amount obtained by individuals. The use of equipment that rapidly delivers food to all animals simultaneously, or computer-controlled feeders to ration individual animals, has replaced individual stalls as a means of evenly rationing pregnant sows.

Adult boars

To preserve libido and semen quality, and to avoid their becoming obese and injuring sows during mating, working boars are normally given limited amounts of food.

Dairy cattle

Restricted concentrate feeding of dairy cattle is normal in most production systems. In the lactating cow, reduced energy intake from concentrates can be offset by increased catabolism of body fat reserves or by increasing forage intake, but protein reserves are less readily mobilized. Protein catabolism during lactation is an indicator of reduced welfare in lactating cows, because it represents loss of an essential body tissue. Forage intake can be reduced for periods of about 3 weeks by up to 40% of *ad libitum* intake of the forage, but more than this will cause a reduction in milk production, in particular milk protein output, and considerable losses in body weight.

Bulls

Bulls kept predominantly indoors for semen production are prone to over-fatness and this is controlled by regular exercise, by a moderate restriction of food intake and by offering bulky forage foods. (JMF, MFF, CJCP, JSav)

Retention time The time that food is retained in any compartment of the digestive tract, especially the stomach, rumen, caecum, etc. (MFF)
See also: Gastric emptying; Particle size

Retention, energy: *see* Energy balance

Retention, nitrogen: *see* Nitrogen retention

Retention, protein: *see* Protein retention

Reticulum The second compartment of the ruminant stomach. It communicates with the rumen through the wide ruminoreticular opening and with the omasum via the reticulo-omasal orifice. It is lined with a stratified squamous epithelium, which is raised into ridges around the numerous small reticular cells. It contracts first in the sequences of reticuloruminal contractions. (RNBK)
See also: Forestomach (figure)

Retinoic acid: *see* Vitamin A

Retinoids Retinoids are all compounds, natural or synthetic, that are structurally related to retinol (vitamin A). Retinol supports all known functions of the vitamin, including growth and cellular differentiation, reproduction and embryogenesis and vision. In contrast, not all retinoids exhibit vitamin A activity. (MC-D)
See also: Carotenoids; Vitamin A

Retinoid-binding proteins A number of cellular and serum proteins in addition to the nuclear retinoic acid receptors have been identified that bind to vitamin A metabolites. Cellular retinol-binding protein (CRBP or CRBP type I) and CRBP type II bind to retinol and retinal but not retinoic acid. A newly described CRBP type III binds only retinol isomers. Cellular retinoic acid-binding protein (CRABP or CRABP type I) and CRABP type II bind to retinoic acid but not retinol or retinal. In addition to the cellular binding proteins, a serum retinal-binding protein (RBP) is responsible for transporting retinol from the liver storage site to the target tissues. (MC-D)
See also: Vitamin A

Retinol: *see* Vitamin A

Retinyl acetate Retinyl acetate is formed when retinol is esterified to the two-carbon acetic acid molecule. (MC-D)
See also: Vitamin A

Retinyl palmitate Retinyl palmitate is formed when retinol is esterified to the fully saturated 16-carbon long-chain fatty acid, palmitic or hexadecanoic acid. This is the most common retinyl ester found in animal tissues. (MC-D)
See also: Vitamin A

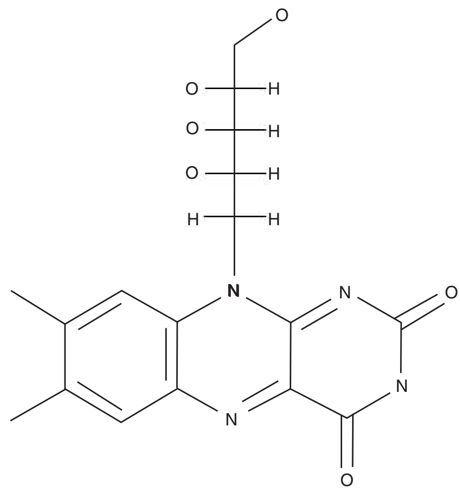
Retrograded starch: *see* Resistant starch

Rhamnogalactouronans Heteropolysaccharides of rhamnose and galactouronic acid residues, also known as rhamnogalacturanans frequently occurring as segments of the main chain in complex pectic substances and thus commonly classed with pectins. (JAM)
See also: Carbohydrates; Dietary fibre; Galactouronans; Pectic substances; Uronans

Rhamnose A deoxysugar of mannose, $C_6H_{12}O_5$, molecular weight 164, in which the hydroxyl group on carbon 6 is replaced with a hydrogen, making it 6-deoxy-L-mannose. It is a constituent of glycoproteins, plant glycosides, storage polysaccharides and plant gums. (JAM)
See also: Carbohydrates; Dietary fibre; Gums; Pectic substances; Rhamnogalactouronans; Storage polysaccharides

Rhinitis An upper respiratory tract disease caused by viral, bacterial, fungal or parasitic agents, and hypersensitivity reactions. It is characterized by exudates and erosion and ulceration of nasal mucosa. Atrophic rhinitis in swine results in severe ulceration and breakdown of the nasal turbinates, including distortion of the nasal septum and jaw deformity. Infectious agents (*Bordetella bronchiseptica*, *Pasteurella multocida*) and environmental factors (dust, ammonia) are involved. Sneezing, coughing and lacrimation are common signs. Antibiotic treatment and vaccination programmes are used to keep rhinitis under control. (PC)

Riboflavin Vitamin B_2, one of the water-soluble B vitamins. Riboflavin is a heterocyclic three-ring compound (isoalloxazine,



$C_{17}H_{20}N_4O_6$) attached to a five-carbon sugar alcohol, ribitol.

When the alcohol group of the ribitol is phosphorylated by ATP the vitamin becomes the co-factor flavine mononucleotide (FMN). FMN reacts with ATP, adding AMP to the phosphorus of FMN to form another riboflavin vitamin co-factor, flavine adenine dinucleotide (FAD). Both FMN and FAD are intimately involved in lipid and carbohydrate metabolism. They are found in foods derived from both plant and animal products. Digestion and absorption of the food-derived coenzyme forms of riboflavin occur in the upper small intestine. After conversion of the coenzyme forms (FMN and FAD) to the vitamin, absorption is by a sodium- and ATP-dependent transport system. Riboflavin is transported through the bloodstream bound to proteins (albumin and globulin). It is excreted in the urine as free riboflavin. The vitamin co-factors of riboflavin are the prosthetic groups of oxidoreductase enzymes such as amino acid oxidase, xanthine oxidase glycerol-3-phosphate dehydrogenase and succinate dehydrogenase, sarcosine dehydrogenase and as part of the electron-transferring flavoprotein in fatty acid oxidation.

Riboflavin is required for the metabolism of the vitamins, pyridoxine, niacin and folic acid, thus it is not surprising that a riboflavin deficiency can affect multiple components of metabolism and a deficiency of riboflavin gives rise to no specific symptom. Riboflavin deficiency may be due to limited riboflavin intake or inadequate conversion to the coenzyme forms, FMN and FAD. The reported deficiency symptoms are failure to grow, loss of hair, scaliness and incrustation of a red-brown material in skin, a normocytic anaemia, degenerative changes in the nervous system and impaired reproduction. The erythrocyte enzyme glutathione reductase is an FAD-requiring enzyme and is used to assess the degree of deficiency of riboflavin. Erythrocytes from deficient animals have lower concentrations of FAD and thus the enzyme glutathione reductase is less saturated with co-factor and the activity measured *in vitro* declines. *In vitro* the activity can be stimulated by addition of FAD. Thus, as with other erythrocyte enzymes that require a B-vitamin co-factor, the activity of glutathione reductase can be measured without and with supplemental FAD and the degree of stimulation noted. An increase in the activity of 20% (an activity coefficient of 1.2) is expected in animals with adequate intakes of riboflavin. Activity coefficients of 1.4 or more reflect a deficiency state. Requirements for this vitamin are in the range of mg kg^{-1} diet. (NJB)

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Ribonuclease A cellular enzyme that hydrolyses ribonucleic acids. Ribonucleases cleave internal phosphodiester bonds of RNA to produce either 3′-hydroxyl and 5′-phosphoryl terminals or 5′-hydroxyl and 3′-phosphoryl terminals. They are classified as endonucleases. In the process of digestion of food, ribonuclease from the pancreas is involved in the digestion of the RNA in food. (NJB)

Ribonucleic acid (RNA) A polymer of purine and pyrimidine ribonucleotides linked together by 3′,5′-phosphodiester bridges. RNA is a single strand whereas DNA may have two strands. The two purines in RNA, adenine and guanine, are also found in DNA but of the two pyrimidines in RNA only cytosine is also found in DNA; the other, uracil, is not. The sugar in RNA is ribose whereas that in DNA is deoxyribose. In cells, RNA is found in three forms. rRNA is associated with ribosomes, subcellular particles involved in protein synthesis. Messenger RNA (mRNA) is the RNA template that codes for the amino acid sequence of a protein being synthesized. Transfer RNA (tRNA) binds individual amino acids and associates with a specific triplet of ribonucleotide bases in mRNA, ensuring that amino acids are added in the correct order to the developing polypeptide chain. (NJB)

Rice Rice (*Oryza sativa*) is a member of the *Gramineae* (grass) family and is the principal cereal crop of eastern and southern Asia. About 60% of all rice is grown and consumed in China and India. It is grown as an annual crop and requires a subtropical or warm temperate climate. Little rice is grown in Europe north of latitude 49°.

The seeds are firstly sown in prepared beds; once the seedlings are 25–50 days old, they are transplanted into paddy fields which are under 5–10 cm of water. The transplanted seedlings and subsequent rice crop are grown in water throughout the growing season, the crop reaching a final height of about 1.2 m. Additionally, rice may be grown on dry ground but this results in lower crop yields. The leaves are long and flattened, and its panicle, or inflorescence, is made up of spikelets bearing flowers that produce the fruit, or rice grain.

Rice grain is an important food product and the grain is also used in the manufacture of starch. As a result of processing rice grain for human food purposes, a number of by-products are produced for livestock feeding. The harvested rice grain (kernel), also called paddy or rough rice, is enclosed in a fibrous outer hull and a layer of bran. The first stage of milling rice grain into white rice for human consumption involves the removal of the outer hull, which represents about 20% of the total grain weight. This process yields brown rice. Following hulling, the bran is removed together with the rice germ and part of the aleurone layer to produce white rice. The by-product of this process is called rice bran. To produce a glossy appearance, a coating of glucose and talc may be applied to white rice, which is then called polished rice.

The by-products of rice grain processing are rice hulls, rice germ and rice bran. Rice hulls are rich in crude fibre, in the range of 470–550 g kg^{-1} dry matter (DM) and have a high ash content (180–270 g kg^{-1} DM) (see table). The ash fraction is mainly silica (170–250 g kg^{-1} DM). The crude protein (CP) content of rice hulls is very low (20 to 50 g kg^{-1} DM). Rice germ has a high protein content (210–230 g kg^{-1} DM) and the protein is of better quality than that of most other cereal grains. The oil content is high (210 g kg^{-1} DM) but the ash (90–100 g kg^{-1} DM) and crude fibre (30–70 g kg^{-1} DM) contents are low. Rice bran generally contains about 120–125 g CP kg^{-1} DM, 100–110 g ash kg^{-1} DM and 110–180 g oil kg^{-1} DM; this oil is rich in unsaturated fatty acids.

The high oil levels present in both rice germ and rice bran mean that they share similar problems in terms of their use for animal feeding. Both are difficult to store, particularly during the summer, since the oil becomes rancid very quickly and reduces digestibility, the availability of vitamin E and the quality of deposited fat in growing animals. For these reasons the oil is generally removed by wet pressure (expelled rice bran meal) or by solvent extraction (extracted rice bran meal and rice germ meal). The expeller and extracted meals can be fed to cows at a level of 3 kg per head per day and represent about 20% to 30% of the concentrate portion of the feed. Rice bran meals can be fed to horses as a partial substitute for oats but they are not recommended for fattening pigs, due to their relatively high fibre and ash contents. In the preparation of starch from rice, a product known as rice sludge or rice slump is produced as a residue. This product, when dried, has a CP content of about 280 g kg^{-1} DM and low levels of crude fibre and oil; it is suitable for feeding to both ruminants and pigs. (ED)

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Ricin A toxic lectin isolated from castor beans and the first lectin to be isolated (by Stillmark in 1889). Like other lectins, it has the ability to agglutinate the red blood cells of humans and animals. (SEL)

See also: Lectins; Phytotoxins

Rickets A disease affecting the physeal region, or growth plate, of the bones of growing animals. Rickets is most commonly caused by a dietary deficiency of vitamin D or phosphorus. In some cases, dietary calcium deficiency induces a mild form of rickets. During vitamin D or phosphorus deficiency, the cartilage in the zone of hypertrophy within the physis fails to undergo mineralization. It seems that normal concentration of blood phosphorus (and to a lesser extent blood calcium) is needed before bone mineralization can proceed. As a result the cells of this zone continue to divide and proliferate, expanding the cartilaginous zone within the physis. In severe cases this can result in bones that are bendable, with enlarged physes. This leads to pain, particularly at the joints. Costochondral junctions within the ribs are commonly greatly enlarged and readily palpable in animals with rickets. Vitamin D is a pro-hormone required for the production of the calcium regulating hormone, 1,25-dihydroxycholecalciferol, without which dietary phosphorus and calcium are only poorly absorbed, which can lead to rickets. In addition 1,25-dihydroxyvitamin D seems to have direct effects on the growth and metabolism of cartilage cells within the physis. (JPG)

See also: Hypophosphataemia; Vitamin D

Chemical composition of rice by-products (as g kg^{-1} DM unless stated otherwise). (Source: MAFF, 1990.)

By-product	DM (g kg^{-1})	CP	Starch	EE	NDF	GE[a]	ME[a]
Rice bran meal, expeller	902	128	302	90	370	18.9	11.0
Rice bran meal, extracted	896	154	236	7.3	451	16.7	7.1

[a] As MJ kg^{-1} DM.

DM, dry matter; EE, ether extract; NDF, neutral detergent fibre; GE, gross energy; ME, metabolizable energy.

Roasting: *see* Heat treatment

Rock phosphate Naturally occurring, phosphorus-containing rock comprising mainly fluor- and chlor-apatites with the general formula $Ca_2(PO_4)_3^-$ (Cl, F). Besides fluorine, rock phosphates contain significant levels of other undesirable contaminants such as cadmium and arsenic. Without some form of decontamination it does not meet feed grade standards. (CRL)
See also: Calcium phosphate; Diammonium phosphate; Dicalcium phosphate

Rolling The process of crushing a feed, usually a cereal grain or other seed, between two rotating rollers, to break the pericarp and expose the embryo and endosperm so that they can be better digested by the animal when the seed is eaten. (JMW)

Roots: *see* Carrot; Cassava; Fodder beet; Jerusalem artichoke; Potato; Sugarbeet; Swede; Sweet potato; Turnip; Yam

Rotational grazing A system in which a grazing area is subdivided to give paddocks for alternating periods of grazing and resting, allowing time for application of fertilizers, recovery, etc. The duration and intensity of grazing can be varied. Grazing may be interspersed with conservation, especially early in the growing season, to maximize use of high quality material. (TS)
See also: Grazing

Rotifer A small marine crustacean. The rotifer *Brachionus plicatilis* is an essential part of the first feeding of many marine fish larvae. It may be 10–300 μm in size and can be cultivated in batches or semi-continuously at high densities and warm temperatures year round. Recent improvements have led to intensive ultra-high-density mass culture techniques. Although rotifers can grow on simple media such as yeast enriched with marine oils, much work has been dedicated to improving their nutritional value with emulsions containing highly unsaturated fatty acids, eicosapentaenoic (20:5 n-3) and docosahexaenoic acid (22:6 n-3). Bacterial pathogens associated with intensive rotifer culture may have a negative impact on larviculture. (KP)
See also: Aquatic organisms; Fish larvae; Live fish food; Phytoplankton

Roughage Coarse fodder, plant material that is fibrous in nature and relatively indigestible. As feed, it is most valuable to ruminants because of their ability to digest cellulose. Roughage is normally dry and includes cereal crop residues. Any forage allowed to reach maturity takes on the characteristics of roughage. (TS)
See also: Stover; Straw

Rubber seed (*Hevea brasiliensis*) This by-product of the rubber tree is a high-protein product, equivalent to 35% of the weight of the seed. The protein has a digestibility of 53% in ruminants. The cake contains 90 mg hydrogen cyanide (HCN) kg^{-1} DM, a low concentration which is unlikely to have adverse effects. Rubber seed cake can be included in calf concentrate up to 30% and up to 25% for dairy cattle. Although some reports indicate that it can be included in pig and poultry rations up to a level of 20%, it is low in methionine and relatively unpalatable for non-ruminants. There are also reports of poor hatchability after rubber seed meal was fed to breeding hens. (LR)

Further reading

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Rubidium Rubidium (Rb) is an alkali metal with an atomic mass of 85.4678. Its natural presence in the earth's crust is very limited; however, analysis of human brain by neutron activation showed 18 mg Rb kg^{-1} cortex. There are no known physiological or biochemical functions for Rb in animals or plants but recent studies found that the concentrations of a variety of essential mineral elements in tissues could be affected in rats fed diets containing variable amounts of Rb.

Nutrient composition of rubber seed cake (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Rubber seed cake	20.6	35.1	7.1	10.5	12.5	34.8	1.00	0.80

CF, crude fibre; CP, cruide protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Goats fed < 200 μg Rb kg^{-1} diet had decreased growth and increased spontaneous abortions. Rb may support cell differentiation in bone marrow. (PGR)

Further reading

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Rumen The first and largest compartment of the ruminant stomach. The oesophagus enters via the cardiac orifice and the rumen communicates with the reticulum through the wide ruminoreticular opening. It is partially subdivided by muscular folds of its wall into a number of smaller compartments or sacs. It is lined with a stratified squamous epithelium, raised into numerous small papillae that enlarge the absorptive surface area. (RNBK)

See also: Forestomach (figure)

Rumen development: *see* Forestomach development

Rumen digestion The rumen is a large organ. Together with the reticulum, to which it is closely connected, the rumen occupies most of the left side of the abdomen. The volume of the rumen and reticulum may be as much as 200 l in an adult cow, and its contents are continually being mixed by strong cyclical muscular contractions, which occur about once a minute. In ruminant livestock, most of the **digestion** of food occurs in the rumen, with additional digestion of protein, including microbial protein, in the abomasum. Most of the **absorption** of nutrients occurs in the small intestine. Further digestion and absorption occur in the large intestine, but this is relatively insignificant compared with the digestion in the rumen.

The two most important factors affecting digestion in the rumen are its speed (the rate of particle breakdown) and its extent (the proportion of the original food that is solubilized and absorbed into the blood).

Digestion in the rumen comprises the relatively slow microbial breakdown of plant cell wall components, mainly cellulose and hemicellulose, at up to 48 h for particles of straw, and the relatively rapid breakdown of plant cell contents, mainly sugars and proteins, which takes a few minutes for urea and molasses.

Food arrives in the rumen having been eaten, chewed and mixed with saliva in the mouth for a relatively short period of time. Particle size is reduced during subsequent rumination, when additional saliva is mixed with the food.

Rumination effectively increases the surface area of the food to facilitate colonization by the **rumen microorganisms**. Bacteria, protozoa and fungi invade and attach themselves to the particles of food and secrete their digestive enzymes, further reducing the particle size until the digesta can pass through the reticulo-omasal orifice to the omasum, where considerable amounts of water are removed prior to digestion in the abomasum.

The speed with which food particles are reduced in size during digestion in the rumen determines how long they remain there. The reticulo-omasal orifice acts as a barrier to the onward passage of large particles along the alimentary tract and is especially important when most of the diet is slowly digested cell wall material: the level of ‘fill’ or the bulk of food in the rumen then limits the amount the animal can eat. Physical processing, such as chopping or milling, by artificially increasing the surface area of food particles, increases intake by accelerating digestion in the rumen.

The second important aspect of digestion in the rumen is the extent of digestion, which is a reflection of the accessibility of the plant cell wall material to the rumen microorganisms. The major component of foods responsible for reducing the extent of digestion in the rumen is lignin. Foods generally contain low concentrations of lignin, less than < 10% of the dry matter, but small amounts of lignin have large effects on the extent of digestion in the rumen. The cell wall component of foods that contain relatively high concentrations of lignin (e.g. straw) is digested relatively poorly (about 50%), whilst the cell walls of foods that contain relatively little lignin (e.g. young pasture grass) are digested to a much greater extent (about 80%).

Digestion of food proteins in the rumen results in the production of ammonia in rumen fluid, which helps to buffer the acetic, propionic and butyric acids that are also produced. The bacteria in the rumen have a requirement for ammonia, and if the concentration of ammonia in the rumen is inadequate then both the rate and extent of digestion are likely to be reduced. It is important to avoid large losses of ammonia from the rumen to the liver, because of the toxic nature of ammonia. The rate at which the liver can detoxify ammonia to urea is limited and excess ammonia in the blood can, in extreme situations, cause toxicity symptoms. The extent to which protein is digested in the rumen varies from 40% for heat- or formaldehyde-treated foods such as fish meal, to 90% for fresh pasture grass. Generally, the greater the extent of protein digestion, the more rapidly it occurs.

Sugars are normally digested almost completely in the rumen. Starch is digested to a variable extent, depending on its physical form. Normally 70–80% of the starch in ground cereal grain is digested in the rumen, a further 20–30% being digested further along the alimentary tract. Processes such as gelatinization and treatment with concentrated sodium hydroxide slow the rate of digestion of starch so that less is digested in the rumen and more in the small intestine. This has the advantage of providing more glucose than would occur if it were all digested in the rumen.

Lipids are often included in the diet of ruminants in an attempt to increase energy supply. Unsaturated fatty acids such as linoleic acid and linolenic acid tend to be hydrogenated to oleic acid in the rumen, acting as a sink for hydrogen. Fat in the diet can reduce the digestion of fibre, because the fatty acids coat the fibre surfaces and prevent bacterial colonization. To reduce this effect, fat can be saponified. (JMW)

See also: Fermentation; Fermentation products

Rumen fluid Fluid accounts for 80–90% of total ruminoreticular content. It is important that the solids are held in fluid suspension to allow free mixing of the content, microbial activity, rumination and onward passage. The fluid arises mainly from saliva and also from drinking water and food water. Its composition is affected by dietary and salivary composition, the products of microbial fermentation, absorption of solutes and passage of water across the rumen epithelium. Typical values are shown in the table overleaf, though they will vary considerably with food intake, time since feeding and other circumstances. (RNBK)

See also: Rumen; Rumen digestion

Rumen microorganisms The bacteria, protozoa and fungi that colonize the rumen, either attached to food particles or free in the rumen liquor. The ruminant host provides them with a favourable environment and regular food supply which enables them to proliferate rapidly. In return the ruminant has access to the products of microbial digestion, including those from fibrous polysaccharides which are normally not digestible by mammals. The majority of the rumen microflora are strict anaerobes. They digest by fermentation, yielding large quantities of volatile fatty acids, which are mainly absorbed through the rumen wall, and microbial cell mass which is rich in protein and vitamins for the ruminant to digest in its abomasum and small intestine. The symbiotic relationship between the ruminant and its microflora concludes with the digestion of the latter.

The rumen environment, notably the temperature, neutral pH, turnover rate and nutrient supply, is maintained relatively constant by the ruminant. This favours the establishment in the rumen of a stable, very mixed, microflora, and the rapid digestion of ingested feeds. The composition of the microflora is thus controlled by the host to its own benefit. Any organism within the immediate environment that can live and reproduce in the rumen is likely to be present. Regular constant feeds maintain the stability and variety of the microflora. Rapidly imposed feed changes can disturb this equilibrium. For example the sudden introduction of acid feeds, or rapidly degradable ones, may reduce rumen pH to

The typical contents of rumen fluid.

Diet	VFA mmol l^{-1}	Ac mol%	Pr mol%	Bu mol%	Na mmol l^{-1}	K mmol l^{-1}	OP mOsm l^{-1}	pH
Hay	80	70	20	10	100	30	250	6.6
Hay + concentrate	120	60	25	15	100	30	280	6.1
Green fodder	140	65	25	10	60	70	300	6.4
Mainly grain	100	55	25	20	90	40	250	5.8

VFA, volatile fatty acids; Ac, acetate; Pr, propionate; Bu, butyrate; OP, osmotic pressure.

cause acidosis and indigestion. Reduction of pH below 6 reduces the activity of fibrolytic organisms, favours the domination of the rumen by acidophilic bacteria, and interferes with the digestion of roughages. Rumen microflora concentration tends to be lowest 2–4 hours post-feeding and gradually increases until 16 hours post-feeding. Increasing feeding frequency can reduce this effect.

Young ruminants acquire their microflora early in life through their contacts with adults and the environment generally. In calves, cellulose fermenters are detectable by 1–3 weeks old with most species being established by 6–9 weeks.

Rumen bacteria represent the largest population of microflora in the rumen. The concentrations of bacteria may be as high as 10^9–10^{10} ml^{-1} of rumen contents and may comprise up to 200 species. These bacteria are simple unicellular organisms which reproduce by fission. Many of the rumen bacteria are ciliate and motile. The majority of them are found attached to or contained inside food fragments. They can be classified by their principal digestive activities as in the examples given in the table on the facing page. However, rumen digestive function is the total of the activity of many species. For example, many species in isolation will attach to cellulose particles and digest them slowly. The same organisms in cultures combined with non-cellulolytic organisms will deliver greatly increased rates of digestion. An example of this is *Fibrobacter succinogenes* which has a much brisker action in the presence of *Butyvibrio* species.

Ciliate protozoa are present in the rumen fluid in bulk equal to that of the bacteria, in concentrations of about 10^6 cells ml^{-1}. The many species come from two families, the Isotrichidae and Ophryoscolecidae (see table below). Their interaction with rumen bacteria is complex, and their importance in rumen digestion is still debatable. Ophryoscolecidae protozoa engulf and digest bacteria, their main nitrogen source, in vast numbers and are the major cause of microbial turnover. This may account for the increased flow of nitrogen to the duodenum, and lower rumen ammonia concentrations in rumen liquor, in defaunate animals. They also ingest starch granules which reduces their exposure to amylolytic bacteria, protects the host against lactic acidosis and promotes bacterial cellulolysis. Methanogenic bacteria adhere to protozoa and promote their digestive activity by removing accumulations of hydrogen.

Family	Genera
Isotrichidae (Holotrichs)	*Isotricha*
	Dasytricha
Ophryoscolecidae (Oligotrichs)	*Entodinium*
	Diplodinum
	Epidinium
	Ophryoscolex

Rumen fungi are strict anaerobes which are chiefly found colonizing lignocellulose, indicating their ability to degrade plant components. They are capable of utilizing all plant polysaccharides other than pectin and polygalacturonic acid. They produce motile zoospores, about 10^3–10^4 ml^{-1}, which swim in the rumen liquid phase. These attach to and penetrate plant particles, and form sporangia which complete the life cycle by releasing zoospores. The vegetative phase is substantial, representing about 8–12% of the undegraded dry matter in the rumen. They are most abundant in animals fed on roughage diets, and can be absent on low fibre diets, indicating that they are not necessary for the survival of the rumen system.

There are three morphological types, and

Digestive activities of rumen bacteria.

Activity	Species	Principal fermentation products
Cellulolytic	*Fibrobacter succinogenes*	Acetate, formate, succinate
	Ruminococcus flavefaciens	Acetate, formate, succinate, H_2
	Ruminococcus albus	Acetate, formate, ethanol, H_2, CO_2
Hemicellulolytic	*Butyvibrio fibrisolvens*	Acetate, lactate, butyrate, formate, H_2, CO_2
	Bacteriodes ruminicola	Acetate, formate, succinate
	Ruminococcus spp.	Acetate, formate
Pectinolytic	*Butyvibrio fibrisolvens*	Acetate, butyrate, formate, lactate, H_2, CO_2
	Bacteriodes ruminicola	Acetate, propionate, formate, succinate
Amylolytic	*Bacteroides amylophilus*	Formate, acetate, succinate
	Streptococcus bovis	Lactate, acetate, formate
Ureolytic	*Selenomonas* spp.	Acetate, propionate, lactate, CO_2
	Bacteriodes ruminantium	
Methanogenic	*Methanobrevibacter ruminantium*	Methane
	Methanobacterium formicicum	
Sugar-utilizing	*Treponema bryantii*	
Acid-using	*Megasphaera elsdennii*	Acetate, propionate, butyrate, caproate, H_2, CO_2
	Selenomonas ruminantium	Acetate, propionate, lactate, H_2, CO_2
Proteolytic	*Bacteroides amylophilus*	Formate, acetate, succinate
	Bacteroides ruminicola	Acetate, formate, propionate, succinate
	Butyvibrio fibrisolvens	Acetate, butyrate, lactate, formate, ethanol, H_2, CO_2
	Streptococcus bovis	Lactate, acetate, formate
Ammonia-producing	*Bacteroides ruminicola*	Formate, acetate, propionate, succinate
	Megasphaera elsdennii	Acetate, propionate, butyrate, caproate, H_2, CO_2
Lipolytic	*Anaerovigrio lipolytica*	
	Butyvibrio fibrisolvens	Acetate, lactate, butyrate, formate, H_2, CO_2
	Eubacterium spp.	Acetate, butyrate, formate, CO_2

Modified from Allison (1984).

at least 12 species are found in the rumen. Notable among these are *Neocallimastix frontalis*, *N. patriciarum*, *Orpinomyces bovis* and *Piromyces communis.* (JKM)

See also: Gastrointestinal microflora

References

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Rumen volume The volume of the rumen plus reticulum can be measured most practically by emptying out and weighing the content, either at slaughter or via a rumen fistula. It varies somewhat with feeding habit, from about 13% of body weight in grazing ruminant species to 9% in browsers. It can vary more greatly between breeds, reaching 20–30% in cattle and sheep accustomed to eating straw. A large rumen volume permits a large intake of roughage together with prolonged retention and fermentation of fibre in the reticulorumen. (RNBK)

See also: Rumen

Further reading

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Ruminant feeding In most situations the major objective in feeding ruminants is to maximize voluntary intake. Only in a few specific situations is there a need to limit feed intake (e.g. the pregnant beef suckler cow in winter, when there is a modest loss of body weight, which is regained subsequently at pasture). Failure to maximize voluntary food intake is the most common cause of suboptimal productivity in ruminant livestock. Thus the most important nutritional requirement of the ruminant animal is that for intake of dry matter (DM). Then the animal's requirement for energy should be met, followed by that for protein, major minerals, trace elements and vitamins. The challenge to nutritionists is to be able to predict with accuracy the food intake of the animal in a range of dietary situations.

To maximize the potential voluntary food intake, all ingredients should be free of contaminants and offered *ad libitum* at least once daily with adequate access to food and fresh water at all times. Changes in diet formulation should be made gradually, to avoid digestive upsets. To realize potential food intake, the rumen microbial population should be encouraged to grow as rapidly as possible by being provided with both available protein, from which the microorganisms can derive ammonia for protein synthesis, and available energy. The rumen environment should be conducive to the digestion of plant cell wall material, since in most situations the supply of nutrients to the microbial population is in the form of herbage and other plant material. When poor-quality plant material is offered, the animal should be given the opportunity to select the most acceptable parts and to reject unpalatable material.

Diets for productive ruminants usually comprise two different types of food: forages and concentrates. This distinction is historical and reflects the fact that traditionally most forages were relatively low in energy and protein, and were digested slowly in the rumen. Most concentrates, on the other hand, were relatively high in energy and protein and were digested rapidly in the rumen. Today the division of foods into forages and concentrates can be confusing, since the nutritional specification of some forages, such as young pasture grass, clover and maize (corn) silage, may be similar to that of many concentrated foods. It is better to consider dietary ingredients in terms of their major nutrients, e.g. starch, sugar, cellulose, protein or lipid.

Diet formulation for ruminants involves meeting the requirement of the animal within the specific nutritional constraints of optimizing

Mechanically filled troughs are commonly used in intensive units.

rumen function and avoiding major nutrient imbalances. Thus diets are normally formulated to contain at least 400 g neutral detergent fibre (NDF) kg^{-1} DM to ensure adequate slowly digested plant cell wall material for fermentation in the rumen. If the animal's requirement for energy is particularly high and the concentration of NDF is less than 400 g kg^{-1} DM, then a source of long fibre, or effective NDF such as hay, must be included in the diet to stimulate rumination and saliva production. Total starch and sugar should not exceed 300 g kg^{-1} DM. Effective rumen degradable protein (ERDP) should match the supply of fermentable metabolizable energy (FME). The optimal balance for microbial digestion is 11 g ERDP MJ^{-1} FME.

All dietary ingredients, especially those produced on the farm, should be analysed routinely to determine their composition and adjustments to the formulated diet should be made accordingly. Weekly analyses should be linked to re-formulation twice a month, and monthly analyses to re-formulation once every 2 months to allow systematic changes in composition to be distinguished from random variation.

Feeding systems comprise grazing, self-feeding of conserved forages and trough-feeding of mixtures of forages and other materials. Dairy cows are often fed at the time of milking in a stall or milking parlour. Grazing may be free-range or controlled in paddocks. Range pastures are normally grazed continually for many months and the herd or flock is allowed to roam over large areas to select food. The animals are gathered at specific times of the year for the weaning of young, shearing (in the case of sheep) and disease control.

In controlled grazing situations the supply of herbage is usually more abundant and access to new pasture may be adjusted on a daily basis, in an attempt to match supply with requirement. Thus at times of rapid pasture growth in spring or at the start of a rainy season, the area of land allocated to the herd or flock is reduced, and increased later in the grazing season when the amount of herbage dry matter per hectare, or its daily rate of growth, is reduced.

Herbage surplus to requirements is conserved either as hay or as silage. Storage of conserved forage may be adjacent to, or above, the winter accommodation so that the handling of winter forage is simplified as far as possible. Silos may be built immediately next to the housing for the animals to self-feed the forage directly from the exposed silo face.

Trough-feeding is the most common feeding system on intensive livestock units. The trough should be easily accessible from the animals' lying area and also accessible to machinery for daily replenishment. Troughs should be cleaned out daily to remove rejected food which, if left, deteriorates and reduces the acceptability of new food that may be placed on top and mixed with it. Forage may be the sole food offered in the trough, with concentrates offered as a compounded pellet in the milking parlour, or via a separate food container elsewhere in the animal house. Alternatively, a mixture of foods may be offered in the trough as a total mixed ration. Voluntary food intake, but not the efficiency of food utilization, may be increased by offering the diet as a total mixed ration compared with offering the forage and concentrate part of the diet at separate times of the day or via separate routes of delivery.

Conserved forages and by-products such as brewers' grains and straw may be offered as a 'buffer diet' to rectify deficiencies in the grazed pasture. The specific composition of the buffer diet should be formulated to match the nutrient deficiencies of the grazed pasture. Thus, if the pasture is legume-based or comprises very young leafy grass and is high in protein, a low-protein buffer diet should be offered. If on the other hand the deficiency is simply a shortage of available pasture, then the buffer diet should be fully balanced for all major nutrients. (JMW)

Rumination The regurgitation of reticulorumen content to the mouth for further chewing. Periods of rumination last for 10–30 min, sometimes longer on coarse roughage diets. At intervals of about 1 min, a bolus of digesta is aspirated into the thoracic oesophagus during vigorous reticular and abdominal contractions combined with thoracic expansion. The bolus is transported to the mouth by reverse peristalsis, chewed and ensalivated, then swallowed to mix again with the contents of the reticulorumen. (RNBK)

See also: Particle size; Rumen digestion

Ruminoreticular groove A gutter-shaped structure that runs in the walls of the rumen and reticulum from the cardiac orifice of the oesophagus to the reticulo-omasal orifice. Analogous structures are found in camels and other species that ferment food in a forestomach. Contraction of the muscular lips of the groove shortens and closes the groove, apposing the cardiac and reticulo-omasal orifices, so that swallowed fluid is conducted directly from oesophagus to omasum. Closure occurs reflexly during the sucking of milk by the young ruminant from its dam. Consequently the milk passes directly to the omasum and abomasum, bypassing the reticulorumen and so avoiding microbial digestion. The animal can be trained to drink milk or other fluids from a nipple-bottle or trough so as to elicit reflex closure of the groove, which becomes conditioned to respond to the person and circumstances normally associated with feeding; this response can be maintained into adult life. The groove can also be caused to close by dosing with fluids containing copper sulphate, allowing drugs to be dosed directly to the abomasum. (RNBK)

See also: Abomasum; Reticulum; Rumen

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Runt A pig that is of small body size relative to others of its litter or age group. This results from growth retardation caused by poor nutrient supply or utilization at any stage of life. It can occur in the uterus during fetal development, during the suckling period if an adequately yielding teat is not accessible, or during later life if social competition limits feed access or ill health stunts growth. (SAE)

Rye Rye (*Secale cereale*) is a cereal grown predominantly in parts of Europe and North America, generally where climate and soil are unfavourable for other cereals or as a winter crop where temperatures are too low for winter wheat. The plant, which thrives at high altitudes, has the greatest winter hardiness of all small grains and grows to a height of 1–2 m. Flower spikes comprise two or more spikelets that bear the florets which develop into single-seeded fruits, or grains.

Rye is the only cereal grain other than **wheat** to have the necessary properties for bread making. However, rye flour is inferior to that of wheat since it lacks the necessary elastic properties for baking. For this reason rye and wheat flours are frequently blended for baking purposes. Rye grain is also used for making whisky, particularly in the USA. Rye has a similar nutritive value to wheat grain, being rich in carbohydrates and providing small quantities of protein, potassium and B vitamins (see table). The amino acid profile of rye is similar to that of wheat, slightly higher in the essential amino acid lysine but lower in methionine.

Like wheat, rye grains should generally be crushed or coarsely ground for feeding to livestock, though whole grains are often fed to sheep. The use of rye grains in animal production is similar to that of barley but it should be mixed with other cereals for most livestock, in order to avoid digestive disturbances. Sheep can be fed rye grain alone as the entire concentrate supplement. Coarsely ground rye can be included to about 40% of the total compound feed for dairy cows while maintaining the same level of performance as seen with barley and maize. Growing cattle can receive coarsely ground rye as part of a cereal mixture including maize, oats and barley, while pre-ruminant and ruminant calves can be fed rye meal mixed with linseed meal and wheat bran. Rye can be fed to horses as a replacement for oats and can be fed at levels of 3 kg per head per day without digestive disturbances. Growing pigs can be fed rye (digestible energy value 15.3 MJ kg^{-1} dry matter) in a mixture with other cereals up to 0.1 to 0.2 of total daily intake. Rye is not given to poultry, because of appetite-depressing and growth-depressing factors in the bran and whole grain, respectively.

In addition to providing grain, rye is also grown as a forage and is particularly important in the spring. Forage rye is very palatable and has a higher digestibility than fresh grass pasture. Preserved as silage, it can be fed to dairy cows up to 40 kg per head per day, but mixing rye and maize silages is generally recommended to achieve the best levels of production. (ED)

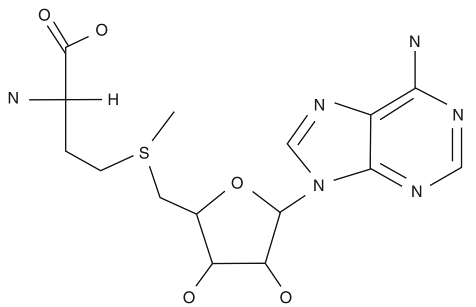
Chemical composition of rye grain and forages (as g kg^{-1} dry matter unless specified). (Source: MAFF, 1990, *UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs*; Piccioni, M., 1989, *Dizionario degli Alimentii per il Bestiame*, 5th edn, Edagricole, Bologna, Italy.)

Product	DM (g kg^{-1})	CP	EE	Starch	NDF	CF	Ash
Grain	869	119	12	–	357	20	18
Forage	223	26	8	–	–	76	17
Hay	913	67	21	–	–	325	50
Silage	303	35	10	–	–	108	25

DM, dry matter; CP, crude protein; EE, ether extract; NDF, neutral detergent fibre; CF, crude fibre.

S

S-Adenosylmethionine Often abbreviated to SAM, this compound ($C_{15}H_{22}N_6O_5S$, molecular weight 398.4) is not a component of protein. It is synthesized when methionine is adenylated by ATP. *S*-Adenosylmethionine functions as the most important donator of methyl groups in the body.



(DHB)

See also: Methionine

Safety factor A safety factor (normally 5–10%) is usually incorporated in calculating nutrient allowances from nutrient requirements to take account of animal variability and unforeseen environmental factors.

(KJMcC)

Safflower Also known as bastard saffron, safflower (*Carthamus tinctorius*) belongs to the *Asteraceae*. It is an annual broad-leaved plant with a thistle-like appearance and orange to yellow flowers. The crop flourishes in dry conditions. Historically the importance of safflower was the use of the dye (carthamin) within its flowers to colour food and clothing red or yellow. Currently the primary product of this crop is the edible oil derived from the seeds, which contain up to 45% oil and are comparatively rich in vitamin E. Varieties have been developed with high levels of linoleic acid (up to 75% – considerably higher than other vegetable oils). Uses for this linoleic-rich oil are primarily for salad oils and non-dairy spreads. The other type of safflower varieties are rich in oleic acid. The uses for this heat-stable oil are either as a cooking oil or as an industrial oil. After processing, the meal or cake that remains is used as a protein supplement for livestock. The crude meal contains approximately 24% protein, the decorticated meal 40%. After harvesting, the stubble can be grazed profitably by ruminant livestock. The seeds also contribute to birdseed products.

(DA)

Sago An edible starch extracted from the pith-like centre of several South-east Asian palms, chiefly *Metroxylon sagu*. Sago is obtained by grinding the inner stem content of fully mature (12-year-old) sago palm that is beginning to flower. The starch is extracted with water and dried. Sago is an important part of the human diet in some parts of East Asia. The sago pith, or rasps, is obtained by mechanical rasping of the barked sago trunks. The sun-dried rasps can be fed to cattle and older pigs and it has been included at < 50% in pig diets and < 25% in poultry diets. Feeding higher levels of sago rasps decreases production and reduces feed conversion efficiency. The dry matter (DM) content of rasps after starch extraction is 773 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 27, crude fibre 101, ash 210, ether extract 3 and NFE 659, with ME 10 MJ kg^{-1}.

(JKM)

Sainfoin A leguminous perennial herb, *Onobrychis viciifolia*, of the family *Leguminosae* (pulse family) indigenous in southern Europe and temperate western Asia. It is cultivated widely as a forage crop for its high protein content (*c*. 240g kg^{-1} dry matter) and its ability to thrive on calcareous soils too dry or too barren for clover or lucerne (alfalfa), but is of less economic importance than lucerne. In the UK it is confined to a few areas in the south-east. The high feed value of the hay makes it a good feed for racehorses. The aftermath of hay production is very good for fattening lambs. As in other forages, the leaf contains higher levels of protein, ether extract, calcium and other minerals than the stem and so the composition of the plant is greatly affected by the increasing proportion of stem to leaf as the plant matures. The protein content declines rapidly at flowering, with a subsequent increase in fibre content. (JKM)

Sal seed (*Shorea robusta* Gaertn.) The seed of the sal tree, used for oil extraction. The oilcake, although high in tannins (8–14%) which render the protein indigestible, is a valuable energy component. It can be included up to 20% in ruminant rations and up to 10% for non-ruminants. Replacement of maize in pig rations by de-oiled sal seed meal has been reported in India for finishing pigs. Tannin levels can be reduced by treatment with 0.1 M NaOH, which allows higher levels of inclusion in rations. (LR)

Nutrient composition of sal seed (% dry matter).

	CP	CF	Ash	EE	NFE	Ca	P
Sal seed meal	8.6	1.3	3.1	2.5	84.4	0.20	0.20

CF, crude fibre; CP, crude protein; EE, ether extract; NFE, nitrogen-free extract.

Further reading

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Saliva A highly viscous fluid containing salts and mucoproteins secreted from the salivary glands into the mouth. The salivary glands represent a network of accessory structures, each of which drains into a main gland that opens into the mouth. The network includes three pairs of major glands: parotid glands (located under the ears), lingual glands (located in the base of the tongue) and mandibular (or submaxillary) glands (between the other pairs). Minor glands in the tongue and buccal mucosa, with numerous secretory ducts emptying into the mouth, also contribute.

The composition and volume of secreted saliva is influenced by the diet and can be highly variable. Two basic types are produced: one is very thick, with a high content of mucus; the other is serous, i.e. watery and thin, and contains various enzymes. Saliva of non-ruminant animals is slightly acid and that of ruminants alkaline. On average, sheep secrete 5–10 l day^{-1}, pigs 15 l day^{-1} and cattle 130–180 l day^{-1}.

Saliva aids in mastication, bolus formation and swallowing. A large quantity of bicarbonate is secreted via saliva and serves to buffer the digesta. In ruminants, which produce large quantities of saliva, bicarbonate is essential for neutralizing the considerable microbial production of short-chain fatty acids in the rumen. Other components of saliva, e.g. urea, mucin, phosphate, sulphate, magnesium and chloride, are essential for microbial metabolism in the rumen. Enzymes such as ptyalin, an α-amylase (in omnivores), and lipase (in suckling and young milk-fed animals) can initiate the digestion of macromolecules. Finally, saliva solubilizes a number of the compounds in the feed and thereby makes them detectable by the taste buds on the tongue. (SB)

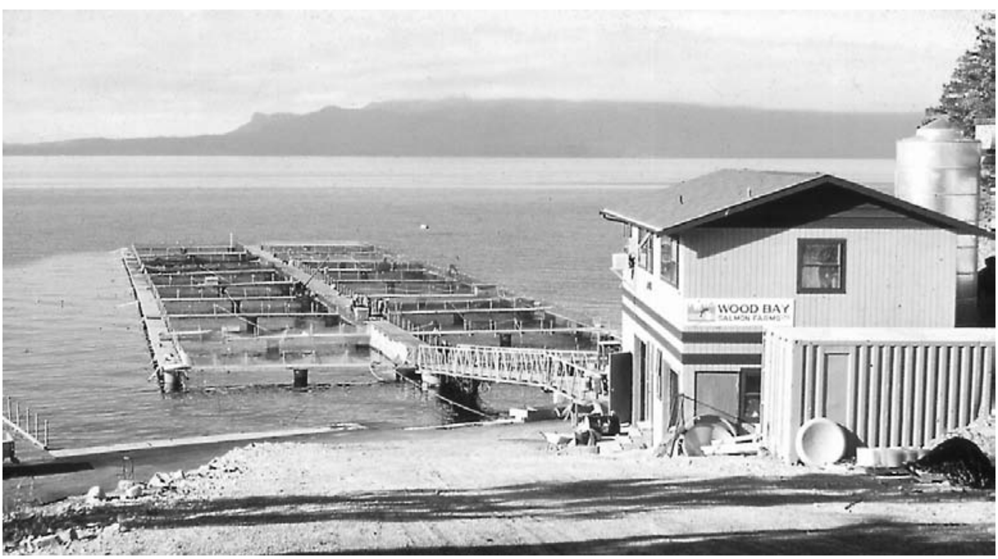
See also: Digestion

Salmon culture Culture of salmon freshwater stages began in Scotland in the 1850s but commercial culture of the marine phases essentially began in Norway in the 1960s. Atlantic salmon (*Salmo salar*) is the principal cultured species (883,858 t worldwide in 2000), with coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon cultured in smaller amounts. The major countries that farm Atlantic salmon include Norway, Chile, the United Kingdom, Canada and Australia.

All salmon species are anadromous. In the early stages they require culture in freshwater hatcheries and are transferred to sea cages at the smolt stage (seaward migrant phase). Adult salmon typically mature in autumn or early winter, but maturation may be manipulated by variation of temperature and photoperiod regimes and synchronized by injection of luteinizing hormone-releasing hormone (LHRH). Adults may be ripened in sea water but better quality eggs are obtained from final maturation in fresh water. Spawning should utilize water of 4–7°C. The eggs and milt are stripped from adults manually by exerting pressure on the abdomen, mixed for a few minutes (1–10 million sperm per egg), then hardened in running fresh water during which time the eggs swell through water uptake. Eggs (4–6 mm diameter) are reared in hatching trays supplied with running water at 0 to 8°C. Most commercial facilities use high temperature to shorten hatching times (about 2 months at 8°C). Use of water recirculation and biofiltration is becoming more common to make more efficient use of heated water.

The salmon hatchlings (alevins) have a large yolk sac that comprises *c*. 70% of their wet weight at hatch. Most of this must be absorbed prior to exogenous feeding. Alevins may be reared at 0–12°C, which may be increased to 16°C just before feeding. Many commercial hatcheries rear alevins at elevated temperatures to reduce the time to first feeding (*c*. 1 month at 12°C). Alevins should be reared in artificial substrate to reduce locomotor activity and promote better yolk utilization efficiency. Fry (*c*. 30 mm long at first feeding) may be started on commercial starter diets. The optimal rearing temperature from fry to smolt for most salmon species is near 15°C. The majority of Atlantic salmon smolts currently produced are '1+' smolts, at 14–16 months post-fertilization and an average weight of 80 g. The production of '0+' smolts at less than 12 months is becoming more prevalent. Many male smolts tend to become precociously mature at the end of the first summer, resulting in growth reduction and necessitating an extra year's growth to smolt size ('2+' smolts).

Most smolts are placed in sea cages in the spring at 5–7°C, with 0+ smolts placed in sea water in the autumn. Smolts are vaccinated against infectious bacterial pathogens, furunculosis and vibriosis, prior to seawater transfer. Smolt stocking densities are 4–12 m^{-3}, depending upon whether they will be divided among several cages later. Coho salmon have a freshwater phase of similar length to Atlantic salmon but chinook salmon, particu-



Sea cages for salmon may be as large as 10,000 m^3.

larly the ‘ocean type’, can tolerate full sea water at 6–7 g. Culture cages may be made of wood, steel or plastic, with plastics becoming more prevalent. Industry development has resulted in increasingly larger cages and more offshore locations. Sea cage volumes may vary from a few hundred cubic metres for older cage types to over 10,000 m^3 for more modern cages.

Salmon in sea cages are fed extruded dry feeds (7% moisture) containing 40–45% protein and 22–35% lipid, with supplements of pigments and micronutrients. Market sizes of 3–6 kg are attained in 16–24 months after smolt entry, at a final stocking density of 15–20 kg m^{-3} of cage volume. Potential hazards to salmon cage culture include various bacterial and viral pathogens, sea louse infestations, bird and seal predation, toxic algal blooms, low lethal temperatures and low dissolved oxygen. Some bacterial pathogens (e.g. bacterial kidney disease) are controlled by antibiotics. Sea lice are controlled by insecticide baths and feed additives (e.g. Ivermectin). Predator nets and ultrasonic seal repellents reduce predation risks, while proper site selection and stocking densities can minimize the dangers of temperature, algae and low dissolved oxygen. (RHP)

Salmonellosis Infection with bacteria of the *Salmonella* group can cause disease in animals and may be important as a cause of food poisoning in humans. There are many different serotypes of salmonella: some have distinct host-species preferences and there is a wide range in pathogenicity. Some salmonellae transmit vertically (parent to offspring), others laterally (animal to animal). Salmonellae can survive for long periods, weeks or months, in the environment. Food may be a source of infection, either at source or by subsequent contamination. (EM)

Salmonid fishes Pacific salmon and rainbow trout are members of the genus *Oncorhynchus*, of the family Salmonidae, which includes Atlantic salmon, trout, char, grayling, whitefish and several other groups. There are five species of Pacific salmon, but only two – the chinook (*Oncorhynchus tshawytscha*) and the coho (*Oncorhynchus kisutch*) – are farmed for food production. Rainbow trout (*Oncorhynchus mykiss*) are by far the most widely farmed trout, having been transplanted over the past century from their native environments in the northern, temperate areas of the eastern and western Pacific to South America, Japan, China, Europe, parts of Africa, Australia and New Zealand. Atlantic salmon (*Salmo salar*) are native to the northern, temperate areas of the eastern and western Atlantic and are the most widely farmed salmon species in the world, being farmed in Norway, Scotland, Iceland, Ireland, Chile, Canada, the USA, Tasmania and New Zealand. Other farmed species include the Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). Salmonids exhibit considerable plasticity with respect to freshwater and seawater existence as post-juveniles, but all spawn and live in fresh water as juveniles. Salmon prefer a seawater post-juvenile existence; they undergo a metamorphosis in spring that prepares them for migration to the sea. Salmon are farmed in floating sea cages, whereas trout are generally farmed in freshwater raceways and tanks. However, rainbow trout can be adapted to sea water after they reach *c.*100 g, and in Norway and Chile are commonly farmed in marine cages like salmon.

Salmonids are carnivorous fish that consume zooplankton and aquatic insects as fry and juveniles, and small fish, shrimp (krill) and squid as post-juveniles and adults. They grow best when fed high-protein, high-lipid feeds containing highly digestible protein. They have a limited ability to utilize carbohydrates and become hyperglycaemic when fed diets containing high levels of digestible carbohydrates. Salmonids require 10 essential amino acids and 15 vitamins (Tables 1 and 2). Like most other fish, they require ascorbic acid. Salmonids also require dietary sources of omega-3 fatty acids, preferably docosahexaenoic (22:6) and eicosapentaenoic (20:5) acids. Salmonids can obtain many of the minerals they need directly from the water, but diets are generally supplemented with copper, iodine, manganese, zinc and sometimes selenium, plus sufficient available phosphorus to meet dietary requirements (*c.*0.6% minimum). Salmonids are adept at utilizing dietary protein for metabolic energy, in part because they readily excrete ammonia via the gills. While it is desirable to feed high lipid diets to spare expensive dietary protein, digestible protein:energy ratios are kept within a narrow range for grow-out fish. Various ways of expressing desirable protein:energy ratios are reported, such as 18–22 mg digestible protein MJ^{-1} digestible energy, about 42% digestible protein and 4.1 kcal g^{-1} diet, or 100 kcal g^{-1} protein. Salmonids vary in their tolerance of high-lipid diets according to their size and species. Atlantic salmon exhibit higher growth and protein retention rates when fed high-lipid (*c*.35%) diets, in contrast to Pacific salmon or rainbow trout which tend to accumulate fat when fed diets containing more than 25% lipid, perhaps associated with their life cycle in nature (food scarcity in winter, voluntary starvation during long spawning migrations).

A unique attribute of salmonids is their pigmented flesh and skin. In nature, they obtain the pigments, mainly astaxanthin and canthaxanthin, via the food chain; they cannot synthesize carotenoid pigments *de novo*. Astaxanthin has been shown to be an essential dietary nutrient for Atlantic salmon. Fry from female Atlantic salmon deprived of dietary astaxanthin exhibit slow growth and high mortality if not fed diets containing astaxanthin. Other salmonid species probably also require a dietary source of astaxanthin, canthaxanthin, or both, to produce viable off-

Table 1. Dietary amino acid requirements for salmon and trout (expressed as percentage of diet).

Amino acid	Salmon[1]	Trout
Arginine	2.04	1.5
Histidine	0.61	0.7
Isoleucine	0.75	0.9
Leucine	1.33	1.4
Lysine	1.7	1.8
Methionine + cystine	1.36	1.0
Phenylalanine + tyrosine	1.75	1.8
Threonine	0.75	0.8
Tryptophan	0.17	0.2
Valine	1.09	1.2

[1]Adapted from NRC (1993).

Table 2. Dietary micronutrient requirements and their deficiency signs for Atlantic salmon.

Micronutrient	Requirement[1]	Deficiency sign
Vitamin E	35 mg kg^{-1} diet	Muscle degeneration, anaemia, reduced carcass protein, increased carcass moisture and fat
Pyridoxine	15–20 mg kg^{-1} diet	Nervous disorders, anorexia, reduced alanine transferase activity
Vitamin C	50 mg kg^{-1} diet	Scoliosis, lordosis, anaemia, mortality
Vitamin K	Required	Not determined
Riboflavin	Required	Not determined
Pantothenic acid	Required	Not determined
Phosphorus	0.7% of diet	Low bone ash, calcium, phosphorus and magnesium, bone abnormalities, poor growth
Manganese	20 mg kg^{-1} diet	Reduced haematocrit and vertebral manganese
Copper	6 mg kg^{-1} diet	Reduced serum copper and liver cytochrome C oxidase activity
Iron	73 mg kg^{-1} diet	Reduced haematocrit, red blood cell count and tissue iron level
Selenium	Required	Muscular dystrophy-like signs
Iodine	Required	Not determined
Astaxanthin	5 mg kg^{-1} diet	Poor growth, mortality in fry from females deprived of dietary astaxanthin

[1] Dietary requirements determined in one or two studies only, and generally with fry or fingerlings. Adapted from Hellend, Storebakken, and Grisdale-Helland (1991) in: *Handbook of Nutrient Requirements of Finfish* (ed. R.P. Wilson), CRC Press, Boca Raton, Florida, pp. 13–22.

spring. In farming, salmon and trout diets are supplemented with astaxanthin, either from natural sources, such as krill, crustacean waste, *Phaffia* yeast and algae, or from astaxanthin produced by industrial synthesis, e.g. Carophyll pink®. Diets are typically supplemented to contain between 45 and 60 μg pigment g^{-1} and supplemented diets are fed during the grow-out period before harvest.

Feed formulations for salmonids are relatively simple: fish meal, fish oil, ground wheat or gelatinized maize, vitamin and trace mineral supplements, plus carotenoid pigment for grow-out stages (Table 3). Depending upon the relative prices of fish meal and other protein supplements, formulations often contain other protein sources, such as maize gluten meal or soybean meal, in place of a portion of fish meal. There are also concerns about long-term dependency upon fish meal as the main protein source in salmonid feeds. Rendered animal products have long been used in salmonid diets but in Europe, because of concerns about BSE transmission and excessive phosphorus losses from farms, they are now limited to poultry by-product meal and feather meal. Another developing concern is the presence of organic contaminants in fish meals and oils originating from the North Atlantic.

Special diet supplements are used to increase diet efficiency or enhance disease resistance. As more plant protein introduces higher levels of phytate in salmonid diets, supplementing diets with phytase is an effective means of increasing the availability of phosphorus. Immune stimulants and immune enhancers are also used, to enhance disease resistance.

Because salmonid diets contain high levels of unsaturated lipids, there is potential for auto-oxidation. This can be minimized by using only batches of fish oil with low oxidative status, and by addition of antioxidants to fish oils. Dietary supplements of α-tocopheryl acetate, ascorbic acid and selenium provide additional metabolic protection against free-radical damage *in vivo*.

In trout farming, a kind of demand feeder is commonly used that delivers feed when fish move a rod suspended in the water. Wave and wind action limit the use of demand feeders in sea cages, so feed is delivered mechanically, using pipes and blowers programmed to supply each cage with an appropriate amount of feed, divided into an appropriate number of meals per day. In some part of the world, feed is delivered by hand, or by mechanical dispersing devices on each cage that are programmed to feed at intervals. In any case, feeding amount is based upon expected growth and feed efficiency ratios that vary with season (photoperiod and water temperature).

Table 3. Generalized formulations (g kg^{-1}) used for grower and fingerling Atlantic salmon feeds and for grower rainbow trout.

Feed ingredient	Grower salmon	Fingerling salmon	Grower trout
Fish meal	480	600	360
Soybean meal	50	0	100
Poultry by-product meal	50	0	100
Feather meal	0	0	60
Wheat by-products	0	274	90
Ground whole wheat	104	0	104
Vitamin premix	10	10	10
Trace mineral premix	1	1	1
Choline chloride (60%)	4	4	4
Ascorbic acid	1	1	1
Fish oil	300	110	170
Proximate composition:			
Moisture	8%	8%	8%
Crude protein	41%	48%	44%
Crude fat	35%	17%	22%

Salmonid feeds are expensive, and the potential for feed waste, especially in sea cages that can be 10 m deep, is relatively high. This has led to the development of sophisticated systems to detect pellets reaching the bottom of cages and recovering them for reintroduction at the surface, or stopping feeding when feed is detected at the bottom of pens. These systems are very effective and, as a result of their use, feed waste in salmon farming is low. Overall, the use of high-quality ingredients, cooking-extrusion pelleting, and effective vaccines to prevent disease have made salmonid aquaculture one of the most efficient farming systems to convert ingredients not consumed directly by humans into high-quality food; feed conversion ratios of 1.0 to 1.2 on a farm basis are routinely obtained. (RH)

See also: Atlantic salmon; Pacific salmon; Salmon culture; Trout

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Salt The compound formed when the hydrogen atom of an acid is replaced by a metal (e.g. sodium, potassium). Common salt is sodium chloride (NaCl). Both sodium and chloride are required nutrients. (NJB)

Sample A small portion representative of the whole. To sample is to select a small amount of a larger mass or to take a number of units to represent a large number of units, or a population, for statistical analysis. For sampling certain populations or materials, there are three distinct ways in which a selection can be made: random, systematic or authoritative. In random sampling, each individual of a population or each part of the mass of material has an equal chance of being selected as part of the sample. In systematic sampling, individuals are chosen at fixed intervals, e.g. every fifth animal in a population or every tenth bag of fishmeal. Authoritative sampling requires individuals who are well acquainted with the material or the population to take a representative sample without regard to randomization. Other sampling procedures include stratified random sampling and sampling with replacement. For many materials, sampling error (the difference between the sample and the whole) is minimized by complete mixing, or homogenization, so that any one sample has the same composition as the whole. (SPL)

Saponification The chemical process in which a fatty acid ester is hydrolysed by an aqueous alkali (e.g. sodium hydroxide, NaOH) to form the salt of the fatty acid and an alcohol. For example, when animal or plant **fats** (i.e. triacylglycerols) are saponified, the sodium salt of the fatty acid (now a soap) is produced along with free glycerol (an alcohol). (NJB)

Saponins Natural detergent-like glycosides found in a variety of plants used for human and animal feeds. Their detergent activity derives from a steroid or triterpenoid nucleus with one or more side chains of water-soluble carbohydrates. Saponins have multiple biological effects, some positive but many negative. Because of their foaming properties, they are extremely toxic to fish and have been used as fish poisons in native tropical rainforest cultures. Saponins are bitter and irritate mucous membranes of the mouth and gastrointestinal tract and may cause frothy bloat in ruminants. Many plants containing saponins cause clinical signs of toxicity: depression, anorexia, diarrhoea, weight loss, liver and kidney lesions and photosensitization. Low levels of dietary lucerne meal can reduce the growth rate of poultry and pigs. Saponins affect nutrient metabolism and mineral absorption (especially iron) by interacting with mucosal cell membranes, causing permeability changes or loss of activity of membrane-bound enzymes. (KEP)

Satiety A state which, following the ingestion of a food, suppresses further ingestion. Satiety occurs after the termination of a meal and continues until the onset of hunger or initiation of a subsequent meal. It is defined as the period between meals that is characterized by a lack of hunger or desire to eat. Satiation is the inhibition of feeding that occurs during the consumption of a meal, and contributes to the termination of a meal. Because satiation occurs within a meal, it is dependent upon the positive and negative feedback signals that initiate and stop ingestion. Positive feedback signals are responsible for initiating and maintaining eating, and arise from the sensory properties of food. Negative feedback signals increase during a meal and eventually terminate ingestion. Negative feedbacks arising from stomach distension, hormonal release, chemoreceptor stimulation and metabolism of ingested nutrients seem to be the primary factors that contribute to satiation. Peptides released from the gastrointestinal tract during a meal that may be candidates for controlling meal size include cholecystokinin, bombesin-like peptides, pancreatic glucagon, insulin, amylin, somatostatin, neurotensin, enterostatin, apolipoprotein AIV and glucagon-like peptide. Termination of a meal as a result of satiation should be differentiated from termination due to reasons such as competition from rival activities, malaise or depletion of the food source. (NJB)

Saturated fatty acids Fatty acids with the general formula $CH_3(CH_2)_nCOOH$, where n may be 0 to 30 but in most natural fats is an even number. Odd-numbered and branched-chain saturated fatty acids are not uncommon in ruminant fats. The lower members are liquid at room temperature but those with more than ten carbons are solid, with melting points increasing with chain length. Saturated fatty acids do not absorb iodine. The physical characteristics associated with longer chain length and higher melting point decrease the ability of the fatty acids to interact with amphipathic molecules to form soluble micelles; thus, higher homologues of saturated fatty acids have lower intestinal digestibility than shorter chains. Saturated fatty acids are found in lower proportions in cholesteryl esters and phospholipids of plasma and tissue membranes than are unsaturated fatty acids. Palmitic acid (16:0) is the main product of fatty acid synthesis in animal adipose tissue, whereas ruminant mammary tissue synthesizes 4:0 to 16:0. Milk fat typically contains 70% saturated fatty acids. Stearic acid is the primary product of ruminal biohydrogenation of dietary unsaturated fatty acids. Saturated fatty acids with 12–22 carbons can be desaturated by δ-9 desaturase, the product being the *cis* δ-9 monoene. Stearoyl-CoA (18:0) is the favoured substrate. (DLP)

Scales The primary purpose of scales is to give fish external protection. Most bony fish have one of two types of scales: cycloid and ctenoid. Cycloids have a smooth edge whereas ctenoids have a toothed edge. The scales grow with the development of fish and leave rings like the rings of a tree, and so the age of most fish can be determined by examining their scale rings. Scale sizes vary greatly between species; freshwater eels have small embedded scales, the tunas have tiny scales and the scales of the Indian mahseer can reach over 10 cm in length. (SPL)

Scallops Bivalve molluscs of the family Pectinidae. The shells are usually rounded, with radiating ribs and wing-like projections (called 'ears') on either side. The outline and appearance have been much used in heraldry, murals, decorations, ornaments and jewellery. Many species are fished and cultivated worldwide, principally for the single large adductor muscle which the animal uses to swim by rapid 'clapping' movements of the shells, and which is good to eat. (DJS)

Scorch The result of overheating of feed materials during processing which results in discoloration and a reduction in nutritional value, especially as a result of Maillard reactions. New technologies in processing, such as low-temperature and spray drying, can prevent scorching. (JKM)

Scour: *see* Diarrhoea; Digestive disorders

Sea urchins Sea urchins belong to the invertebrate phylum Echinodermata, meaning 'spiny skins'. The typical sea urchin is a rounded, globular organism, a few centimetres in diameter, with a rigid, hard internal shell made of many interlocking calcareous plates, and covered with a dense layer of moveable spines. The species may be of different colours with spines of different lengths. They occupy a range of habitats in all the oceans of the world, mostly browsing on rocky surfaces and among corals. 'Heart' urchins are heart shaped and live buried in sand. Sand dollars are quite flat and browse on the surface of the sand. All echinoderms have a unique natural hydraulic 'water vascular' system that powers the tube feet, allowing the urchins to 'walk' and grasp their food.

Edible sea urchins are captured by trapping, dragging or by diving. They have no conspicuous musculature and are fished exclusively for their roe, which is considered a delicacy. Most fisheries are seasonal, linked to the period when roe quality is at its best. Current landings are in the order of 100,000 t year^{-1}. Principal consumers are Japan and France. Some progress is being made with the culture of sea urchins but the amounts harvested to date are nominal. Some wild-caught urchins are being held in captivity and fed selected diets to improve roe quality and yield. (DJS)

Sea water A complex solution of inorganic and organic solutes and dissolved gases with suspended particles such as mineral grains, aggregates of organic particles and living plankton. The term 'salinity' is a measure of concentration of salt in sea water. The following dissolved ions (percentage of total salt) make the water saline: sodium, 55.04%; chlorine, 30.61%; sulphate, 7.68%; magnesium, 3.69%; calcium, 1.16%; potassium, 1.1%; bicarbonate, 0.41%; bromine, 0.19%; borate, 0.07%; strontium, 0.04%; and fluorine, 0.003%. Many of the elements in sea water are found in nearly constant proportions although the total salinity varies from place to place. The salinity of sea water ranges between 33 and 37 parts per 1000 (g kg^{-1}), of which approximately 85% is sodium chloride. Freshwater discharge from rivers as well as evaporation and freezing may affect the salinity and concentrations of various ions in the sea water.

Exchange of ions occurs across the gills, skin and oral epithelia in fish. Inorganic ions present in sea water such as calcium, magnesium, sodium, potassium, iron, zinc and copper can partially satisfy the mineral requirements of aquatic organisms. (DN)
See also: Freezing

Seasonal variation The value of grass, either for grazing or for conservation, changes as the growing season progresses, largely due to increasing maturity, with climate and management causing changes between seasons. As the interval between defoliations increases, so does total dry matter (DM) yield, but increased fibre concentrations reduce the digestibility of DM. This is compounded by an increase in lignin content which, because it complexes with cell walls, further reduces the digestibility of the fibre fraction. Metabolizable energy (ME, kg^{-1} DM) falls. Delaying the time of the first cut of the season increases yield at that cut but delays secondary growth. This can result in a reduced total yield (see table). Crude protein concentration falls (e.g. from 300 to 30 g kg^{-1} DM) but total stored nitrogen increases.

In temperate regions, the growing season is largely controlled by ambient temperature but the time of plant maturity varies between species and between varieties within species. Perennial ryegrass is generally regarded as an early-flowering variety and timothy as late flowering. Management of grassland through the growing season must ensure adequate grazing with sufficient material for conservation for winter feeding. In long-term leys and permanent pasture it is also essential to allow the plant sufficient rest time to replenish root reserves.

In the tropics, growth is controlled by rainfall – both the amount of rain and its distribution through the year. Tropical grasses exhibit a rapid fall in protein content and increased fibrousness at the end of the rains. The quality of standing hay is usually not greater than that of crop residues, depending on the amount of termite damage and the amount of senescence that occurs. Management of grazing for intensive production can mitigate this extreme seasonality of production by: (i) timely application of fertilizer; (ii) conservation of excess biomass; (iii) seasonal breeding programmes and the use of mixed-species swards, includ-

Effect of cutting frequency on grass yield and quality (from Leaver and Moisey, 1980).

(a) Three-cut system

Cut	DM yield (t ha^{-1})	ME (MJ kg^{-1} DM)
Late May	4.6	10.6
Early July	3.2	9.8
Mid-August	1.8	9.6
Total	9.6	Mean 10.0

DM, dry matter; ME, metabolizable energy.

(b) Two-cut system

Cut	DM yield (t ha^{-1})	ME (MJ kg^{-1} DM)
Early June	7.8	9.6
Mid-August	3.7	9.0
Total	11.5	Mean 9.2

DM, dry matter; ME, metabolizable energy.

ing legumes; and (iv) introduction of leguminous multipurpose trees to give the option of browsing. In smallholder livestock production systems, particularly in the drier areas, there is no tradition of conservation of forages to offset dry-season feed shortages. Fertilizer application to communal rangelands is not a practical option. There is little or no evidence to suggest that cattle breed to coincide with the grass flush (peak kidding times in goats are more predictable). (TS)

See also: Cutting frequency

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Seaweed Seaweeds are multicellular algae of marine and brackish waters, more usually the readily visible larger forms. They come in three basic colours (red, brown and green) and display a large variety of forms and life histories. Seaweeds are typically rich in complex polysaccharides, which make up their cell walls, and usually contain significant amounts of protein, vitamins (especially A and B) and trace elements. Of about 9000 known species, only about 50 are utilized, via either direct consumption or extraction of contents. Limited digestibility of the cell walls restricts human consumption of seaweed to relatively few (albeit very valuable) species, but ruminant livestock pastured along seacoasts traditionally have fed and thrived on kelps, rockweeds and other accessible seaweeds. Meal from the brown seaweeds *Ascophyllum* and *Laminaria* is used as a supplement to livestock feed, and the addition of *Chondrus* to diet has ameliorated cases of ovine ill-thrift. Seaweeds also provide a natural food source for aquacultured marine herbivores such as abalone and sea urchins, with certain species being more nutritious and more palatable to the animals. The other major commercial use of seaweeds is as sources of extractives, par-

Laminaria is one of several species that may be used as a livestock feed.

ticularly gelling agents (carrageenan (*Chondrus*), agar (*Gelidium*, *Gracilaria*) and alginates (*Ascophyllum*, *Laminaria*)) derived from their cell walls and used as binders, emulsifiers and stabilizers in foods, pharmaceuticals and various industrial applications. Lesser uses are the production of foliar fertilizers (*Ascophyllum*), soil conditioners (especially calcified forms such as *Phymatolithon*) and sources of therapeutants (e.g. *Alsidium* and *Chondria* as vermifuges). Few species are toxic, although some are a nuisance as aggressive weeds. (CB)

See also: Algae; Marine plants

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Secretin Secretin was the first hormone to be discovered (by Bayliss and Starling in 1902). It is a 27-amino-acid polypeptide that is released into the circulation from endocrine cells of the small intestine. Sometimes referred to as nature's own antacid, secretin is released in response to the presence of the acidified meal entering the small intestine. It acts through a cyclic-adenosine monophosphate (cAMP)-mediated intracellular pathway to inhibit gastric emptying and stimulate the secretion of a bicarbonate-rich fluid from the pancreas. (GG)

Selection, feed: *see* Feed selection

Selenium Selenium (Se) is a mineral element with an atomic mass of 78.96. It exists in three oxidation states of +6, +4 and –2, and shows both metallic and non-metallic properties. Selenium is present in all organs, with kidney, liver and bone having the greatest concentration; however, muscle and skeleton, as a whole, contain most of the Se found in the mammalian body. Selenium is an essential nutrient and is required for full activity of a number of enzymes, including the various isozymes of glutathione peroxidase, thioredoxin reductase, and iodothyronine 5′-deiodinase types 1, 2, and 3, and is a component of selenoproteins P and W. Selenium can also be incorporated into most types of proteins in the form of selenomethionine as a substitute for methionine. Thus, Se is present in plant and animal products bound to certain proteins or incorporated into proteins as selenomethionine and selenocysteine. Methylselenocysteine is a soluble form of Se. Small amounts of Se can also exist in the body as

An adequate selenium intake by ewes during late pregnancy is essential for good lamb vigour at birth and the ability to generate heat from their brown adipose tissue, essential for survival in cold outdoor environments.

inorganic selenite and selenate salts. The inorganic forms are reduced to selenide before incorporation into selenocysteine. Most of the Se in plant material is selenomethionine and that in animals is both selenocysteine and selenomethionine.

In non-ruminants, Se is absorbed primarily from the upper intestinal tract. More than 90% of intake is absorbed if Se is in the organic form, and 60% if in the inorganic forms of selenite or selenate. This suggests that Se homeostasis is not controlled to a large extent by absorption. Se absorption in ruminant animals is somewhat less than in non-ruminants, which could be the result of chemical processes in the rumen that reduce Se to insoluble forms. The rate at which Se is eliminated from the body depends largely on the form of ingested Se. Selenium that is incorporated into proteins as a substitute for methionine, or as selenocysteine, has the slowest turnover, because it is eliminated only when the proteins are degraded. Before urinary excretion, all forms of Se are reduced in the liver to selenide and methylated. In animals, most of the Se is excreted in urine as the trimethylselenonium ion. It can also be eliminated through the breath as dimethyl-selenide.

Variable signs of Se deficiency can occur in animals. Muscular dystrophy, or white muscle disease, is seen in lambs and calves that consume a selenium-deficient diet. Exudative diathesis is seen in poultry and liver necrosis in other species. Because Se is associated with enzymes with antioxidant properties, some of the signs of Se deficiency will respond to vitamin E supplementation; others will not.

The dietary requirement for Se is somewhat consistent among farm species. The US National Research Council recommends 0.1 mg Se kg^{-1} diet for growing beef cattle and 0.3 mg kg^{-1} for dairy cattle. The requirement for pigs depends on their age: young growing pigs require 0.5 mg Se kg^{-1} diet and older pigs require only 0.15 mg kg^{-1}. The requirement for horses and poultry is about 0.1 mg Se kg^{-1} diet, and for sheep the value is between 0.1 and 0.2 mg kg^{-1} diet. The maximal tolerable dose of Se for cattle and horses is 5 mg kg^{-1} diet and for sheep it is 2 mg kg^{-1} diet.

Selenium toxicity in grazing animals can be a problem, especially in areas where soil Se is relatively high. Numerous plants tend to accumulate Se in their leaves and, if consumed, can lead to Se toxicosis. The exact mechanisms involved in Se toxicity are not understood, but may include the inhibition of sulphydryl enzymes or the production of excess methylated selenium metabolites that are toxic. Excess Se can also bind glutathione and remove it from critical biological reactions. (PGR)

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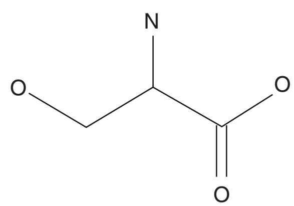
Selenocysteine An amino acid, $HSeCH_2{\cdot}CHNH_3^+{\cdot}COO^-$, molecular weight 168, identical to **cysteine** but with **selenium** (Se) in place of the sulphur moiety. Selenocysteine is incorporated into proteins and, in some, forms part of the active site. Examples of selenocysteine-containing proteins are: thioredoxin reductase, which is involved in the conversion of ribonucleosides to deoxyribonucleosides; glutathione peroxidase, which is involved in the destruction of peroxides; and iodothyronine deiodinase, 5′ DI, which converts thyroxine (T_4) to 3,5,3′ triiodothyronine (T_3). (NJB, DHB)

Semi-purified diets Diets based largely on purified ingredients. Semi-purified diets are useful biological tools in establishing responses to specific dietary ingredients/nutrients in the absence of confounding factors. Thus, for example, a response to a vitamin should ideally be assessed under conditions where no other dietary ingredient contains that vitamin. Semi-purified diets should, wherever possible, be nutritionally adequate (except for that nutrient under investigation). Common ingredients are purified starch, glucose, soya protein isolate, casein and vitamin/mineral premixes. Vegetable oil is often added for textural reasons (to reduce dust and maintain palatability). JW

Serine An amino acid ($HO{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 105.1) found in protein. It is synthesized from glucose or glycerol, with alanine serving as the amino donor. In addition to its role in protein synthesis, serine serves as a metabolic precursor of glycine, and in this process a hydroxymethyl group is contributed to the folate pool. Serine is thus considered the most important precursor in the body for *de novo* methyl group synthesis. Phospholipid synthesis also involves serine; after diacylglycerol reacts with ethanolamine to form phosphatidyl ethanolamine, serine can be exchanged with ethanolamine to produce phosphatidyl serine. Both of these phospholipids can then serve as precursors for phosphatidyl choline (lecithin) biosynthesis. In this process, three methyl groups (from *S*-adenosylmethionine) are added to phosphatidyl ethanolamine to form phosphatidyl choline, which can be converted to choline.



A series of so-called serine proteases exist in which serine 195 of the enzyme becomes acylated. This can trigger proton shifts from serine through histidine to aspartate. Proton shifts of this type can affect the catalysis potential of an enzyme, e.g. chymotrypsin.

Serine is catabolized in one of two ways. Most is thought to be metabolized first to glycine and N^5, N^{10} methylene tetrahydrofolate. Glycine is then oxidized to CO_2 and NH_4^+, with N^5, N^{10} methylene tetrahydrofolate again being formed. Serine can also be deaminated by serine dehydratase to pyruvate, and this reaction yields NH_4^+ and H_2O. (DHB)

See also: Glycine; Phospholipids

Serotonin 5-Hydroxytryptamine (5HT, $C_{10}H_{12}N_2O$). Serotonin is formed from L-tryptophan by hydroxylation of position 5 in the benzene ring followed by a decarboxylation of the carboxyl carbon. It is found in high concentration in blood platelets and in the enterochromaffin cells in the intestine and in smaller amounts in brain and retina. Serotonin is a neurotransmitter produced by neurones in the hypothalamus and brainstem. It functions in pathways that relate to sleep and sensory perception. It is inactivated by the enzyme monoamine oxidase (MAO) which converts it to 5-hydroxyindoleacetic acid (5-HIAA), which is excreted in the urine. Serotonin can be converted to melatonin in a two-step process. High concentrations of melatonin are found in the pineal gland. (NJB)

Sesame Sesame (*Sesamum indicum*) has a long history of cultivation, being an important oil-yielding crop 4000 years ago. A member of the family *Pedaliaceae*, it is an annual, erect plant 0.5–2.5 m high, depending on the variety. Flowers are bell-shaped, white to pale pink. The fruit is an elliptical pod containing up to 100 seeds. It is highly tolerant of dry conditions, though very intolerant of waterlogging. The seeds contain about 50% oil and 25% protein. The primary fatty acids in sesame seed oil are oleic (47%) and linoleic acids (39%). The oil is used for cooking, salad oils and non-dairy spreads and has various industrial uses. The oilcake or meal that remains after the oil has been removed is protein rich (34–50%) and is palatable to all livestock, including poultry. Sesame cake can have a laxative effect and it can taint milk if fed as a high proportion of the ration ($<$ 3 kg day^{-1} in the case of the dairy cow). High concentrations of phytate can bind calcium and prevent its absorption, so care should be taken to increase the calcium provision in the ration when feeding sesame meal. Although sesame oil contains an antioxidant, sesamol, which delays deterioration, sesame meal will become rancid if stored for long. (DA)

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Sex differences Sex differences affect appearance, psychology, **carcass** attributes and **meat quality**. Strictly speaking there are only two sexes, male and female, defined by the genotype and the presence or absence of a Y chromosome. In mammals the male is the heterogametic sex whilst in birds it is the female. In mammals, the genetic information on the Y chromosome facilitates the initiation and development of the testes whilst in birds it initiates the ovary. The sex-related aspects of growth are driven by the sex steroids: androgens secreted by the Leydig cells of the testis and oestrogens secreted by the ovary. Although the activity of the testes is suppressed until early puberty, the Leydig cells from an early stage secrete androgens into the bloodstream at a rate that affects growth and the development of genitalia. In cattle, the female twin of a mixed-sex twin pregnancy is adversely affected by the androgens of its bull-calf sibling so that it is sexually undeveloped and becomes a ‘freemartin’.

At birth, male sheep and cattle tend to be larger than their female siblings and in normal circumstances this advantage continues through to puberty and thereafter in an exaggerated way to adulthood. Prior to puberty the main effect of sex differences is on growth rate and the adipose tissue depots associated with growth, males growing about 5–10% more rapidly and having up to 25% less fatty tissue than females. After puberty a considerable degree of sexual dimorphism occurs. Adult males are some 20% larger than females of comparable age. The choice of animals for domestication showed an understandable preference for those with herding or flocking tendencies. Related to this is the fact that the males compete for mastery of groups of females and tend to establish harems. The males of species that have evolved with these characteristics tend to be much larger and more muscular than the females. They also have differentiated features related to their ability to fight and to impress rivals.

Bulls and rams are equipped for head-on confrontation, with massive heads, reinforced frontal bones on their skulls and substantial horns. The muscles of the neck are thickened and there is increased musculature in the shoulders. The characteristic male profile and weaponry signals not only maleness but also relative strength and may intimidate a rival without physical contact. An extreme example of this is the North American bison or buffalo, which has specially elongated dorsal spines on the cervical and upper thoracic vertebrae that increase the impressiveness of the profile. Boars grow larger than sows and have exaggerated weapons for attack in the tusks that protrude laterally from the mouth. They also have a remarkable defensive adaptation in the so-called shield fat that covers the shoulder region. This fat is specially reinforced with cross-linked collagen and is resistant to penetration by opponents’ tusks (and butchers’ knives). It is detectable in entire males of market weights above 100 kg liveweight.

The production of meat from entire male animals is a subject of ongoing debate. In agricultural terms, the castrated male forms a third sex category and on rare occasions the spayed or ovariectomized female a fourth. In most countries bulls, rams and boars are castrated if destined for meat, though for different reasons. In the case of bulls, the safety of stock people amongst a herd of bulls is a major consideration. Extra fencing and handling facilities are required and there will be some damage and even losses from fighting. Bulls, however, grow faster and are leaner and require less feed per kilogram of carcass gain than castrates or females. Though skilled tasting panels may detect a degree of extra graininess in the meat and a lack of intramuscular fat and succulence, many tests have shown the general public to be less perceptive and unaware of any difference. Sinclair *et al*. (1998) actually showed a reduced shear force for biceps femoris in meat from bulls relative to that from steers. A disadvantage of bulls in relation to castrates is that butchers note a lower killing-out percentage and a poorer carcass conformation. The relatively large muscle groups in the forequarters mean a higher proportion of the less valuable cuts.

In the case of sheep, a major concern of leaving males entire is that it would be impracticable in the context of hill sheep in that young rams would be capable of indiscriminately serving females in the flock, wrecking breeding protocols. Entire lowland male lambs have the same advantages as bulls in terms of efficiency and similar problems in terms of carcass conformation and meat texture.

The use of entire boars for meat production is controversial for a rather different reason. The problem is the presence of so-called ‘boar taint’ in the meat or, more exactly, in the fat. The offensive odour is now known to comprise two main components: androstenone or 5α-androst-16-en-3-one (an unpleasant musk-like steroidal ketone elaborated in the testicles) and skatole (1-methyl indole), a definitive contributor to faecal odours. Androstenone is converted by the submaxillary glands to androstenol, which is the male pheromone of the pig and is distributed by an aroused boar in the frothy saliva that it generates in the presence of females. Skatole is a product of bacterial breakdown of tryptophan in the gut but, under the influence of testosterone, the gut preferentially absorbs it into the bloodstream, from which it is recruited as part of the sex odour of the boar when exhaling and is also liable to dissolve in the body fat. It is only a serious consumer problem in boars slaughtered in excess of 120 kg liveweight. **Castration** of boars is not routinely practised in the UK, Ireland, Australia or Denmark, though the latter country has on-line taint testing to eliminate tainted carcasses. Boars grow more rapidly to slaughter weight than do castrates or females, and because they are leaner they are more efficient at converting feed to liveweight gain. The leanness makes the appearance of the meat more acceptable and several studies have shown that meat from boars is more tender than that from gilts, a factor that is attributed to the beneficial effect of growth rate on tenderness (Blanchard *et al*., 1999).

In cattle slaughtered between 400 and 500 kg liveweight, the carcasses of females contain on average about 4% and castrates 3% more fatty tissue than those of bulls. In sheep slaughtered between 35 and 40 kg liveweight, similar differences in percentages of fatty tissue in the carcass are found for the respective sex categories. In pigs, the differences are greater, castrates being about 6% and females 5% fatter than boars (Lawrence and Fowler, 2002).

The anabolic properties of sex steroids as manifested in intact males and females have developed an impetus to deliver exogenous sex steroids to animals kept for meat. This is a practice that is banned in many countries but not in others. In the past, birds have been caponized using hexoestrol and cattle implanted with either natural steroids or analogues of sex steroids such as zearalenone and trenbolone. It is difficult to envisage the continued use of exogenous sex steroids or analogues in a world where consumers have become sensitized to the possible health risks of such practices. On the other hand, it is possible to foresee a diminution of castration as a routine agricultural practice and the development of appropriate husbandry systems for entire males. (VRF)

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Sex ratio Unlike many animals, in farmed species of poultry it is the female, not the male, that determines the sex of the offspring. This is a result of the female chicken carrying the Z and W sex chromosomes while the male carries only Z chromosomes. Prior to ovulation the formation of the first polar body provides the opportunity for either the Z or W chromosome to be excluded from the reproductive process, the remaining chromosome being incorporated into the female pronucleus. While there have been claims to be able to manipulate the phenotype (for example, through altered incubation conditions), there is little evidence for the sex ratio being anything other than 50:50 in commercially farmed species of bird. (NS)

Sexual maturity The stage in the life of an animal when the sex glands become fully functional so that the male is capable of producing fertile sperm and the female is capable of becoming pregnant. The age at sexual maturity varies between species and is generally somewhat lower in the male. (PJHB)

Sheep Sheep belong to the order Artiodactyla (even-toed ungulates), suborder Ruminantia, family Bovidae, subfamily Caprinae, genus *Ovis*. There are more than 800 breeds of domesticated sheep (*Ovis aries*). Their classification into types (Franklin, 1997) involves visual features such as shape and length of tail, length and diameter of wool fibres and ear type (lop or erect). Commercially, the most important are the fine-wool breeds (Merino and those derived from the Merino), the short-woolled European meat breeds (Suffolk, Texel, Dorset, Île-de-France) and the British long-wools (Leicesters and Romneys). The long-wools are used in the production of cross-bred females which in turn are crossed with meat sires for the production of lamb meat. The fat-tailed breeds of Asia, Africa and the former USSR, which produce coarse wool for carpets as well as contributing meat and milk, are regarded as another type; so too are the haired sheep of tropical regions that are kept mainly for their meat.

Despite major differences between breeds in the quantitative expression of production traits, some of which can be single gene effects (e.g. the *collipyge* gene for increased muscularity), it is extremely difficult, at the whole-animal level, to demonstrate differences between breeds in the amounts of energy or protein required for maintenance and gain. None the less, selection within a breed for increased muscle growth is accompanied by alterations in the responses of muscle protein synthesis and degradation, and of oxygen consumption, to feed intake (Oddy, 1999).

Selection for production traits stimulates pre-absorptive as well as post-absorptive effects on efficiency. For example, selection for wool production increased the quantity of rumen microbial protein at a fixed level of food intake, resulting in a 30% increase in the uptake of α-amino nitrogen in portal blood (see review by Oddy, 1999). Pregnancy also enhances by approximately 15% the quantity of α-amino nitrogen reaching the small intestine. So too does cold stress (Kennedy *et al.*, 1976). For these latter two examples there are accompanying decreases in rumen retention time and, in the case of cold exposure, a reduction in diet digestibility equivalent to about 0.2 units per degree fall in the ambient temperature below 20°C.

For breeds kept in high latitudes the males (intact and castrated) exhibit seasonal fluctuations in metabolic rate equivalent to approximately ±15% of the annual mean (Blaxter and Boyne, 1982; Argo *et al.*, 1999); highest and lowest values coincide with the longest and shortest days, respectively. These seasonal effects on metabolism precede similar fluctuations in appetite and correspond to seasonal fluctuations in the circulating concentrations of thyroid hormones. The seasonal effect on appetite is smaller for females than for males and very small in breeds such as the Dorset Horn, which are much less seasonal in their breeding activity than the Soay or Suffolk or indeed the Scottish Blackface and Shetland with which their intakes have been compared (Iason *et al.*, 1994).

Estimates of energy requirements for maintenance are based on calorimetric determinations of fasting metabolism and take into consideration a 15% higher value for intact males than for castrates or females; they also embody a decline in fasting metabolism with age. AFRC (1993) gave the fasting energy requirement (F) of female sheep as F(MJ day^{-1}) = $0.25(W/1.08)^{0.75}$ up to 1 year of age and $0.23(W/1.08)^{0.75}$ beyond 1 year old. In these equations W = liveweight (kg) and 1.08 is the factor used to convert liveweight to fasted weight. Additional energy costs for activity are estimated to be 2.6 and 28 J W^{-1} m^{-1} moving horizontally and vertically, respectively, and 0.42 kJ W^{-1} h^{-1} for standing as opposed to lying. The energy cost of body positional change is estimated to be 260 J W^{-1}. Dividing the sum of fasting metabolism and activity costs by k_m (the efficiency with which metabolizable energy, ME, is used for maintenance) provides estimates of ME requirements for maintenance. Because k_m varies with q_m (the proportion of gross energy, GE, that is metabolizable, i.e. q_m = ME/GE), it is calculated for diets of different metabolizability using the relationship $k_m = 0.35q_m + 0.503$.

Energy requirements for liveweight gain in growing lambs are calculated from estimates of their energy gains in fat and protein (39.3 and 23.6 MJ kg^{-1}, respectively). For practical application, energy gains (EVg, MJ kg^{-1} liveweight gain) are estimated to be $2.5 + 0.35W$ for males, $4.4 + 0.32W$ for castrates and $2.1 + 0.45W$ for females, where W = body weight (kg). Dividing these values by k_f (the efficiency of ME utilization for growth) provides estimates of ME requirements for growth; in this case $k_f = 0.78q_m + 0.006$. For wool production, the energy gain is estimated to be 23.6 kJ g^{-1}. Using the CSIRO (1990) estimate of efficiency (18%) of use of ME for its production gives an ME requirement of approximately 130 kJ g^{-1} or 650 kJ day^{-1} for a daily wool growth of 5 g.

The preceding principles are also used to estimate ME requirements for pregnancy. For this calculation AFRC (1993) estimated energy retention in the conceptus, E_c (MJ day^{-1}), to be $0.25W_o$ ($E_t \times 0.07372e^{-0.00643t}$), reflecting the exponential nature of fetal growth. In this equation, t is the number of days from conception, W_o is the total weight (kg) of lambs at birth and E_t is obtained from the relationship $\log_{10}(E_t) = 3.322 - 4.979e^{-0.00643t}$. Again, dividing these estimates for energy gain in the conceptus by k_c, the efficiency of ME utilization for conceptus energy gain, provides estimates of the ME requirements for pregnancy. AFRC (1993) took a standard value for k_c of 0.13 but there is evidence that, as for k_m and k_f, k_c varies with the metabolizability of the diet (Robinson *et al.*, 1980), with the regression coefficient of k_c on q_m being 0.53, i.e. intermediate between the values for k_m and k_f. For energy requirements in lactation, *see* **Ewe lactation**.

AFRC (1993) based protein requirements on metabolizable protein (MP), in which MP = 0.6375(MCP + DUP), where MCP = microbial crude protein and DUP = digestible undegraded feed protein. Requirements of MP are estimated to be $2.1875W^{0.75}$ g day^{-1} for the maintenance of growing lambs and $2.1875W^{0.75} + 20.4$ g day^{-1} for adult ewes. For growth, MP is estimated to be used with an efficiency of 59%. In the AFRC (1993) system this gives a requirement for males and castrates, including the requirement for wool, of $(334 - 2.54W + 0.022W^2) \times \delta W + 11.5$ g day^{-1}, where δW = daily liveweight gain (kg) and W = liveweight (kg). For females the coefficients for W and W^2 are 4.03 and 0.036, respectively. Pregnancy requirements, according to AFRC (1993), are based on an efficiency of utilization of MP for conceptus protein gain of 85% and are estimated to be $0.25W_o(0.079\ TP_t \times e^{-0.00601t})$ where t = days from conception, W_o = total lamb birthweight (kg) and TP_t is obtained from the relationship $\log_{10}(TP_t) = 4.928 - 4.873e^{-0.00601t}$. For comparisons with the principles involved in the NRC (1985), INRA (1989) and CSIRO (1990) feeding systems, see Sinclair and Wilkinson (2000). *See also* **Ewe lactation**.

AFRC (1991) used the preceding principles for estimating the requirements for the major mineral elements calcium and phosphorus, but linked them to energy intake, the major determinant of animal performance. For growing lambs the AFRC (1991) estimates for calcium requirements increase from 0.7 g day^{-1} for a 20 kg lamb maintained on a diet of q_m 0.5, to 4.0 for the same lamb gaining 200 g day^{-1} on a diet with a q_m of 0.7. The latter value rises to 5.4 g day^{-1} at the higher growth rate of 300 g day^{-1}. Corresponding values for phosphorus are 0.5, 2.5 and 3.7 g. During pregnancy, estimates of daily calcium and phosphorus requirements (g) for a diet with a q_m of 0.5 fed to a 40 kg ewe carrying a single fetus increase from 1 to 3.6 g for Ca and from 1.1 to 2.8 for P over the last 12 weeks of pregnancy. For a 75 kg ewe with twin lambs and receiving a higher quality diet (q_m = 0.7), the corresponding values for Ca are 1.2 and 6.9 and, for P, 0.8 and 3.5 g. (JJR)

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Sheep feeding There is a wide variation in both the productivity of sheep systems and the quality of the feed resources that they utilize. Thus the practical application of feeding strategies involves matching flock requirements with the availability of feeds. As a result of the ability of sheep to digest and utilize feed of widely different quality, there is considerable latitude in the choice of feeds. Factors that govern this are nutrient requirements in relation to appetite, the cost of feedstuffs relative to their nutrient content, the ease of transport and handling of feeds and how well forage conservation during times of surplus can be accommodated within the production system in order to provide for times of feed deficit.

For grassland flocks in temperate regions, nutritional management during the **grazing** season is based on sward height. In the case of spring-lambing ewes and their lambs grazing high-quality pasture (organic matter, OM, digestibility 75–80%) there is no benefit, in terms of lamb production, from feeding cereal-based supplements when sward height exceeds 3 cm (Treacher, 1990). Above this level of availability of a highly digestible pasture, substitution rates (i.e. the reduction of herbage intake per unit of supplement) are large (> 0.9 g OM g^{-1} herbage OM), thereby cancelling out the ability of additional starch-based concentrate feeds to boost the ewe's energy intake. Oddly, despite the high crude protein content of pasture (about 17% of dry matter), substitution rates are much lower and ewe milk yields and lamb growth rates significantly higher when protein-based, rather than starch-based, concentrates are given, particularly when the protein source is high in rumen undegradable protein (Penning *et al.*, 1988). The same is true for 6-week-old lambs weaned on to either ryegrass or clover pastures even though, in the case of clover, its crude protein content appears to exceed requirements (Robinson, 1990).

As the grazing season progresses and both the ewe's milk yield and the digestibility of her

The nutritional management of grazing lambs is based on sward height.

grazings decline, a gradual increase in pasture height from 3 cm to 6 cm is required, to minimize the seasonal decline in lamb growth rates. Following their weaning at 12–16 weeks, the growth of those lambs that have not been marketed for meat is particularly sensitive to herbage availability. If the aim is to ensure that these animals gain weight, sward heights should be increased to above 5 cm. At this point further increases in lamb growth rate can be achieved by again providing a small amount of a protein-rich concentrate. Alternatively, if the aim is to arrest the growth of the lambs for later marketing, the adoption of lower pasture heights and higher stocking densities is indicated. Subsequent realimentation of these animals in preparation for feeding for slaughter is best achieved by giving them, for a 2-week period, a diet rich in a high quality rumen undegraded protein such as that supplied by fish meal (Ørskov, 1987). This ensures repletion of body proteins lost during the period of growth arrest, thus allowing the lambs subsequently to achieve normal growth on the lower-protein diets recommended for the pre-slaughter period.

When, through delays in marketing, lambs become overfat, making them unacceptable to the meat industry, dietary manipulations can be used to bring their body composition into line with carcass specifications. The procedure involves reducing their energy intake to just under **maintenance** needs by, for example, the feeding of barley straw to appetite while at the same time providing them with about 2 g day^{-1} kg^{-1} body weight of a high quality rumen undegraded protein. This feeding regimen is highly effective in reducing the fat content of the carcass, while at the same time promoting the growth of lean tissue (Vipond *et al.*, 1989).

After their lambs are weaned and prior to remating, ewes usually have to replace body fat reserves lost during lactation. Achieving target body condition scores at mating involves adjusting stocking densities and pasture availability or, where pastures are inadequate, the provision of conserved forage with or without energy and protein supplementation. Where sward heights and green leaf masses are above 3 cm and 100 kg ha^{-1}, respectively, voluntary intake of herbage energy equates to 2–2.5 × maintenance in ewes of body condition score 2 (Treacher, 1990). This means that approximately 2 months are required to bring their body condition up to the optimum of 3–3.5 for maximum ovulation rate. If supplements are required, it is best to provide them in the form of high quality conserved forage or as small amounts of fibrous concentrates (e.g. sugarbeet pulp or whole oats) that are slowly fermented in the rumen. This avoids the risk of acidosis and its accompanying adverse effects on the oocyte and early embryo (McEvoy *et al.*, 2001). Whole lupin grains are also a useful supplement for enhancing ovulation rate, particularly as their beneficial effect is expressed following a relatively short pre-mating period (about 1 week) of supplementation (Nottle *et al.*, 1990).

Although conserved forages can be used to improve ewe nutrition and body condition premating, they are mostly reserved for the peak nutrient demands of late pregnancy and early lactation. Where ensiling is used as the conservation method, care must be exercised to avoid soil contamination of the herbage during the harvesting process as this can lead to listeria-induced abortions and ewe deaths. For this reason, many sheep producers prefer to conserve forages by drying. This has the added advantage that voluntary intakes of hays are higher than of silages that have a similar nutritive value but, when supplemented with cereal-based concentrates, hay intakes decline more rapidly than those of silage (Robinson, 1990b).

Home-grown cereal grains for on-farm mixing with high quality protein balancers are widely used for supplementing conserved forages during late pregnancy and early lactation. In the case of pregnancy, they can be given at a constant level along with free access to forage or in gradually increasing amounts in proportion to fetal growth. Unless conserved forage is in the form of silage, there is no need to process the cereal grains, as the losses of whole grains in faeces are usually < 5%, which is the approximate cost of processing the grains. Even for silages, the extent of the comminution of the grains should be minimal in order to reduce the detrimental effects of their rapid fermentation in the rumen on the growth of the cellulolytic bacteria and thus on fibre digestion and forage intake. For lambs abruptly weaned on to all-concentrate diets at

5–6 weeks of age, there is the additional advantage that feeding cereal grains whole reduces the incidence of unacceptable soft fat in their carcasses (Ørskov, 1987). The preferred cereal grains for these early-weaned lambs are barley, maize and wheat. Because of their high content of husk, oats are unsuitable for feeding whole. Their undigested husk component remains in the rumen for an extended period, restricting the intake of digestible energy, and consequently their growth rate, to about 60% of that obtained using the other cereal grains. (JJR)

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Sheep meat The edible component of sheep carcasses. It is usually classified by age of animal into lamb (up to approximately 8 months), hogget (approximately 8 months to 2 years) or mutton (> 2 years).

Pre-cooked presentation to the consumer can be as chilled whole carcasses to be barbecued intact or to be cut into joints (hindlegs, loin, shoulder, breast, shank, flank and neck, in declining order of value) and portions (chops, cutlets, mince, etc.). These joints and portions may be cooked and used immediately or stored frozen (–20°C) for subsequent thawing and cooking.

Reducing the fat content of sheep meat is a major goal. This can be achieved by slaughtering at lighter weights, using breeds that are known to have a high lean:fat ratio in their carcasses or by selecting sires within a breed that have a high index for lean tissue growth. The most commonly used method for estimating the composition of the carcass of a live animal to be used for the breeding of slaughter lambs is ultrasonic scanning. By giving information on fat and muscle depths over the lumbar region, the procedure provides an index of the lean meat in the carcass.

The nature of the carcass fat is also important. High dietary intakes of processed cereal grains result in fat that is high in branched-chain fatty acids, which makes it soft and unacceptable to the consumer. (JJR)

Shell-less eggs: *see* Egg formation; Eggshells

Shellfish Shellfish are generally considered to include all edible marine and freshwater invertebrates that have some sort of external or internal shell. In addition to the molluscs, they include crustacean groups such as shrimps and prawns, crabs, lobsters and crayfish, as well as planktonic krill, which are normally considered to be the food of the great baleen whales. Sea urchins are also considered to be shellfish by reason of their calcareous tests.

Crustaceans in particular have been the subject of important fisheries. Total landings of shellfish exceeded 5.7 million tonnes (Mt) in 1998, of which 47% was shrimp and 17% crabs. Many species are now being cultivated

intensively; landings in 1998 exceeded 1.2 Mt, principally of shrimp. Some tropical marine shrimps are cultivated traditionally by allowing naturally spawned juveniles to enter lagoons which are then sealed from the open sea. The shrimp are then fed until such time as they are large enough for harvest. Hatchery technology has developed to the point that some crustaceans can be cultivated independently of wild larval production. Freshwater species are also cultivated. Technology is now being developed for the culture of lobsters, crayfish and crabs. (DJS)
See also: Mollusc culture; Molluscs; Sea urchins; Shrimp

Shellfish culture Shellfish, principally molluscs and crustaceans, have been cultivated for centuries. In some cases, such as the marine shrimp and prawn, people have taken advantage of natural seasonal migrations of the species by trapping naturally spawned larvae in shallow lagoons and estuaries. The young shrimp are allowed to feed naturally until they are of harvestable size.

People have also captured naturally spawned spat of molluscan shellfish species such as mussels and oysters and retained them on the seabed, or on artificial structures, where they grow naturally until they can be harvested. Scallop seed are now being captured and grown in nets or cages to a size where they are less vulnerable to predation and are then released back on to the seabed for further natural growth before being harvested by traditional fishing techniques.

The development of hatchery and nursery technology now allows some species, both crustaceans and molluscs, to be cultivated from the egg stage through to market size. This has opened opportunities for selective breeding and the enhancement of desirable market qualities, and the culture of the species beyond its normal range.

While shellfish culture has made extremely rapid strides, it has also been accompanied in some places by serious problems of disease which plague some segments of the industry. The cultivated tropical shrimp industry has also caused environmental degradation, which is only now being rectified. (DJS)
See also: Mollusc culture; Shellfish

Shells: *see* Eggshells; Oyster shell

Short-chain fatty acids Saturated fatty acids with chain lengths from two to six carbons. They include acetate ($CH_3{\cdot}COO^-$), propionate ($CH_3{\cdot}CH_2{\cdot}COO^-$), butyrate ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$), valerate ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$) and caproate ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$). With the exception of caproate, all are end-products of fermentation. (NJB)

Shrimp Shrimp are related to other animals with jointed appendages such as insects (Phylum Arthropoda) but are further characterized by a hard shell or exoskeleton (Subphylum Crustacea). Grouped with other large crustaceans (Class Malocostraca) such as lobsters and crabs, they have the five pairs of walking legs but lack the large pincers and their body tends to be laterally flattened. The abdomen or shrimp 'tail' makes up about half the body and is filled with muscle. This muscular tail can be contracted suddenly to escape from danger. The high demand for shrimp tail meat stimulated the development of culture techniques for marine shrimp in the early 1970s. Shrimp aquaculture has grown rapidly and now produces almost a billion tons of shrimp each year. (DEC)
See also: Crustacean feeding; Prawn

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Shrimp aquaculture now produces almost a billion tonnes of shrimp each year.

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Shrimp culture: *see* Shellfish culture

Silage Ensilage originates from the Greek *en* (in) and *siros* (pit), with the product being called silage. Silage making is an anaerobic fermentation process and if silage is well made the predominant acid is lactic acid, with lesser amounts of acetic, propionic and butyric acids. Silage has become one of the main methods of storing green nutritious fodder in times of plenty for feeding ruminants and horses when feed is scarce. A wide range of crops and by-products can be ensiled and a brief but by no means exhaustive list follows: grasses, including ryegrasses (*Lolium* spp.), cocksfoot (*Dactylis glomerata*), timothy (*Phleum pratense*), fescues (*Festuca* spp.) and brome grass (*Bromus* spp.); legumes, including clovers (*Trifolium* spp.), lucerne (*Medicago sativa*), sainfoin (*Onobrychis viciifolia*), peas (*Pisum sativum*), beans and vetches (*Vicia* spp.) and lupin (*Lupinus* spp.); brassicas such as kale, turnip, mangolds, rape (*Brassica* spp.) and radish (*Raphanus sativus*); whole-crop cereals such as maize (*Zea mais*), barley (*Hordeum* spp.), sorghum (*Sorghum vulgare*), wheat (*Triticum sativum*) and oats (*Avena sativa*); and by-products of sunflowers (*Helianthus annus*), potatoes (*Solanum tuberosum*), sugarbeet (*Beta vulgaris*), sugarcane (*Saccharum officinarum*) and citrus fruits. The type of crop ensiled has a significant impact on silage composition. For instance, legume silages are high in true protein and low in metabolizable energy, and vice versa for whole-crop silages. With grasses, the more mature the crop is at harvesting, the lower will be the digestibility and crude-protein concentration.

There are two key parameters that give an indication of crop ensilability: the concentration of water-soluble carbohydrate (WSC) and the buffering capacity (BC). The WSC is fermented by lactic acid bacteria to lactic acid, which preserves the forage. Thus the higher the WSC concentration, the easier a crop will be to ensile. The BC is the ability of the crop to neutralize the lactic acid. The higher the BC, the greater is the acid requirement to lower the pH. The BC is related to the amount of protein in the forage. Low-protein crops generally have high WSC levels and vice versa. Legumes, with high protein contents, have a high BC but low WSC concentrations and are more difficult to ensile than, say, a whole-crop cereal with a low protein content and a high WSC level. However, successful ensilage of the legume can give large benefits in terms of the nutritive value of the protein conserved for animal feeding.

The process of ensiling starts when the

Whole crop maize (*Zea mais*) makes a palatable, high energy silage.

crop is tightly packed into a container and sealed to prevent the access of oxygen. Provided that forage is packed tightly, sealed quickly and maintained in an oxygen-free environment, silage fermentation should proceed and a stable product result. The container can, in reality, be anything, as long as it is clean and can be sealed to prevent the ingress of air. The advent of polythene has widened the scope of shape, size and form of silo.

Four main silos are commonly used.

1. Clamp or pit. These types of silo are the most common permanent structures. They consist of two side walls and usually a back wall and they can be made of earth, wooden sleepers or concrete. Herbage is packed into the silo in thin layers (ideally no more than 30 cm at a time) and consolidated. The layers are built up and finally sheeted with polythene and sealed. The polythene sheet is weighted down with tyres or sandbags to minimize air ingress.
2. Bales. These are placed into polythene bags or wrapped in polythene film.
3. Towers. These are tall cylinders built of concrete or steel, typically 5 m in diameter and can be 20 m high. They are an ideal way of making silage as there is minimal air exposure. However, if the herbage is not wilted sufficiently then the extreme weight can cause problems at the base of the structure.
4. 'Sausage'. This is a polythene sausage, typically 2.4 m in diameter and of variable length up to 30 m, that is sealed at one end, packed by a silo packer machine and subsequently sealed at the other end.

Once the material to be ensiled has been sealed in the silo, the in-silo processes begin. There are four main phases.

Aerobic phase

Residual oxygen trapped in the silo during packing is removed by plant respiration or by aerobic microorganisms present on the plant material at ensilage. Oxygen is depleted from the silo within a matter of minutes provided that further ingress of air is inhibited.

Fermentation phase

This can take from 2 days up to a month to complete, depending on factors such as crop type, crop dry matter and whether an additive was applied. Initially two bacterial populations develop: the undesirable enterobacteria group of Gram-negative, facultatively anaerobic organisms producing mainly acetic and formic acids, ethanol, carbon dioxide and hydrogen; and the desirable lactic acid bacteria (LAB), which are Gram-positive facultatively anaerobic organisms that are either homofermentative, producing solely lactic acid from hexoses, or heterofermentative, producing a mixture of predominantly lactic and acetic acids from hexoses. The LAB will dominate in the production of a good silage. At pH 6, both enterobacteria and LAB can grow and produce lactic and acetic acids. As the pH falls the enterobacteria die out, while within the lactic acid fermentation there is a succession from the *Lactococcus* and *Enterococcus* spp. at the more neutral pH range to the *Pediococcus* and *Lactobacillus* spp. at the more acid pH range. Provided that there is sufficient available energy, the fermentation will continue down to a low enough pH (*c*. pH 4 or below, depending on crop type and dry matter) to remain stable. However, if the pH does not fall below approximately pH 4.2, depending on dry matter (DM) content and crop type, the enterobacteria continue to grow and ultimately saccharolytic clostridia can increase in number. These organisms convert lactic acid into butyric acid, which results in a rise in pH followed by growth of the proteolytic clostridia that deaminate protein and amino acids. The end-product of such a fermentation is a noxious-smelling unpalatable silage. A rapid fermentation to a low pH brings about a better silage quality because it inhibits detrimental biochemical changes more rapidly. The rate is affected by many factors but most significant is the make-up of the natural flora, which in turn is affected by the cleanliness of the silo and the herbage being ensiled. Clean crops result in lower numbers of undesirable bacteria. However, even a natural flora of predominantly LAB can contain many organisms that are not efficient at carrying out a rapid silage fermentation and so by inoculating the silage the silo is swamped with the best type of silage-fermenting bacteria.

Stable phase

This occurs between the end of fermentation and feed-out. Provided that anaerobic conditions are maintained, and a sufficiently low pH within the silage mass has been obtained, then few if any changes occur.

Aerobic feed-out phase

This applies predominantly to silage produced in clamps; it is less important for silages made by other procedures in which air ingress at feed-out is less problematic. Once the clamp has been opened the silage face becomes aerated and spoilage organisms, particularly yeasts, moulds and acetic acid bacteria, can proliferate. If yeasts (in grass and whole-crop silage) and acetic acid bacteria (in whole-crop silage) have survived the ensiling phases and the silage has been poorly compacted, then fermentation of lactic acid and residual sugars to acetic acid occurs, resulting in a rise in pH and silage heating. The rise in pH enables secondary colonizers such as moulds to grow and so composting begins and there is great loss of nutritive value. Ironically, high quality silages are more prone to aerobic deterioration and poor quality silages with high concentrations of acetic and butyric acids are unlikely to deteriorate aerobically. (DD)

See also: Volatile fatty acids (VFAs)

Key reference

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Silage additives Four categories of material are added to silage to improve crop preservation and feeding value, or to reduce silage losses.

1. Fermentation stimulants to promote rapid lactic acid fermentation. They can be inoculants containing lactic acid bacteria from the genera *Lactobacillus*, *Pediococcus*, *Lactococcus* and *Enterococcus*, which convert forage water-soluble carbohydrate into lactic acid, or enzymes, cellulases, xylanases, hemicellulases, pentosanases and amylases, which release water-soluble carbohydrates from forage polysaccharides. These enzymes are often applied alongside inoculants and are frequently called biological additives. Alternatively, carbohydrate-rich by-products such as sugarbeet pulp, citrus pulp and molasses may be added as energy sources to promote the activity of epiphytic lactic acid bacteria.

2. Fermentation inhibitors to inhibit microbial growth. These may be sulphuric, hydrochloric, formic or benzoic acids, which work by direct acidification, or other chemicals with antimicrobial activity such as formaldehyde, sodium nitrite, sodium chloride, sodium hydroxide and ammonia. Clostridia phages are viruses that inhibit clostridial growth.

3. Absorbents to retain silage effluent in the clamp and avoid environmental pollution. These are often by-products such as straw and sugarbeet pulp, but can include rolled barley, polymers and bentonite.

4. Inhibitors of aerobic deterioration. These include long-chain organic acids such as propionic and caproic acids, or salts of sulphite or benzoate, or bacteria with anti-fungal end-products such as *Propionibacteria*, *Bacillus* or *Serratia*.

Additives were traditionally used as an insurance against poor ensiling conditions. More recently additives, and particularly inoculants, have been shown to improve animal performance under ideal ensiling conditions. (DD)

Silage effluent The juice that flows from low dry-matter silage. Silage effluent can range from 0 to 250 l t^{-1} herbage ensiled, depending on the herbage dry-matter content. Environmental pollution from silage effluent in watercourses is attributed to its high biochemical oxygen demand in the range 12,000–83,000 mg O_2 l^{-1}. In the initial stages of fermentation the composition of effluent reflects that of the cell sap of the ensiled crop. The predominant change is the disappearance of soluble carbohydrates and the production of organic acids, mainly lactic acid, in well-fermented silages. The ranges in composition reported for major constituents are (g l^{-1}), 6–110 dry matter; 0–26 lactic acid; 0.5–6.5 acetic acid; 1–31 water-soluble carbohydrate; 1–5 total nitrogen; 2–22 total ash. Much of the total N is in the form of non-protein nitrogen but significant quantities of nutritionally important amino acids have been reported. Mineral elements are found in effluent in the same proportions as in herbage but their concentration in dry matter is higher.

Potassium (1–8.5 g l^{-1}) and calcium (0.2–3.6 g l^{-1}) are the predominant elements but significant quantities of manganese, copper and zinc have also been reported. (RJ)

Silica Silicon dioxide (SiO_2), the main component of sand or glass. (PGR)

Silicon Silicon (Si) is a non-metallic element with an atomic mass of 28.086, and is one of the most abundant elements in the earth's crust. Earlier studies in laboratory animals suggested that silicon might be an essential nutrient but those studies have not been validated. Some of these studies indicated that silicon is associated with connective tissue and bone metabolism, because animals fed diets low in Si had less bone collagen and hexosamine content than animals fed higher amounts; however, bone mineral content and animal growth were not affected. No dietary Si requirement has been set for any of the farm animal species. (PGR)

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Simulation models Mathematical models of a system that describe the nature and behaviour of the system in terms of its component parts and the interaction between these parts. Also called mechanistic models, in contrast to empirical models, which describe a system purely in terms of external measurements made on the system. In practice, most models are developed using some knowledge of the inner workings of the system and are tested and modified based on data obtained from measurements on the system itself. Therefore most models contain both mechanistic and empirical aspects.

The core of any simulation model is the specified state of the system under investigation. The state is usually described by a number of state variables, which are measurements of components of interest in the system. As an example, suppose there is an interest in predicting the energy requirements of a farm animal. Various state variables could be considered to describe the state of the animal: measurements of its weight, shape and carcass composition, feed composition, and its ambient environment. With the goal of predicting energy requirements, a small subset of these may be chosen. For example, the weight of protein and lipid in the body are two state variables that allow calculation of the energy required for maintenance of the body and its further growth. To this should be added the energy expended through heat loss, which can be calculated from a further two state variables: the surface area of the animal, and the ambient temperature. A crucial decision for the modeller is what small set of state variables, representing the most relevant aspects of a typically very complex system, should be selected for the model. In the example above, state variables describing feed composition, which may be used to predict energy lost through waste, have been omitted. The energy requirement model described above is static. Relationships are specified between state variables and model predictions, but there is no specification of how these relationships may change with time. Simulation models with a time dependence are called dynamic.

Dynamic models usually contain some feedback mechanism: the rules governing how state variables change over time may depend on the current values of those variables. For example, suppose that the above model is expanded by predicting feed intake itself based on the predicted energy requirement of the animal in its current state. The animal's feed intake will determine its growth, and how its protein and lipid weights and body surface area will change over time. Changes in these state variables will feed back into changes in energy requirements and hence feed intake. Dynamic simulation models often consist of a set of state variables, together with a set of differential equations that describe the evolution of these variables and their iteration over time. A growth curve such as the Gompertz (*see* **Growth equations**), which is derived from differential equations, is a simple example of such a model. In simple examples such as this, the differential equations can be solved exactly, yielding an equation or set of equations predicting the behaviour of the system over time. More typically, no analytic solution is available. In this case the behaviour of the system over time can be predicted computationally, predicting values of the state variables step by step over small increases in time.

Simulation models may be further classified into deterministic and stochastic models. The state variables of a deterministic model are assumed to be known exactly. The predicted evolution of a dynamic, deterministic model is also assumed to be exact. Of course, state variables cannot usually be measured exactly, and their evolution is usually based partly on the influence of unmeasured factors external to the model. Stochastic simulation models introduce random variation into the state variables themselves and their predicted change over time, in order to model this uncertainty. Stochastic models may therefore be used both to predict and to estimate the uncertainty of these predictions. This estimate of uncertainty is particularly useful when there is an economic value associated with the predictions of the model. Predictions are usually obtained from stochastic models using computational Monte Carlo methods. Statistical distributions are specified on the state variables. Values are drawn randomly from these distributions and predictions are obtained for the model under this state. Values are drawn again from these distributions, predictions are obtained, and the process is repeated many times, yielding a range or distribution of model predictions. Simple measures of predictive uncertainty (for example, the standard deviation of this distribution) can then be obtained.

The energy requirement model as presented above is deterministic. A stochastic element may then be introduced by assuming a distribution of carcass compositions for the animal, rather than a particular composition, and predicting from this a distribution of energy requirements. This is therefore no longer a model of an individual animal, but rather of a typical animal drawn from a population with this distribution of body compositions. The distribution of predicted requirements for the population as a whole can then be obtained.

Many examples of simulation models exist, from simple relationships to complex interactions between variables. Some of the more complex simulation models include the prediction of the timing of egg laying, taking account of the hen's internal cycle length, the external cycle length to which she is being subjected, and the rate at which follicular maturation occurs; some models account for unconstrained and constrained growth in which information about the animal, the feed and the environment are integrated (*see* **Growth models**); rumen digestion and metabolism have been modelled, as has the depletion of lipid reserves in cattle to assist in meeting the energy requirements for lactation. The reputation of simulation models varies considerably. Mechanistic models are more respected than those based purely on empirical relationships of correlation and association between two or more variables that imply nothing about the underlying mechanisms controlling the operation of the system. However, most mechanistic models ultimately rely on empirical relationships at, for example, the cellular level.

Through the integration of simulation models with relevant economic inputs, systems may be not only modelled but also optimized. The objective function chosen could be any one of a number of the output variables simulated by the model, and with the use of suitable optimization techniques this function could be either maximized or minimized, thereby making the model more useful for management purposes. (RG)

See also: Mathematical models

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Sinapic acid A hydroxycinnamic acid derivative that occurs in woody angiosperms worldwide. Part of the biosynthetic pathway of lignin, sinapic acid is dehydrogenated to the corresponding sinapyl alcohol, a primary substrate for peroxidate-catalysed oxidation. Free radicals are generated by peroxidase activity and condense to form **lignin**. Lignin greatly reduces the digestibility of cell wall carbohydrates. (JAP)

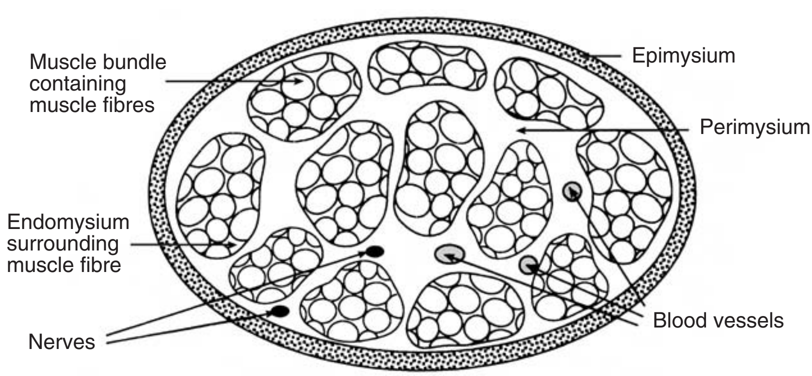
See also: Cinnamic acid

Single-cell protein A generic name for protein derived from algae, yeasts, fungi and bacteria grown on a multitude of substrates, including carbohydrates, ethanol, methanol, mineral oils and their by-products and other organic waste materials. The crude protein content is 400–800 g kg^{-1} but up to 25% of the nitrogen (considered as crude protein) is nucleic acid nitrogen. Despite this, amino acid contents are high and digestibility coefficients in pigs are about 0.8. Crude protein digestibility in poultry is 0.5–0.6, due to the excretion of nucleic acid nitrogen as uric acid. The apparent metabolizable energy values are 12–16, depending on the type of single-cell protein and the animal consuming it. Inclusion levels in diets are normally less than 100 g kg^{-1}. (TA)

Skatole 3-Methyl-H-indole, C_9H_9N. Skatole is formed from the amino acid **L-tryptophan** by intestinal bacteria. Indole, 2,3 benzopyrrole (C_8H_7N), is also produced by fermentation of L-tryptophan. Both are responsible in part for the odour of faeces. (NJB)

Skeletal muscle Striated muscle having fibres connected at one or both extremities with the bony skeleton of the body, i.e. the axial and appendicular muscles. The major function of skeletal muscle is the generation of force or the performance of work in the form of movement or support of the skeletal structures. The outstanding property of muscle is therefore contractility. Skeletal muscles, both avian and mammalian, contain the contractile proteins actin and myosin, whose filaments are arranged in an interdigitated pattern, giving rise to the 'striated' appearance. Muscle cells also contain the regulatory contractile proteins troponins I, C and T, tropomyosin and α-actinin. Skeletal muscle contraction is generally initiated by the arrival of an excitatory electrical signal at the neuromuscular junction which is transduced into the physical interactions between the contractile proteins. This process by which muscle membrane depolarization is linked to contraction is known as excitation–contraction (EC) coupling.

Skeletal muscle fibres can be broadly divided into three different categories of twitch muscle fibres: types 1, 2a and 2b. Many muscles are mixed in nature in that they have varying proportions of the different muscle fibre types but one particular type may predominate, depending upon the muscle's primary function. Type 1 fibres are termed slow oxidative and possess many mitochondria (oxidative), have high myoglobin contents (red), high capillary densities, small fibre diameters, low glycogen storage, slow contraction rates and a tonic contractile action. The speed of contraction is due to the presence of a myosin isoform that hydrolyses ATP very slowly, resulting in a slow cross-bridge formation cycle. Such muscles are very efficient for slow repetitive movements or for sustaining isometric force, e.g. in the maintenance of posture. Thus muscles such as trapezius (shoulder) and soleus (leg) which are active a great deal of the time tend to have a very high proportion of type 1 fibres.



Diagrammatic representation of cross-section of a skeletal muscle.

Type 2a fibres are fast oxidative-glycolytic. These 'reddish' fibres are intermediate between the other fibre types in terms of their capillary density, fibre diameter, mitochondrial numbers and glycogen storage. They have high myoglobin contents and fast, phasic contractile properties. Group 2b fibres are fast glycolytic; these too are fast phasic fibres and, in common with type 2a, possess myosin isoforms and other contractile proteins capable of very rapid ATP hydrolysis and cross-bridge formation. They can thus develop force very quickly and predominate in muscles involved in high power output over a short period (e.g. longissimus in pig, semitendinosus in cattle and pectoralis major in poultry). Type 2b or 'white' fibres have relatively large diameters, are low in myoglobin, capillary density and mitochondria but exhibit high glycogen storage capacities. In meat animals, fibre type has some marked implications for meat quality. Glycolytic fibres, as might be expected, tend to exhibit high post mortem glycolytic rates and thus produce more lactate and have a lower pH_u.

In poultry, genetic selection for desirable production traits has led to differences in fibre-type composition and fibre growth. Thus the modern broiler chicken possesses pectoralis major muscles (breast) composed exclusively of large-diameter type 2b, an observation not made in any other animal. In addition, transformation of small-diameter type 2a fibres to large-diameter type 2b in some selected lines has contributed greatly to increased muscle production. For a description of the nature and pattern of growth and development of skeletal muscle, *see* **Muscle**. (MMit)

See also: Body composition; Growth; Meat composition; Meat quality

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Skimmed milk: *see* Dairy products; Dried skim milk

Skin diseases Nutritional factors in skin diseases include minerals (e.g. zinc) and essential fatty acids. Parakeratosis is a zinc deficiency in pigs, characterized by excessive keratinization of the epidermis with skin lesions and scaling (dandruff). Excessive dietary calcium and dietary phytates provoke zinc deficiency. Pruritus (itching) is a common problem in dogs. A deficiency of linoleic acid causes dry, itchy skin, dermatitis, and an unkempt, lustreless hair coat. Fatty acid supplements containing mixtures of omega-3 and omega-6 fatty acids are effective in treating atopic pruritus in dogs. Evening primrose oil, containing *cis*-gamma linolenic acid (GLA), is also an effective treatment; it promotes synthesis of prostaglandins which have anti-inflammatory properties. Provision of these fatty acid supplements increases dietary vitamin E requirements. (PC)

Slaughterhouse waste Most slaughterhouse waste is further processed for use in other industries to produce meat and bone meal, bone meal, blood meal, feather meal and tallow; however, some unprocessed waste may be fed directly to animals such as mink. Processed by-products have traditionally been used as sources of high quality protein in the feed of all farm species. However, since **bovine spongiform encephalopathy** these practices have now ceased in Europe, with specific exceptions. (MG)

Small intestine The section of the digestive tract between the stomach and the large intestine. It is divided into duodenum, jejunum and ileum and is the principal site of **digestion** and **absorption** of nutrients. (SB)

Smoltification A process in some salmonids of transformation from the juvenile freshwater phase to the seaward migrant phase (smolt). It includes morphological changes (silvering of the scales, lowered condition factor, darkening of paired fins), physiological changes (increased hypo-osmoregulatory capacity; increased levels of cortisol, thyroid hormone and growth hormone) and behavioural changes (development of schooling behaviour, loss of territorial behaviour). Smoltification is under control of temperature and photoperiod. (RHP)

Smooth muscle Smooth muscle lacks the visible cross-striations (the Z lines associated with actin and myosin filaments) of skeletal and cardiac muscle. In smooth muscle, actin fibres are attached to dense bodies in the cytoplasm and to the cell membrane so no repeat striations are apparent. Rather than discrete structures, smooth muscle can be found in sheets as in the walls of the hollow viscera, uterus and ureters or in multi-units such as those found in the iris of the eye. Smooth muscle is characterized by irregular contractions that are not dependent on a nerve supply. (NJB)

Sodium Sodium (Na) is an alkali metal with an atomic mass of 22.9897. Sodium is usually associated with the chloride ion in mammalian systems. They, along with potassium, maintain the electrolyte balance of the body. Sodium is essential in the diet of animals and humans. It constitutes one of the main extracellular ions and helps to maintain water balance. However, the intracellular concentration of Na is quite low. Intestinal absorption of Na is not regulated; simple diffusion accounts for most of that which is absorbed, but Na entry into the cell occurs with the co-transport of glucose and amino acids, and the transport of hydrogen ion. The body balance of Na is controlled through excretion by the kidneys and involves many factors, including the hormones aldosterone, angiotensin, rennin and antidiuretic hormone, as well as plasma Na concentration and renal blood flow.

One of the key roles of Na is the maintenance of an electrical potential across the membranes of all cells. This is accomplished to a great degree by the Na^+/K^+ pump in the membrane that exchanges three Na ions inside the cell for two K ions outside the cell. The Na/K pump is an ATPase and is especially important in the propagation of impulses in muscle and nerve cells. Other ion transporters located in cell membranes involving Na exchange are the Na-H exchanger, the Na-K-Cl co-transporter and the Na–Ca exchanger.

Almost all farm animal feedstuffs have very low Na concentrations and so most animal diets require supplementation with common salt, NaCl. Grazing animals will supplement their own diet either from natural salt licks or from salt blocks provided for them, or sodium fertilizers can be used. The US National Research Council recommends from 600 mg Na kg^{-1} diet for growth to 1000 mg kg^{-1} for early lactation in beef cattle, and 1800 mg kg^{-1} diet for lactating dairy cows, but only 1000 mg kg^{-1} diet for growing heifers and bulls. The Na requirement for pigs ranges from 1000 to 2500 mg kg^{-1} diet, depending on the stage of growth: young growing pigs require more than mature adults. The requirement for poultry is 1500 mg Na kg^{-1} diet, regardless of the age of the birds. For growth and maintenance of horses the requirement is 1000 mg kg^{-1} diet but increases to 3000 mg kg^{-1} diet for working horses. For sheep, the requirement is between 900 and 1800 mg kg^{-1} diet.

Animals that are Na deficient can have depressed plasma Na concentrations; they become lethargic and appear weak and confused. Signs of high Na intake include increased water intake; however, very high intakes can even result in reduced water consumption, probably because of the accompanying anorexia. Cattle have been shown to tolerate as much as 9% NaCl in the diet without ill effect, but sheep have been observed to reduce their food consumption at 10% dietary NaCl. Pigs seem to be more sensitive and cannot tolerate 5% NaCl in their diets without developing tremors and convulsions. There was increased mortality in chickens fed 4% dietary NaCl. (PGR)

See also: Chloride; Potassium

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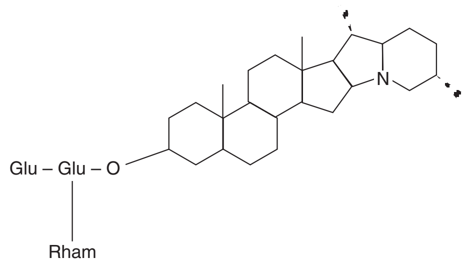
Sodium chloride Common salt, NaCl, molecular weight 58.5, a crystalline white solid, abundant in nature. Widely used as a source of sodium and chloride in animal feeding. Also used to prepare physiological saline (0.9% sodium chloride) with osmolality comparable to that in living organisms. (JAM)

Sodium hydroxide treatment: *see* Alkali treatment

Soil ingestion Soil may be ingested either voluntarily or involuntarily by farm animals. Involuntary soil ingestion occurs mainly in herbivores consuming pasture that is short. The soil may be consumed directly or attached to plant roots, or leaf material when rain has splashed it on to lower leaves or livestock convey it from poached areas of the field on to leaves. Soil may also contaminate harvested root crops for ruminants, such as fodder beet, or it may be incorporated into grass silage when the soil surface is not flat or the mower is set too low. Soil ingested in this way can increase teeth wear in sheep, especially, and the high content of silicon (90% of some sandy soils) may complex essential minerals, such as magnesium, iron and manganese. Most silicon ingested directly is excreted without being absorbed, but that in leafy plants is more readily absorbed and high concentrations of silica in the urine can cause the formation of siliceous calculi and urolithiasis. This condition is most likely if water intake is low and less urine is passed.

Voluntary soil consumption is typically observed in mineral-deficient herbivores, especially in cattle deficient in sodium (*see* **Geophagia**). Apart from minerals, herbivores also consume many microorganisms in the soil, some of which may be beneficial, others harmful. For example, cara inchada, a progressive periodontitis in young Brazilian cattle whose teeth are erupting, is believed to be due to enhanced actinomycete concentrations in newly cultivated land. The actinomycetes produce an antibiotic, which facilitates the attachment of a pathogenic bacterium, *Bacteroides melaninogenicus*, to the gums. Conversely, the consumption of benign soil mycobacteria may protect grazing cattle from developing tuberculosis when they are challenged by *Mycobacterium bovis*. (CJCP)

Solanin (solanine) A glycoalkaloid commonly found in fresh potato sprouts and other *Solanum* species. $C_{45}H_{73}NO_{15}$, molecular weight 868. The glycoside of solanidine may also be classified as a solanum alkaloid.



Solanin is a cholinesterase inhibitor primarily causing neurotoxicity. Solanum alkaloids are also known for teratogenic effects and gastrointestinal tract irritation through inflammation of the intestinal mucosa and ulceration. Symptoms include apathy, drowsiness, salivation, laboured breathing, trembling, weakness and paralysis. (DRG)

Sole A name commonly applied to a large number of flatfishes (Pleuronectidae), frequently as trade names. The more important include: Dover sole, applied to *Solea vulgaris*, an important European species, and to *Microstomus pacificus*, a commercial species on the west coast of North America; lemon sole (*Microstomus kitt*) of Europe; petrale sole (*Eopsetta jordani*), an important North American west-coast species; and grey sole (or witch flounder) (*Pseudopleuronectes americana*), important in the western North Atlantic. Scientifically the name applies to the flatfish family Soleidae of Europe and North Africa, which includes the Dover sole. (RHP)

Solid-state fermentation A microbial fermentation that occurs in a solid medium, in contrast to liquid fermentations such as brewing. Some fungi have evolved to take advantage of multiple food sources. Solid-state fermentation using white rot fungi *Pleurotus florida* is an effective delignifier of brassica haulms that can increase the protein content by 7.8% to produce highly digestible mycoprotein-rich fermented ruminant feed. Oyster mushrooms degrade cellulose in sugarcane bagasse or spent rice straw, trapping and consuming nematodes, which provide additional nitrogen. The addition of oilseed cake to the rice straw can increase fat and protein content of the mushrooms. (JKM)

Solids-not-fat The non-fat solids (SNF) of **milk** are primarily carbohydrate (mainly sugars) and protein. SNF may be determined by difference after lipid and moisture analyses. Milk carbohydrate is predominantly lactose with smaller fractions of glucose, galactose, oligosaccharides and numerous glycoconjugates (glycolipids, glycoproteins, glycosaminoglycans, mucins, etc.).

Methods for carbohydrate determination include enzymatic hydrolysis of lactose and determination of glucose, fractional crystallization and modern chromatographic procedures, including preparative thin-layer chromatography, molecular sizing, affinity chromatography and high-pressure liquid chromatography (HPLC).

The protein fraction of milk consists mainly of casein and whey proteins with numerous minor proteins and enzymes occurring in milk that are derived from either the epithelial cell or from the blood. The other major nitrogen-containing fraction is the non-protein nitrogen, which may represent 4–5% of the total nitrogen. Milk protein concentration is most commonly assayed by the Kjeldhal method. The total nitrogen value obtained by the Kjeldhal method is multiplied by a conversion factor of 6.38 (based on an average nitrogen content of 15.7% in bovine casein and whey proteins). Factors affecting milk solid composition include stage of lactation, environmental temperature, nutritional status, breed differences and seasonal differences. (JSA)

Further reading

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Solubility The tendency of one substance to be taken up homogeneously into another. Examples include solids taken up in a liquid (such as sugar in water, when the sugar loses its crystalline form and becomes molecularly dispersed in the water). Other examples are miscible liquids such as ethanol in water, when the ethanol is distributed uniformly in water, in contrast to immiscible solvents (oil vs. water) where identifiable layers are apparent. Other mixtures can be a gas in a gas (e.g. hydrogen in nitrogen). Solubilities vary from 0 to 100%. (NJB)

Somatotrophin A protein hormone also known as growth hormone (GH). It is produced in an episodic manner by the anterior pituitary gland. It may act directly on the metabolic activity of some tissues through the presence of GH receptors on the cell membrane and indirectly via its stimulation of the production of insulin-like growth factors 1 and 2 (IGF-I and IGF-II) in the liver and peripheral tisssues. Originally extracted and purified from pituitary glands, it is now available in much larger quantities due to the use of genetic engineering to enable bacterial production of human (HST), porcine (PST) and bovine (BST) somatotrophin. In pigs, it has been used to increase growth rate and lean carcass mass. In dairy cows, it is used to increase milk yield by as much as 40%. The use of PST and BST is permitted in North America but not in the EU. (JRS)

Sorbic acid 2,4,Hexadienoic acid, $CH_3{\cdot}CH{=}CH{\cdot}CH{=}CH{\cdot}COOH$. Sorbic acid is found in the berries of mountain ash and can be produced commercially. It is used as a fungicide, in drying oils and as a plasticizer and lubricant. (NJB)

Sorghum Sorghum (*Sorghum bicolor*) is a cereal grain plant of the *Gramineae* (grass) family that originated in Africa. Those sorghums cultivated mainly for their grain belong to the species *Sorghum vulgare*, which includes varieties of grain sorghums and grass sorghums, grown for hay and fodder, and broomcorn, used in making brooms and brushes. Grain sorghums include durra, milo, shallu, kafir corn, Egyptian corn, great millet and Indian millet. Sorghum is especially valued in hot and arid regions for its resistance to drought and heat. It is the main food grain in Africa, Asia and China. It is also grown in the southern parts of the USA, where it is the second most important feed grain.

The plant grows to a height of 0.5–2.5 m and may reach a high of 4.5 m. Stalks and leaves are coated with a white waxy bloom and the central portion or pith of the stalks of certain varieties is juicy and sweet. The grains vary widely in colour, shape and size among different types but they are smaller than those of wheat (about 66% the weight of wheat grains). Kafir sorghums, originally from South Africa, have medium-sized seeds which may be white, pink or red. Milo sorghums, originally from East Africa, tend to be more tolerant to heat and drought than the kafir types and have large seeds, which are pale pink to cream in colour. Feterita sorghums, from Sudan, have very large seeds, which are chalky white. Durra sorghums, from the Mediterranean area and from the Near and Middle East, have large, flat seeds. Shallu sorghums, from India, have pearly white seeds; the plant is late maturing, thus requiring a relatively long growing season. Koaliang sorghums, typically grown in China and Japan, have brown seeds with a bitter taste. Hegari sorghums, also from Sudan, are similar to kafir sorghums and have chalky white seeds.

Nearly all the sorghum grain cultivated in the USA is used for livestock feed. Where used for human food, the grain may be roughly ground and made into bread-like preparations, used after grinding and stewing as a porridge or made into flour for mixing with wheat flour for breads. Varieties with waxy endosperms are a source of starch, having properties similar to tapioca. The grain is used in native beers, particularly in Africa.

The grain or kernel comprises about 84% endosperm (largely starch), 10% germ and 6% bran (pericarp or surface layers). Sorghum contains a similar protein content, at a mean 113 g crude protein kg^{-1} dry matter (DM) to that of wheat and higher than that in maize. Starch concentration ranges from 690 to 761 g kg^{-1} DM and is concentrated in the endosperm, as in other cereal grains. The grain is generally low in fibre (mean 107 g neutral detergent fibre kg^{-1} DM) and contains about 30 g oil (as ether extract) kg^{-1} DM (see table).

In common with maize, sorghum grain is wet-milled to produce starch. The starch is also used in the manufacture of glucose for human use. Starch from ‘waxy’ sorghums is used in adhesives and for sizing paper and fabrics, also in the ‘mud’ used in oil drilling. The grain is also used in grain distilleries and butyl alcohol production. As a livestock feed, sorghum can be grown for grain production, giving sorghum stovers and leaves as by-products, or grown to provide a forage crop that can be fed to livestock as a fresh forage or following conservation as hay or silage. Conservation as hay or silage helps to eliminate the risk of toxicity due to the presence of a cyanogenetic glycoside which, as a result of the enzymatic activity in the gut, releases cyanidric acid. Sorghum grains can be fed fresh to livestock after removal of fibre or ensiled. Stover and leaves may also be ensiled. The nutritive value of the grains is similar to barley grains, while the stover and leaves have a higher nutritional value than maize.

Tannins, which confer resistance to insect and bird damage, are present in sorghum grains. They bind to protein and starch and thereby reduce the availability of these nutrients to the animals consuming them. The depression in digestibility is more marked in non-ruminants than in ruminants, because of the positive effect of rumen degradation. Treatments to reduce the tannin content (seed skinning, flaking, etc.) are not always economically viable. The grains are generally processed by coarse grinding and this is particularly effective for cattle and horses.

Sorghum grains can be used as a substitute for maize grains in dairy cow diets without any detrimental effect on milk but their nutritive value for beef cattle is about 90% of yellow dent maize, mainly due to their lower oil content. Feed conversion ratio for milk and meat production is improved by 0.2 and 0.3, respectively, following the grinding or pelleting of sorghum grains. The grain can be fed to dairy cows or beef cattle at about 500 g per head per day as part of a feed mixture containing other cereal grains, cereal brans, linseed meal and soybean meal. Sorghum is also a useful feed for fattening lambs, with no differences in terms of nutritive value between

Chemical composition of sorghum grain and forages (as g kg^{-1} DM unless stated otherwise).

	DM (g kg^{-1})	CP	EE	Starch	CF	Ash	GE (MJ kg^{-1} DM)
Grain	897	113	30	730	20.1	17	18.7
Grain silage	686	68	–	–	25	12	–
Stover hay	828	57.9	12.7	–	342	140	–
Stover silage	346	55.7	18.2	–	296	112	–

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; GE, gross energy.

the grain and meal. Sorghum can be substituted for maize in pig diets with a relative feeding value of over 0.9; however, it presents some difficulties in ration formulations for poultry owing to its low overall content of pigments, which are particularly important for egg yolk colour.

The energy value of sorghum for ruminants is 13.2 MJ metabolizable energy (ME) kg^{-1} DM, which is comparable to that of barley and slightly lower than that of maize. The energy value for pigs is similar to that of maize and higher than that of barley grain. The energy value for poultry is intermediate between the values for maize and barley. Sorghum harvested as a forage crop can be fed to cattle following the same recommendations as used for maize, and sorghum silage can be substituted for maize silage for beef cattle, but with a nutritive value 15–33% lower. Sorghum stovers are best utilized when tender and juicy and they can be used by livestock of moderate performance levels. (ED)

Sow A female pig kept for piglet production. A young sow during her first parity may also be referred to as a gilt. Each sow will produce 2 to 2.4 litters of pigs per year, depending on length of lactation, for many years. Under commercial conditions, sows are often culled after six litters as maternal performance deteriorates. (SAE)

Soybean The soybean has been cultivated in China for at least 3000 years but is now of global importance with a world production of over 100 million tonnes annually. Soybean products are estimated to be present in about two-thirds of all manufactured food products today. It is equally important as an animal feed. The reason for its success is its high protein content (40% of dry matter, 50% when decorticated), which is the highest protein concentration of all seeds grown for animal feed. The oil content (20% dry matter) is comparatively low but the oil is commercially important. It contains a high proportion of polyunsaturated fatty acids (< 60%), including linolenic and linoleic acids. Soybean products are good sources of iron, calcium, zinc and most of the B vitamins, though when fed to cattle should be supplemented with vitamin A. The oil is used in salad and cooking oils and in non-dairy spreads. As an emulsifier it is used in a variety of food products and it also has a variety of industrial uses. Soya flour contains no gluten: it is used in baking, as a meat substitute, and as a substitute for cows' milk and other traditional dairy products.

Soybeans, usually cracked or ground, can be fed to ruminants without processing but, before being fed to non-ruminants, must be heated to inactivate the trypsin inhibitors present. Urea should not be fed with soybean seeds as they contain urease, which converts the urea into ammonia. Further antinutrients include phyto-oestrogens, which may reduce the reproductive efficiency of some animals, goitrogens (iodine antagonists) and haemagglutinins. If fed in large quantities (20–25%) the carcass fat may be too soft.

Soybean meal or soybean cake, the residue after the oil has been extracted, is an excellent source of protein (up to 57%), with an amino acid profile similar to that of milk. For non-ruminants, the efficiency of digestion of these proteins is impeded as they are bound within the cell wall carbohydrates. Nevertheless, soybean meal is an animal feed for both ruminant and non-ruminant livestock,

including pigs, poultry, horses and fish, and also companion animals. The hulls that remain after the seeds have been decorticated (also called soybean mill feed), are also of use as a fibre-rich addition to the diets of ruminants. (DA)
See also: Antinutritional factors; Digestive enzyme inhibitors; Trypsin inhibitors; Urease.

Spawning The release of eggs and sperm from mature parent fish. Spawning may be allowed to proceed naturally by placing sexually mature males and females together in a spawning container, or fish may be spawned artificially by manually stripping eggs and sperm by manual pressure or injection of air or isotonic fluid into the body cavity. Manual stripping is most easily performed on species (e.g. salmonids) where the ova are shed into the body cavity prior to spawning. In species where the ovarian lumen is continuous with an oviduct, natural spawning may be required.
(RHP)

Specific gravity A physical measure, the weight of a given volume relative to the same volume of water at the same temperature and pressure. Because fat (adipose tissue) is much less dense than lean meat, specific gravity is sometimes used to estimate the ratio of fat to lean meat in a **carcass** by weighing it first in air and then in water. The estimate is somewhat affected by the proportions of skin, bone and muscle in the carcass, and by the mineralization of the bone. (MFF)

Spermidine: *see* Polyamines

Spermine: *see* Polyamines

Sphingolipids Complex lipids containing the basic unit sphingosine (a complex amino alcohol derived from palmitic acid and serine), a long-chain fatty acid, phosphate and choline: it contains no glycerol. Sphingolipids are found in cell membranes and particularly in brain and spinal cord lipids. (DLP)

Spinach *Spinacta olerecea*, a hardy annual vegetable with edible leaves, grown in Europe, the Americas and the Far East. It is suitable for inclusion in ruminant diets and can be fed to dairy and beef cattle at 30% and ewes at 20% of total diet. The dry matter (DM) content of spinach is 90 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 190, crude fibre 100, ether extract 15, ash 105 and neutral detergent fibre 215, with MER 9.5 MJ kg^{-1}. (JKM)

Sprouted grain: *see* Germination

Stability Maintenance of the form and activity of a chemical substance. In animal feed certain components such as **vitamins**, **enzymes** and **unsaturated** fats are liable to become changed in form or function during processing or subsequent storage. The stability of enzymes and vitamins can be improved by encapsulation within a protective layer. The stability of unsaturated fats can be improved by inclusion of antioxidants.
(KJMcC)

Stachyose A tetrasaccharide of galactose-galactose-glucose-fructose, $C_{24}H_{42}O_{21}$, molecular weight 667. Also called lupeose, it is a constituent of the seeds of many *Leguminosae*. It is resistant to the digestive enzymes of animals but is readily fermented by the intestinal microflora. (JAM)
See also: Carbohydrates; Fructose; Galactose; Glucose; Oligosaccharides

Stages of growth Stages of growth are subsets of the overall growth process, usually separated by physiologically significant events such as birth, weaning, puberty and maturity. Almost every description of a stage is an oversimplification. For example, prenatal growth is not a *continuum* of one type of event; the blastocyst (in polytocious species) goes through a repertoire of changes as it stakes its claim on uterine space by rapid elongation. The fetus then becomes a template for subsequent growth and there is a phase in which most tissues and organs are initiated. Postnatal growth is a reflection of the animal's need to achieve functional independence at weaning and reproductive competence after puberty. The initial part of the postnatal growth curve indicates a steadily increasing increment of gain in mass per unit of time, described as the 'self-accelerating phase'. The second feature is that part of the curve in which the change from acceleration to deceleration takes place. This is usually at puberty. The final part of the curve shows a steady decline in the increment of mass gained each day, called 'self-decelerating', until the 'mature' or asymptotic weight is attained. The final stages of growth are degeneration, senescence and death. (VRF)

Stallion An adult uncastrated male horse or pony, normally over 4 years old. In Britain entire males over 2 years old must be licensed.

The stallion is subject to the same seasonal influences as the mare. His fertility is greatest in summer and least in winter. Seasonal changes in blood concentrations of luteinizing hormone, follicle-stimulating hormone and testosterone, and consequential changes in testicular size, sperm production and libido, are functions of changes in photoperiod. Increased fertility earlier in the season may be obtained by increasing the photoperiod artificially and increasing the energy and protein content of the daily feed.

Physical activity of the stallion increases in the breeding season, increasing his energy expenditure. However, at no time should the stallion be allowed to fatten. In consequence, high-fibre balanced feeds are satisfactory when given out of the breeding season in accordance with the equations under '**Horse feeding**'. Proposed minimum nutrient requirements for the stallion are also given under the latter entry but there is little published research work to establish these. (DLF)

Standardized digestibility: *see* Digestibility

Starch A polysaccharide consisting of two main macromolecules: amylose, a linear polymer of α-D-glucopyranose units linked by 1→4 bonds (molecular weight 100,000–600,000); and amylopectin, linear chains of D-glucopyranose linked by (1→4)-α-D linkages with about 5% of (1→6)-α-D bonds at branch points (molecular weight 100,000–1,000,000). After cellulose, starch is the most abundant carbohydrate in plants and the principal reserve substance of most higher plants. Found in high concentrations in cereal grains, pulses and tubers, it is the major dietary energy source for many animals. (JAM)

See also: Carbohydrates; Maltodextrin; Maltose; Maltotriose; Storage polysaccharides

Starch equivalent (SE) The starch equivalent system (developed by Kellner in Germany) can be considered the first widely adopted net energy system. It expresses the efficiency with which 1 kg of feed is used for lipid deposition relative to 1 kg of pure starch. (JvanM)

See also: Energy systems

Starvation Complete or almost complete absence of food for a prolonged period, as distinct from anorexia or malnutrition. This necessitates mobilization of body reserves, resulting in loss of weight, slimming, emaciation and eventual death. After an initial weight loss, the total energy expenditure is similar to that in normal individuals, with a decrease in resting energy expenditure and an increased energy-related physical activity. The time taken to die in the absence of food depends on the size of the animal's body energy reserves in relation to its maintenance requirement. Typically, the smaller the animal, the shorter is its period of survival – from a few hours for a shrew to many weeks for an elephant. Starvation induces a reduction in activity and metabolic rate, which falls to as little as one-half of normal. Blood glucose is maintained at normal levels in non-ruminants so that neural function is initially not seriously affected. However, the ketones produced from fat breakdown, although capable of being utilized by the brain, are toxic and may eventually cause damage to kidneys and other organs. Triiodothyronine, the steroid hormones and leptin, a protein expressed in the adipocytes, are among the most sensitive indicators of starvation. During starvation, all tissues are affected but the adipose tissues of the body are metabolized to the greatest extent, then muscle, bone and finally nervous tissue, thereby protecting the vital organs and tissues during undernutrition. (JMF)

Steam-volatile fatty acids: *see* Volatile fatty acids (VFAs)

Steaming: *see* Heat treatment

Stearic acid Octadecanoic acid, $CH_3 \cdot (CH_2)_{16} \cdot COOH$, shorthand designation 18:0. A saturated long-chain fatty acid found in many animal and some plant fats. Saturated long-chain fatty acids such as myristic acid (14:0), palmitic acid (16:0) and stearic acid (18:0) as triglycerides or mixed triglycerides give rise to what are called hard fats.

(NJB)

Steatorrhoea The passage of excess fat in the faeces, resulting in bulky, pale, foul-smelling, greasy stool. It is frequently a symptom of disease of the exocrine pancreas in which lipase is inadequate to hydrolyse dietary fat, or of biliary disease in which there are insufficient biliary components for the emulsification of digested dietary fat necessary for absorption. It may also involve malabsorption of the fat-soluble vitamins A, D, E and K.

(JAM)

Steroids Steroid hormones are produced by the adrenal cortex and by tissues of the reproductive tract in both sexes. The adrenal cortex synthesizes as many as 50 different steroid molecules, which can be classified as glucocorticoids, mineralocorticoids and androgens. The glucocorticoids are involved in adaptation to stress. The glucocorticoids cortisol and corticosterone are 21-carbon steroids involved in gluconeogenesis. The mineralocorticoids are 21-carbon steroids necessary for maintaining normal Na^+ and K^+ balance. The mineralocorticoid aldosterone is the most potent in this class. Sex steroids are hormones produced by the adrenal cortex, ovaries and testes. Small amounts of testosterone (the male sex hormone) are produced in the adrenal but other tissues produce the bulk of testosterone. The androgen precursor dehydroepiandostrone and the weak androgen androstenedione are also produced in the adrenal cortex. The sterol cholesterol is the starting compound in the biosynthesis of oestrogen and progesterone (the female sex hormones) and of testosterone. Oestrogen is produced by the follicile and has effects on the central nervous system, the mass of uterus and secondary sex characteristics such as the mammary glands. Progesterone is produced by the corpus luteum, placenta and adrenal and facilitates the preparation of the uterus for implantation of the fertilized egg. It is involved in the maintenance of pregnancy and in mammary development. Testosterone maintains the function of the male reproductive tract, spermatogenesis, accessory glands and mating behaviour.

(NJB)

Steroids, anabolic Androgenic (masculinizing) and oestrogenic (feminizing) hormones produced by the testes of the male (testosterone and dihydrotestosterone) and ovaries of the female (oestrogen and progesterone). In steers and heifers, these hormones have an impact on growth by changing the relative rates of protein synthesis and protein catabolism in a coordinated manner among organs, so that the difference is greater, resulting in enhanced growth. Like other steroid hormones they bind to intracellular receptors, travel to the nucleus, bind to DNA and result in the gene-directed production of protein. The commercially produced hormones, oestradiol, zeranol, trenbolone acetate (TBA) and melengestrol acetate (MGA), enhance growth and decrease the proportion of carcass fat and have therefore been used in meat animal production.

(DMS)

Key references

Anonymous (1994) *Metabolic Modifiers. Effects on the Nutrient Requirements of Food-Producing Animals*. National Academy Press, Washington, DC.

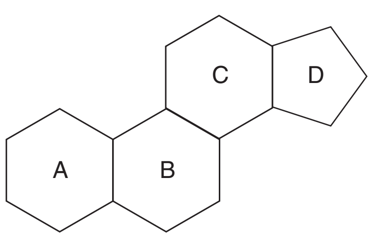
Meyer, H.H.D. (2001) Biochemistry and physiology of anabolic hormones used for improvement of meat production. *Acta Pathologica Microbiologica et Immunologica Scandinavica* 109, 1–8.

Steroids, sex Hormones produced in the testes and ovaries and released into the bloodstream. They promote sperm and ova production, the development of the reproductive tract, secondary sex characteristics, and sexual behaviour. There are three general classes of sex steroids: the androgens, the oestrogens and the progestins. The structures of these classes are derived from the same compound (cholestane; $C_{27}H_{48}$), which is referred to as the Asteroid nucleus. The testis and the ovary produce the androgens androstenedione and testosterone. In the Leydig cells of the testis, androstenedione is converted to testosterone ($C_{19}H_{28}O_2$). Andro-stenedione is also produced by ovarian thecal cells. It is converted by granulosa cells to oestrone or testosterone and subsequently to 17β-oestradiol ($C_{18}H_{24}O_2$). Several other hydroxylated and methylated derivatives of oestrone and 17β-oestradiol are also found. In regard to progestins, pregnenolone is produced in both the ovaries and testes and converted to progesterone. Other hydroxylated forms of progesterone ($C_{21}H_{30}O_2$) are also found in testes and ovaries. (DMS)

Key reference

Brown, T.R. (1999) Steroid hormones. Overview. In: Knobil, E. and Neill, J.D. (eds) *Encyclopedia of Reproduction*, Vol. 4. Academic Press, New York.

Sterols Sterols are based on the four-ring (A, B, C and D) structure of the cyclopentanoperhydrophenanthrene nucleus. If this nucleus has one or more hydroxyl (OH) groups and no carbonyl (C=O) or carboxyl (COOH) groups, it is a sterol. A number of steroids such as cholesterol, bile acids, adrenocortical hormones, sex hormones and the various forms of vitamin D and its metabolites all have structures related to the phenanthrene (rings A, B, and C) but vary in the groups added to the rings, in the unsaturation of the rings or in the addition of side chains. (NJB)



Stomach The shape and relative size of the stomach varies greatly amongst species. The stomach is divided into four regions: the oesophageal, cardiac, fundic and pyloric regions. The oesophageal region is the only part of the stomach lacking secretory cells. This region occupies a large fraction of the stomach of the horse but is very small in the relatively larger stomach of the pig, in which the cardiac region occupies the major part.

The secretory cells produce hydrochloric acid (HCl), enzymes and mucus. HCl is secreted by the parietal cells in the cardia. Hydrogen ions are secreted into the lumen by a process requiring ATP. Chloride ions originate from blood plasma. The concentration of HCl in most farm animals is about 0.1 M and can lower the pH of stomach contents to 2.0 or less. The low pH established by HCl is bactericidal and may kill pathogenic bacteria entering with the food. The low pH also activates pepsin from its inactive pro-form, pepsinogen, and denatures dietary proteins, making them more susceptible to degradation by pepsin. Finally, minerals such as calcium carbonate and phosphates are dissolved. The secretion of gastric juice is controlled by the hormone gastrin, which is secreted in response to the arrival of food in the stomach. In young suckling animals a more specific enzyme, rennin, is secreted rather than pepsin; its action is to clot milk protein.

The gastric epithelium is protected against attack by HCl and pepsin by mucus, which contains various mucopolysaccharides and mucoproteins. The latter also contain the intrinsic factor that aids the absorption of vitamin B_{12} in the ileum.

There are two types of stomach, one in simple-stomached, non-ruminant animals and one in ruminants, which have four stomach compartments: the rumen, reticulum, omasum and abomasum. The latter is the only true gastric stomach and corresponds to the stomach of non-ruminants.

In non-ruminants the function of the stomach is to store food after a meal, mix it with acid, mucus and pepsin and release it at a controlled steady-state rate into the duodenum.

The food is stored in the proximal stomach (cardia and fundus) where little contraction or mixing occurs. This means that the volume of the stomach in this area can easily be increased during a meal. Amylase from saliva as well as active enzymes in the food, e.g. phytases, may still be active when the food is located in this region.

In the distal stomach, the antrum and pylorus, there is intense slow-wave activity. Strong waves of peristalsis begin at about the middle of the stomach and migrate towards the pylorus, through which only particles smaller than about 2 mm can pass.

The rate of gastric emptying is under both nervous and hormonal control and is regulated to match the rate of digestion in the small intestine.

Some non-ruminant species have a forestomach; for example, birds have a crop, which serves as a storage organ in which microbial fermentation may occur together with a continued action of salivary amylase on starch degradation. The true stomach, in which HCl and pepsin are secreted, is called the proventriculus. In avian species, pepsin is ready for secretion at a high level at the first meal after hatching; this meal can be of the same composition as that eaten by adults and is digested efficiently. The proventriculus is followed by the gizzard, which has very strong muscular walls that grind the food. The gizzard compensates for birds' lack of teeth by physically reducing particle size, often with the help of small stones that are swallowed.

In ruminants, the rumen, together with the reticulum and omasum, can be considered as forestomachs to the abomasum. The reticulum moves ingested food into the rumen or omasum and regurgitates ingesta during rumination. The rumen acts as a fermenter with a large population of microorganisms. The omasum has a role in controlling passage of digesta into the abomasum, the true stomach. (SB)

See also: Gastrointestinal tract

Stomach ulcers Stomach ulcers occur commonly in pigs and are also seen in young foals. Abomasal ulcers occur commonly in cattle. In pigs, the aetiology is uncertain but the condition is associated with finely ground pelleted feed, especially when it contains a high proportion of wheat. The more finely ground the feed, the higher is the pH of the gastric contents and the more fluid their consistency. The pars oesophagea of the stomach appears to lack protection from the acid. *Helicobacter*, found to be associated with the condition in human beings, has recently been found in pigs with gastric ulcers but the condition has not been produced experimentally. In young foals, gastric ulcers are associated with inadequate long fibre in the diet. Abomasal ulcers in cattle are also of uncertain cause but stress and a high proportion of cereal in the diet are commonly thought to be factors. Some prevention of gastric ulcers may be afforded by feeding fibrous material. Stomach ulcers cause signs of abdominal pain, blood loss leading to melaena, and occasionally fatal peritonitis following perforation. (WRW)

See also: Gastric ulcers

Storage polysaccharides Polysaccharides used as energy reserves by living organisms. Major examples include starch in most higher plants, fructans in certain plants and glycogen in animals and bacteria. Starch is present in all green plants and in most of their tissues. It accumulates in leaves in the light, where it is used for energy in the dark, and in storage and seed tissues, where it is used during germination. About 15% of higher plants produce fructans as a storage polysaccharide. Glycogen typically makes up 5% of liver weight and 1% of skeletal muscle weight in animals. (JAM)

See also: Carbohydrates; Fructans; Starch

Stover Stover consists of the dry stems and leaves of tall cereal plants (maize, millets and sorghum) after removal of the grain-bearing structures (ear or cob). Stover is either stored for feeding later or grazed *in situ*. In the tropics it is often the major feed resource for ruminant livestock during the dry season.

Stover is low in crude protein (20–30 g kg^{-1} dry matter, DM) and high in fibre (cell walls 700–800 g kg^{-1} DM, consisting of hemicellulose, cellulose and lignin), limiting intake and digestibility, especially when it is the major component of the diet. The most nutritious fraction is the leaf, with stems often being of little value. The nutritive value of stover can be improved by physical treatment

(e.g. grinding to reduce particle size) or chemical treatment (e.g. by the addition of urea to break down ligno-cellulose bonds and add nitrogen). Supplementation with a nitrogen-rich feed (e.g. urea, oilseed residue or legume straw) also improves the intake and digestibility of these materials. As a component of energy-rich diets, stover can provide the fibre necessary for efficient rumen function. (TS)
See also: Straw

Further reading

Sundstol, F. and Owen, E. (1984) *Straw and Other Fibrous By-products as Feed*. Elsevier, Amsterdam.

Straw The dry cut stalks of grain crops. Whereas the term 'stover' is applied to the stalks from tall grain crops, straw refers to the shorter residues of barley, oats, rice, rye and wheat. Straw is either removed from the field at harvest for threshing or remains in the field, after cutting with a combine harvester, usually to be baled before storage. In intensive livestock production systems, the level of inclusion depends upon the production purpose. In extensive systems, especially those in predominantly cropping areas, straw is often the major or sole component of the diet. Straws are high in fibre (cell walls 700–800 g kg^{-1} dry matter (DM), consisting of hemicellulose, cellulose and lignin) and low in protein (crude protein, 20–38 g kg^{-1} DM). The techniques used to upgrade stover are generally successful with straw. (TS)
See also: Stover

Further reading

Sundstol, F. and Owen, E. (1984) *Straw and Other Agricultural By-products as Feed*. Elsevier, Amsterdam.

Structural polysaccharides Nearly all plants and microbes use carbohydrates as major structural materials. Structural polysaccharides in plants include cellulose, pectic substances, β-D-glucans, hemicelluloses and other heteropolysaccharides of diverse sugar composition. Animal connective tissue includes several polysaccharides, e.g. hyaluronic acid, chondroitin sulphates, heparins, dermatan sulphate and keratin sulphate. Bacterial cell wall polysaccharides include peptidoglycan, lipopolysaccharides, teichoic acids (polyol phosphates) and heteroglycans, frequently containing amino sugars or uronic acids in the repeating oligosaccharide units. Fungal cell wall polysaccharides include chitin, β-D-glucans and glycoproteins with a high proportion of mannose. Algal cell walls contain alginic acid, galactans and sulphated galactans, e.g. carrageenans. (JAM)
See also: Carbohydrates; Dietary fibre; Galactan; Hemicelluloses; Peptidoglycans; Uronic acids

Stunting Stunted growth occurs in farm animals as a result of an inadequate supply of nutrients, infection or genetic factors. It is characterized by delayed and retarded early growth of muscles and bone tissue often caused by an inadequate supply of energy, protein and the minerals that are important for bone growth. Stunting usually occurs at an early age, in which case the growth retardation is likely to be permanent. The critical phase when stunting is most likely usually precedes the period of most rapid accretion of body tissues during prenatal life. Small maternal size is also a risk factor. In rodents, substances that block dopaminergic neurotransmission retard brain development and are implicated in stunting. An infectious stunting syndrome is recognized in poultry, usually caused by enteric or respiratory tract viruses, including the avian influenza virus. The disease is characterized by growth retardation, variability in size, leg weakness, diarrhoea and increased mortality. Despite the association with enteric viruses, the growth retardation is believed to be due to disorders of the metabolism, rather than absorption or digestion. (CJCP)

Sturgeon Fish of the family Acipenseridae, characterized by: a heterocercal tail; lack of adult teeth; four barbels in front of an inferior, protrusible mouth; a largely cartilaginous skeleton; and five rows of bony scutes or plates on the body. All species are either freshwater or anadromous. Some species can attain 4–6 m length and approach 500 kg in weight. There are two genera of sturgeons: *Acipenser*, consisting of 16 species distributed around the northern hemisphere; and *Huso*, with two species, kaluga (*H. dauricus*) and beluga (*H. huso*), confined to the Adriatic and Caspian basins and the Amur river. Several species are prized for flesh and for the caviar derived from the roe. In the past the large swim bladder was used in isinglass production.

All species are long-lived (over 20 years) and have slow growth and reproduction rates. Consequently most wild populations have been drastically reduced. Two principal countries of sturgeon culture are Russia and the USA (California). Russia produces about 100 million fingerlings, largely of the hybrid (called bester) between the beluga and the sterlet (*A. ruthenus*) for stocking purposes. California cultures a few hundred tonnes annually of the white sturgeon (*A. transmontanus*), indigenous to western North America, primarily for commercial markets.

Ovulation and spermiation of broodstock are synchronized with the use of carp pituitary injections. Sperm is collected in hypodermic syringes by exerting pressure on the abdomen of the male, and the eggs are removed by Caesarean operation. After fertilization the eggs are mixed with silt to remove adhesiveness. The eggs of white sturgeon hatch in 5 days at 16°C. The young attain 500 g in the first year, 2 kg in 2 years, 4–5 kg in 3 years, and are marketed at about 6 kg in 3.5 years. Production of good quality eggs from domestic females remains a problem, and wild females are still used for much egg production. (RHP)

Substrates Substances that undergo chemical reactions in metabolism (usually carried out with the aid of a catalyst or enzyme) and are converted into products. Thus, a substrate is changed during the reaction whereas the enzyme is not. (NJB)

Succinate A four-carbon dicarboxylic acid, $HOOC{\cdot}CH_2{\cdot}CH_2{\cdot}COOH$. Because it is an intermediate in the tricarboxylic acid cycle, carbon from succinate, $^{-}OOC{\cdot}CH_2{\cdot}CH_2{\cdot}COO^{-}$, can be found in almost all compounds in the body. (NJB)

Sucking The act of withdrawing milk from the mammary gland. Sucking invokes coordinated neurohormonal reflexes resulting in milk ejection and synthesis, and the control of ovulation in many mammalian species, most notably the sow and cow. A reflex action in the sucking baby ruminant forms a channel (the oesophageal groove) that directs milk away from the rumen and directly into the abomasum. (KDS)

Suckle To nurse; to provide milk to a suckling. (KDS)

Suckling A baby animal that is dependent on milk withdrawn from the mammary gland as its principal source of nourishment. Also, the act of nursing, of providing milk to the suckling. (KDS)

Sucrase A glycolytic enzyme (invertase; α-D-fructofuranoside fructohydrolase; EC 3.2.1.26) that hydrolyses the disaccharide sucrose into its constituents, glucose and fructose. Sucrase is attached to the brush border of epithelial cells in the small intestine, in particular the jejunum. (SB)

Sucrose Common or table sugar. A non-reducing disaccharide of glucose and fructose, α-D-glucopyranosyl β-D-fructofuranoside, $C_{12}H_{22}O_{22}$, molecular weight 342. Sucrose occurs in many plants and is produced commercially from sugarcane, sugarbeet and sorghum. (JAM)
See also: Carbohydrates; Disaccharides

Sugar A general term applied to the simplest carbohydrates, monosaccharides and disaccharides that are soluble in water and 80% ethanol. A 'simple sugar' usually refers to a monosaccharide, which consists of a single polyhydroxy aldehyde or ketone unit. 'Sugar' also refers to the disaccharide sucrose, common or table sugar. (JAM)
See also: Carbohydrates; Sucrose

Sugarbeet The species *Beta vulgaris* (family *Chenopodiaceae*), to which the root crop sugarbeet belongs, also includes mangels and fodder beet. Although morphologically different these are generally classified according to their dry matter and sugar content, mangels having the lowest and sugarbeet the highest content. A temperate crop, sugarbeet is grown throughout Europe principally for sugar production though some roots are either ensiled or fed directly to livestock. Yields vary with variety, location and management practices but fresh weight yields of over 50 t ha^{-1} are common. The crop is harvested from September to January with dry matter yields increasing over this time, but sugar content tends to decline from early December. Sugarbeet has a relatively high dry matter (DM) content (230 g kg^{-1}) similar to potatoes and twice that of other common root crops such as turnips or swedes. Crude protein and fibre levels are low, both about 50 g kg^{-1} DM, with ash content about 30 g kg^{-1} DM. The fibre component is highly digestible (> 850 g kg^{-1} DM), comprising mainly primary cells and containing a high level of pectic substances. The high nitrogen-free extract (870 g kg^{-1} DM) comprises mainly sugars, of which the most important is sucrose (150–200 g kg^{-1} DM). Sugarbeet is high in calcium but low in phosphorus, manganese, zinc and iodine.

Sugarbeet contains betaine, a tertiary amine formed by the oxidation of choline, and young leaves may contain 25 g kg^{-1}. It is this amine that is responsible for the 'fish-like' aroma frequently associated with commercial sugar extraction. Within the ruminant this is normally metabolized to trimethylamine, which is what gives the fish taint to milk produced by cows that have been offered excessive amounts of sugarbeet products. To reduce milk taint, it is recommended that sugarbeet should be offered immediately after milking. If sugarbeet is introduced too rapidly, the high carbohydrate content of the roots can lead to lactic acidosis resulting from rapid fermentation. If this occurs with high-yielding cattle, the accompanying depression of appetite can result in ketosis. Rumen impaction can also occur. As these roots are hard, it is common practice to chop or pulp them prior to feeding. Sugarbeet has caused toxicity in horses and is therefore not recommended.

Commercial extraction of sucrose from beets (a relatively simple process in which the beets are washed, grated and then soaked in hot water to remove sugar) produces two highly valuable by-products: sugarbeet pulp and molasses. In addition, while the tops removed at harvest can be used as a livestock feed, < 5% of this material is actually utilized.

Beet pulp is the residue from the sugar extraction process. It has a high water content (80–85%) and, while it can be fed directly (as pressed pulp), it is usually pre-dried to about 90%. The residue consists mainly of cell wall polysaccharides: as these are highly digestible the product is readily consumed by all classes of ruminant livestock. The incorporation of sugarbeet pulp into rations stimulates fibre degradation in the rumen, enhancing intake, especially when poorer quality feeds such as cereal straw are offered. It is consequently widely used for dairy cattle, with beneficial effects on milk fat content. It is incorporated in the diets of fattening cattle and is a major component of supplementary feed blocks for sheep. The high fibre content makes it a less attractive feed for pigs and poultry. The feed is well tolerated by horses but it is recommended that the material is soaked in water prior to feeding, to prevent impaction. A further use of sugarbeet pulp is as an absorbent to limit effluent losses during ensilage of crops that are low in dry matter.

After crystallization and separation of the sugar from the water extract, a thick dark brown viscous liquid (molasses) remains. Yield is generally about 300 kg t^{-1} sugar. Molasses contains 700–750 g DM kg^{-1}, 50% of which is sugars. The DM has a low crude-protein content, mostly present as non-protein nitrogen, including betaine. At low temperatures molasses is difficult to handle and not easy to mix into feeds on the farm. The use of heated tanks helps to permit accurate metering through calibrated pumps. Molasses can have a laxative effect and is therefore not used at high levels in the diet.

A number of industrial fermentations use molasses as the feedstock: the spent molasses (along with any residual microbial protein) is partially evaporated and sold to the feed industry as condensed molasses solubles. This product is less viscous and has lower sugar levels and higher protein and ash contents than molasses. Molasses is used at inclusion levels of 5–10% in the manufacture of pellets and cubes, not only to improve palatability but also to help to bind the product. In addition, being a rich source of sugars, molasses is used as an additive to silage. Molasses is also combined with beet pulp and the material sold as molassed sugarbeet feed. Although classed as an energy supplement, molasses degrades in the rumen more slowly than starchy feeds such as rolled barley and therefore has a significantly lower impact on rumen fermentation.

Sugarbeet tops comprise the leaves plus part of the upper root and are, therefore, high in sugars. They are also an excellent source of carotene, a precursor of vitamin A. The tops may also contain, depending on the degree of soil contamination, considerable levels of ash. Despite the introduction of single-operation harvesting systems, only 5% of this valuable feed is utilized, the rest being ploughed in. The tops also contain oxalic acid plus soluble sodium oxalate and insoluble calcium and magnesium oxalates. Soluble oxalates are largely detoxified in the rumen to carbonate and bicarbonate. Oxalate poisoning can be manifested as scouring, hypocalcaemia, haemolysis, renal failure and crystallization of oxalate in the brain, causing nervous disorders, paralysis and, in extreme cases, death. The risk appears to be reduced if the leaves are wilted first (up to 1 week). However, oxalate is still present after wilting and so other toxins may be involved. A further problem is the possibility of nitrite poisoning, where nitrates present in the leaves of beet tops are reduced in the rumen to nitrite. This combines with haemoglobin to form methaemoglobin, leaving the blood a characteristic brown colour and greatly reducing oxygen uptake. (FLM)

Sugarcane (*Saccharum officinarum* L)

A tropical or subtropical perennial grass, almost unique in that its carbohydrate reserve is sucrose rather than starch. Nearly two-thirds of all sugar is produced from sugarcane, the remainder being from sugarbeet, which is grown in temperate areas. Sugarcane is widely cultivated: India, Brazil and Cuba account for 40% of cane sugar. Sugarcane is planted by burying short pieces of stem (three-node 'setts') in well-drained soil. When mature, at around 18 months, the plant is about 3 m tall, the sugar concentration is highest and the crop ready for harvesting. At maturity, cane becomes tough and turns pale yellow. After harvesting, the crop regenerates ('ratoon crop') and again matures in about 18 months. Two to three ratoon crops are grown before replanting is necessary due to loss of yield. Sugarcane is reasonably resistant to drought, but *c.* 1500 mm annual rainfall, evenly distributed, is optimal; some irrigation is often employed. Yields are 30–160 t ha^{-1} of cane annually. Cane represents 60–70% of the weight of whole crop, the remainder being tops (20–30%) and leaves (*c.* 10%).

Milling of cane generates 10% sugar plus 70% water, 3% molasses, 2% filter-press mud and 15% bagasse. Traditionally sugarcane is grown in plantations with sugar mills as adjuncts. Tops and leaves are removed in the field and the tops may be used as ruminant feed. Bagasse is normally burnt in mill boilers, processed to paper, board or furfural; use as a ruminant feed is limited. Filter-press mud is used as a soil ameliorant. Molasses is used for alcohol manufacture or livestock feeding. Traditionally, commercial sugarcane production has not been fully integrated with livestock production because the emphasis was on sugar production and its potential as animal feed was not recognized. Since the mid 1970s the use of sugarcane and its by-products in animal feeding has been developed in a number of countries.

Sugarcane tops

The composition of sugarcane tops depends on the point at which the top is cut from the cane and other factors (variety, age at harvest, growing conditions). In Mauritius, the average composition of tops containing 29% dry matter (DM) was (% in DM): ash, 8.5; crude protein, 5.9; crude fibre, 33.5; ether extract, 1.7; nitrogen-free-extract, 50.3. The digestibility of organic matter in sheep and cattle was 56%. Others have reported the structural components of tops to be (% in DM): neutral-detergent fibre 63–67%; acid-detergent fibre, 37–43%; acid-detergent lignin, 4.6–5.0%. Freshly cut tops provide maintenance level feeding for cattle, but for production levels they require supplementing with protein. Smallholder dairy-cow keepers in Mauritius offer tops to cattle at double the appetite rate; this facilitates selection by the animals of the more nutritious growing points and rejection of less digestible leaf. Similarly, trials with African hair sheep showed that intake of chopped tops increased 60% when the amount offered was two to three times the expected intake. Sugarcane tops can be ensiled. In Mauritius, sugarcane tops mixed with 1–5% molasses and 1% ammonium sulphate produced well-preserved and palatable silage.

Molasses

The composition of sugarcane molasses depends on the method of production. The total sugar percentage and the ratio of sucrose to reducing sugars are, respectively: A-molasses, 68, 60:40; B-molasses, 57, 50:50; blackstrap or final molasses, 47, 40:60; high-test molasses, 78, 30:70. The type of molasses is unimportant in ruminant diets but for pigs and poultry high-test and A-molasses are the most suitable. Molasses are used in four ways: (i) in dry feeds as a binder and to reduce dust and improve palatability (< 15% of dry feed); (ii) as an additive to improve fermentation during ensiling of grass (5% of grass); (iii) as a carrier for urea in liquid supplements and feed blocks for ruminants; and (iv) as a substitute for grains in diets for ruminants and, to a lesser extent, pigs and poultry.

Bagasse

Sugar-mill bagasse is of low feeding value, containing 45% cellulose, 35% hemicellulose and 10% lignin. Rumen dry matter degradability is very low (*c.* 30%). High-pressure steam treatment (13 kg cm^{-2}, 200°C, 6 min) solubilizes the hemicellulose and improves rumen degradability to 80%. Steam-treated bagasse supplemented with urea and rumen by-pass nutrients has given rapid growth rates in beef cattle. Hydrolysis with sodium hydroxide is also effective but the method is costly.

Sugarcane

Whole sugarcane, after chopping, may be used as a dry-season forage for ruminants, if economics permit. Although DM digestibility is acceptable (62%), supplementation with minerals (sodium, phosphorus, sulphur), nitrogen (as urea or ammonium sulphate) and rumen bypass nutrients (e.g. rice polishings) is necessary to achieve satisfactory growth rates in cattle. Rice polishings may be replaced by restricted feeding of forage from tree legumes (*Leucaena* or *Gliricidia*). Chopped sugarcane must be fed within hours to avoid fermentation of the sugar, which also makes ensiling difficult without the use of suitable additives (e.g. ammonia). However, the case for ensiling is debatable as sugarcane can be harvested in the dry season and, as a ‘standing crop’, does not deteriorate. Supplemented whole sugarcane for lactating cattle has given disappointing milk yields.

Sugarcane juice

Farm-scale fractionation of sugarcane to produce juice as a feed for non-ruminants, and fibrous residue as a feed for ruminants, has proved more profitable than feeding whole sugarcane to ruminants. The juice is extracted by passing the stalks through a crusher which removes 60–80% of the sugars (sugar mills extract up to 97% of sugars). Consequently, farm-scale bagasse is of a higher feeding value to ruminants than sugar-mill bagasse. Farm-scale cane juice contains 15–23% total solids, 80% of which are soluble sugars, mainly sucrose. Sugarcane juice ferments within 8–12 h but can be preserved for 3–7 days with formaldehyde, ammonium hydroxide and sodium benzoate. For growing pigs, suitable supplements to cane juice include soybean meal (200 g day^{-1}) or groundnut cake (300 g day^{-1}) with a mixture of sweet-potato vines and water plants (for minerals and vitamins). Cane juice is not a suitable substitute for grains in the diets of broiler chickens or laying hens because of the low-energy density of the juice, as well as stress and cannibalism caused by feathers sticking together when splashed with juice. Use of cane juice for ducks and geese shows much more promise. (EO)

Key references
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Sansoucy, R., Aarts, G. and Preston, T.R. (eds) (1988) *Sugarcane as Feed*. FAO Animal Production and Health Paper 72. Food and Agriculture Organization, Rome, 319 pp.

Sulphates Sulphates, $\cdot SO_4^{2-}$, are normal constituents of food. In metabolism, cysteine is the primary source of sulphate. Sulphate is incorporated into glycoproteins via an ATP-like intermediate (adenosine 3′-phosphate-5′-phosphosulphate) or ‘active sulphate’. Sulphate is attached to galactose or *N*-acetylgalactosamine or *N*-acetylglucosamine in connective tissues and other cell surfaces as chondroitin sulphate, keratin sulphate, heparin, heparan sulphate and dermatan sulphate. Sulphate is used to conjugate drugs so as to facilitate their urinary excretion. (NJB)

Sulphur Sulphur (S) is a non-metallic element with an atomic mass of 32.066. The earth’s crust contains approximately 0.05% S as the free element or in combined states as sulphides and sulphates. Sulphur is absolutely required in biological systems; it functions in numerous organic forms and as inorganic sulphate and sulphide. The table lists some of the active organic forms of sulphur found in animal tissues.

Most of the S in the body is in proteins as the amino acids cystine, cysteine and methionine. Another sizeable portion is in the form of sulphated proteoglycans in connective tissues. Other important organic forms are the vitamins thiamine, biotin and lipoic acid, enzyme co-factors, and clotting and anticoagulant factors in blood.

Sulphur is consumed in the diet in both organic and inorganic forms. The organic forms comprise the largest portion, which includes the sulphur amino acids. For the most part, the smaller forms of S are absorbed intact. The sulphate and sulphide forms of S are readily absorbed, and absorption seems to be regulated by a transport mechanism dependent on vitamin D. The absorbed inorganic S is also readily excreted in the urine as inorganic sulphate and/or sulphate esters. The rate of sulphate excretion is proportional to the concentration in plasma, where sulphate constitutes the fourth most abundant anion. The normal value for plasma sulphate is approximately 100 mg l^{-1}.

Organic forms of sulphur found in animal tissues.

Adenosine-5′-phosphosulphate	‘Active sulphate’
Adenosine-3′-phospho-5′-phosphosulphate	‘Active sulphate
Biotin	A member of the B-vitamin complex
Chondroitin sulphate	Mucopolysaccharide containing β-D-glucuronic acid and *N*-acetylgalactosamine
Coenzyme A	Enzyme co-factor
Cystathionine	Intermediate in conversion of methionine to cysteine
Cysteic acid	Precursor of taurine
Cysteine	Amino acid
Cystine	Amino acid
Fibrinogen	Blood clotting factor
Glutathione	A natural reducing agent made of glycine, cystine and glutamic acid
Heparin	Anticoagulant factor in blood
Homocysteine	Amino acid
Lipoic acid	A member of the B-vitamin complex
Metallothionein	Heavy metal-binding peptide
Methionine	Amino acid
Sulphated proteoglycans	Mucopolysaccharide in extracellular matrix of connective tissue
Taurine	Amino acid
Thiamine	Vitamin B_1

Although some inorganic forms of S are used in the synthesis of sulphur-containing compounds in the body, the dietary requirements for S for most animals can be supplied solely through the sulphur amino acids in proteins. However, it has been shown that by adding inorganic sulphate to a low sulphur amino acid diet, the growth rate of chicks and laboratory animals can be improved. Very little response to added sulphate was seen when the animals were fed adequate concentrations of sulphur amino acids. Thus, the US National Research Council recommends 1500 mg S kg^{-1} diet for beef cattle, 2000 mg kg^{-1} for lactating dairy cattle and 1600 mg kg^{-1} for growing heifers, dry cows and mature bulls. There is no dietary S recommendation for pigs or poultry, but 1500 mg S kg^{-1} diet is recommended for horses and 1400–2600 mg kg^{-1} for sheep.

The severity of S toxicity greatly depends on the form ingested. Elemental S is the least toxic form, whereas hydrogen sulphide is extremely toxic. Lactating cattle have been shown to tolerate daily doses of 20 g of sulphur dioxide or sodium metabisulphite, but 50 g day^{-1} reduced food intake. The severity of S toxicity also depends on whether the rumen microorganisms can produce hydrogen sulphide from the sulphur source. The combination of sulphur and molybdenum to form thiomolybdate in the rumen can reduce copper availability, which could lead to copper deficiency. The maximal tolerable concentration of S for cattle is 4000 mg kg^{-1} diet.

(PGR)

See also: Copper; Thiomolybdates; Thiosulphates

Further reading

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Sulphur amino acids A collective term for amino acids that contain sulphur: methionine $CH_3{\cdot}S{\cdot}CH_2{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$, cysteine $HS{\cdot}CH_2{\cdot}HCNH_2{\cdot}$ COOH and cystine $HOOC{\cdot}HCNH_2{\cdot}CH_2{\cdot}S$-$S{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$, are all found in protein. It also includes a number of their derivatives. In the normal catabolism of methionine, four sulphur-containing amino acids are produced in sequence: L-homocysteine $HS{\cdot}CH_2{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$, L-cystathionine $HOOC{\cdot}HCNH_2{\cdot}CH_2{\cdot}S{\cdot}CH_2{\cdot}CH_2{\cdot}HCNH_2.COOH$, L-cysteine $HS{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$ and the β-aminosulphonic acid taurine $NH_2{\cdot}CH_2{\cdot}CH_2{\cdot}SO_3H$. L-Cysteine is in turn the source of sulphur for sulphate.

(NJB)

Sulphuric acid A strong inorganic acid, H_2SO_4, with molecular weight 98.08 and density of 1.84 at 20°C. In the concentrated form (98%) it is a colourless, odourless and highly corrosive liquid (pH < 1) widely used in industry. Combined with hydrochloric acid in the AIV method, it is used to aid pH reduction when ensiling forages. (FLM)

See also: Acid treatment

Sunflower The common sunflower (*Helianthus annus*) belongs to the family *Asteraceae* (*Compositae*) and is native to North America. It is an annual, or perennial, erect plant up to 4 m tall with bright yellow heads up to 30 cm in diameter. The head is not a single flower but is constructed of up to 2000 individual flowers, all joined at a common receptacle. Sunflowers are tolerant of semi-arid conditions and of both high and low temperatures. Cultivars include *H. giganteus* (Russian Giant), and *H. citrinus*. There are 67 species in the genus *Helianthus*. The Jerusalem artichoke (*H. tuberosus*) is of some importance in human and animal nutrition but the other species of sunflower are either weeds or primarily of importance to florists.

The sunflower is principally important for its oil. It is globally the third largest source of vegetable oil, after soybean and palm oil. The oil is of high quality, with a neutral flavour and a high proportion of unsaturated fatty acids, primarily oleic and linolenic. It is used as a salad and cooking oil, in non-dairy spreads and a great variety of industrial applications, including biofuel for diesel engines. There is evidence that feeding sunflower oil to ruminants may be effective in reducing the ruminal ciliate protozoan population and thereby improving the provision of amino acids to the intestine.

Sunflower is a major source of high quality vegetable oil, with a high proportion of unsaturated fatty acids.

The seeds have a high fibre content (about 25–30% dry matter) but are fed to laying hens instead of cereal grain on account of their high energy content. They are a good source of calcium. Sunflower meal, the by-product of sunflower oil extraction, is important as a source of protein in animal feed. Meal from hulled seeds contains 28% protein and 25% fibre; that from dehulled seeds has 42% protein and 20% fibre. High-fibre meals are fed to adult ruminant livestock, whereas dehulled meals are a suitable source of digestible protein for all farm livestock. The protein from sunflower contains a higher proportion of sulphur amino acids than the other commercially available oilseed meals. However, feeding at a proportion greater than one-third of the total protein supplement to pigs can produce a carcass with soft fat. The de-seeded heads can be used for forage, either ensiled if they have a sufficient moisture content, or when dried and chopped. Sunflower silage contains a similar protein concentration to grass hay, up to 12%. (DA)

See also: Jerusalem artichoke

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Superoxide Superoxides (really superoxide anion, $\cdot O_2^-$) are reactive oxygen species (ROS), produced in a series of one-electron uptake steps (or step-by-step reductions) in which an oxygen molecule is reduced to water, the intermediate products being superoxide anion, hydrogen peroxide and the hydroxyl radical, i.e.

$$O_2 \xrightarrow{e^-} \cdot O_2^- \xrightarrow[+2H^+]{e^-} H_2O_2 \xrightarrow[-OH^-]{e^-} \cdot OH \xrightarrow[+H^+]{e^-} H_2O$$

(NJB)

Supplement A feed ingredient, such as an oilseed meal, or a mixture of ingredients, that is added to a forage feed to rectify one or more of the specific nutrient deficiencies in the forage. (JMW)

Surface area of animals The surface area of animals is important in nutrition because heat loss from, and (assuming a constant body temperature) **heat production** by, the body are related more closely to surface area than to body weight. In general, the surface area of a solid is proportional to the square of its linear dimensions and to the two-thirds power of its volume or, if density is constant, to the two-thirds power of its weight (W). The basic mathematical principle is the same for animals and the measured surface areas of animals tend to increase as $W^{0.67}$. However, animals are not simple geometrical shapes and even amongst animals of the same weight, there are differences in surface area between species, between young and old, and between obese and lean. Furthermore, an animal's *effective* surface area can be altered substantially by changes in posture. In **cold environments**, animals tend to reduce their effective surface area by curling up. In hot conditions, they tend to sprawl, with limbs, ears and tails extended, maximizing their effective surface area for both sensible and **evaporative heat loss**. In comparing the adults of different species of very different sizes, metabolic rate varies approximately with the ¾ power of body weight, $W^{3/4}$ ($W^{0.75}$), and this is called **metabolic weight**. (MFF)

Sweat A clear watery liquid secreted by the eccrine glands in the skin of most species. It contains significant amounts of sodium, chloride, bicarbonate and urea. Sweat functions to wet the skin and permit evaporative cooling and is secreted when other heat-loss mechanisms are inadequate to prevent a rise in body temperature. (MFF)

Swede *Brassica napus*, an important temperate root crop grown for both animal feed and human consumption. Swedes provide a good level of energy in an easily fermentable form. They are low in dry matter (DM) but can be used to replace winter forage or concentrate. Swedes should be chopped before being fed to young stock and can be stored in clamps over winter. They taint milk if fed just before milking. The DM of swede is 110 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 95, crude fibre 90, ether extract 10, ash 60 and neutral-detergent fibre 233, with MER 13.5 MJ kg^{-1}. Swedes can be included in the diet of beef cattle and ewes at 20% of the total diet, or for lambs, weaner and grower pigs at 15% and dairy cattle at 10%. (JKM)

Sweet potato (*Ipomoea batatas* (L) Lam) A creeping plant with perennial vines and adventitious roots on which swollen tubers are formed. The tubers are highly digestible and palatable, and an excellent source of energy. Although mainly grown as human food, surplus and cull tubers are used fresh or dry in livestock feed. Sweet potato leaves are an excellent feed for ruminants, being high in both protein and calcium, and highly digestible (see tables). Pigs can also graze the vines. Fresh tubers can replace up to half the cereal in pig rations. Dried tubers can be mixed with molasses and urea up to a

Typical composition of sweet potato products (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh leaves	10.8	19.4	10.2	25.9	3.7	40.8		
Fresh vines	8.7	21.9	15.0	18.0	3.4	41.7	1.79	0.24
Fresh tubers	59.0	5.1	2.3	3.5	1.1	88.0		
Fresh peelings	11.7	6.3	0.3	4.6	1.3	87.5		
Dried tuber meal	87.1	4.6	3.0	3.9	0.3	81.9		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical digestibility (%) and ME content composition of sweet potato products.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Leaves	80.0	55.0	84.0	86.0	10.01
Fresh tubers	37.5	79.3	51.6	95.5	13.58
Dried tubers meal	14.0	37.0	74.0	90.0	11.35

ME, metabolizable energy.

level of 50% of the concentrate for dairy cattle. Dried tubers have about 90% of the feeding value of maize for pigs and can constitute up to 60% of the ration. Fresh tubers are relatively bulky and are better utilized by mature pigs. Sweet potato is high in energy, and a high-protein meal is recommended as a supplement. It is also recommended that dietary intake be restricted to avoid the production of over-fat carcasses. The metabolizable energy content of tubers for pigs is 15.07 MJ kg^{-1} dry matter. However, pigs raised on rations containing sweet potato produce carcasses with hard fat. The protein in tubers has a high biological value. Sweet potato meal can be included up to 50% in poultry feeds, provided that adequate protein supplements are available. Cooking is reported to increase the nutritive value of sweet potato tubers. Sweet potato leaves can be harvested with only a limited effect on tuber production. The leaves are difficult to dry but can be made into silage after wilting. Sweet potato vines and leaves were found to be an excellent milk replacer for goat kids, allowing households to increase milk offtake from does. Vines and leaves have a dry matter digestibility of 70%. (LR)

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Swine: *see* Pig

Synthetic diets Diets composed of pure sources of nutrients, such as starch, cellulose, casein, amino acids, urea, fatty acids and mineral elements. Also called purified diets. (JMW)

T

Taint Abnormal, usually unpleasant, odour or taste of food. Taints in animal products may be due to odoriferous materials (such as fish meal) in the animal's diet or may be produced in the metabolism of an animal given a normal diet. Amongst the latter are boar taint caused by 3-methylindole (skatole) and 5-α-androst-16-en-3-one (androsterone), both of which are odoriferous compounds in pig adipose tissue. There is variable susceptibility to boar taint in humans. Diet-related taints in cows' milk include those from silage, sugarbeet (which can give a fishy taint), garlic, wild onion and other weeds such as stinking mayweed. Contamination of milk with some disinfectants (e.g. phenolics) can cause off-flavours. (JMF)

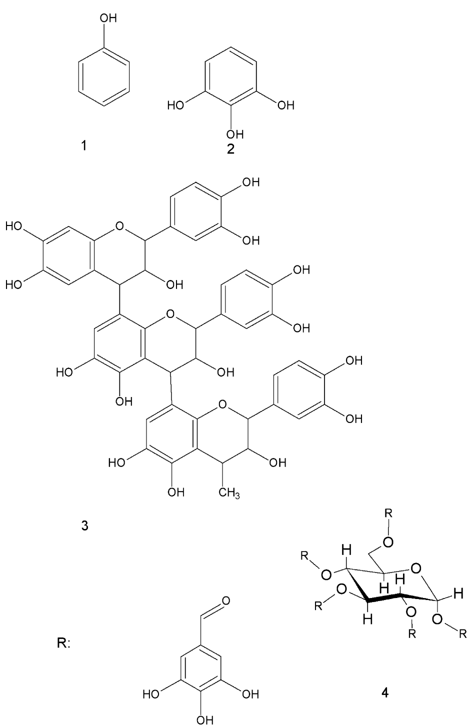
Tallow Fat rendered from animal carcasses, especially of cattle and sheep. Usually solid at room temperature. Beef tallow is hard and typically contains, as a percentage of total fatty acids, 26% palmitic, 17% stearic, 43% oleic and 4% linoleic acids. (JRS)
See also: Animal fat

Tambaqui (*Colossoma macropomum*) Like pacu, a native of the Amazon and Orinoco rivers of Brazil and mainly cultivated in Central and South America. These large, nearly round migratory fish may reach 1 m in length and weigh 20–30 kg. They have a set of large teeth and molars (like those of humans) which can crack open the tough shells of many seeds and fruits. For farmed fish, a market size of 1–2 kg is attained in 18–20 months at water temperatures ranging from 22 to 28°C. Tambaqui do not reproduce in a natural way in captivity and spawning must be induced by hormone injection. (SPL)

Tannins A group of complex polyphenolic compounds (see figure) found in most plant species, mainly in the leaves and seeds. Phenols are aromatic compounds with substituent hydroxyl groups on the aromatic ring (see figure). Polyphenolic compounds have a number of substituent hydroxyl groups. Not all polyphenolic compounds are tannins but all tannins are polyphenols. The structural complexity of tannin molecules confers varying degrees of activity towards other molecules and thus determines their reactivity in biological systems. One of the easiest methods of quantitation is to cause tannins to react to produce colours and then determine these by colorimetric or spectrophotometric methods. However, the spectral properties of reaction products of different tannins vary and cause inaccurate quantitation. This method often also inaccurately predicts the biological reactivity of the tannins.

Tannins exist predominantly (but not exclusively) as two main types: the hydrolysable tannins, based on a central glucose molecule substituted with phenolic moieties (see figure overleaf), and the condensed tannins, based on oligomers of flavonoids. The major difference between the two types is that the ester linkages in hydrolysable tannins undergo hydrolysis readily to produce relatively small molecules such as pyrogallol, while condensed tannins are much more resistant to biological and chemical degradation. Hydrolysable tannins thus tend to produce toxic effects in animals that ingest them whereas condensed tannins are much more stable. The reactions of tannins are pH dependent. They react vigorously, especially with proteins, to reduce the function of proteins such as enzymes. Tannins react with proteins in the gut, whether these are dietary, endogenous or microbial. Often these effects are detrimental to animal performance and nutrient utilization. However, tannins can have beneficial effects in animals by reducing bloat, increasing uptake of some nutrients and reducing intestinal parasites and pathogenic bacteria. These beneficial effects may account for the fact that ruminant animals can often be seen to choose to consume plants that contain tannins, even though alternative plant material is available. Tannins also chelate mineral elements strongly; this can reduce mineral absorption and increase endogenous losses from the gut.

Hydroxylated polymers such as polyethylene glycol (PEG) bind strongly with tannins and reduce their adverse effects. (TA)



Structure of some phenolic compounds and tannins.

(1) Phenol. (2) Pyrogallol; (1,2,3-trihydroxy benzene). (3) Representation of a (tri) flavonoid. (4) Representation of a hydrolysable tannin (pentagalloyl-glucose).

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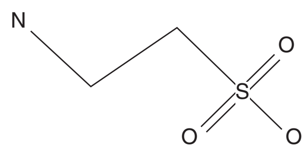
Tapioca: *see* Cassava

Taurine An aminosulphonic acid ($H_2N{\cdot}(CH_2)_2{\cdot}SO_3H$, molecular weight 125.2) not found in protein. It is synthesized from cysteine. Taurine is used in the body to synthesize bile acids. Biosynthesis of taurine is inadequate in feline species, so some taurine must be supplied in the diet to prevent retinal degeneration and cardiomyopathy.



(DHB)

See also: Cysteine; Non-protein amino acids

Tea A small evergreen (*Camellia sinensis* (L.) Kuntze) widely grown for its leaves, which are dried and constitute the tea of commerce. The inclusion of tea leaves or products in animal diets may have health benefits by their influence on the gastrointestinal microflora and by their antioxidant properties: catechins in tea are effective alternatives to vitamin E as antioxidants. The dry matter (DM) content of fresh tea leaves is 920 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is crude protein 266, crude fibre 94.5, ether extract 30.4, starch and sugars 639, and ash 64. (JKM)

Teeth The nutrients primarily required for the growth and maintenance of teeth are calcium and phosphorus. Prolonged dietary deficiency of one or both of these will cause weakening and premature loss of teeth, although the effects of the deficiency on bone, for which adequate dietary supplies of calcium and phosphorus are also required, will probably be noticed before the effects on teeth. Excessive wear can occur in animals eating diets high in soil and is seen especially in ewes folded on root crops and in upland areas. (JMF)

Temperature, body

Species	Average	Range
Cattle	38.6	36.7–39.3
Sheep, goats	39.1	38.5–39.9
Pigs	39.2	38.7–39.9
Horses	37.7	37.2–38.2
Camel	37.5	
Dogs	38.9	37.9–39.9
Cats	38.6	38.1–39.2
Rabbits	39.0	38.5–40
Poultry	40.6	40–42
Small birds	41.0	40–42

In animals, body temperature is controlled by the hypothalamus and usually taken per rectum, but milk temperature will also reflect that of the body. Body temperature varies with age, species, the time of day (highest late afternoon) and stage of the oestrous cycle. Raised temperature (pyrexia) may be a result of exercise, pain, infection or heat stroke. Body temperatures above 41°C are considered dangerous in most mammals.

Hypothermia may be caused by endotoxic shock, starvation or collapse. It is most often associated with neonates, where it may be a result of starvation over the first few hours of life, exposure to unsuitable environmental conditions or a combination of both. Piglets and lambs are particularly susceptible. (EM)

Temperature, environmental: see Environmental temperature

Termamyl Proprietary name for a microbial thermostable (up to 105–110°C) α-amylase (1,4-α-D-glucan-glucanohydrolase; EC 3.2.1.1) purified from a selected strain of *Bacillus licheniformis*. Commonly used in industry and research for rapid and efficient *in vitro* digestion of starch. (SB)

Terpenes A structurally diverse group that occurs throughout nature in various polymeric cyclic and linear forms, with many stereoisomers. The nomenclature is based on the fundamental unit of the unsaturated, branched-chain pentane isoprene; thus hemiprenes (C5), monoterpenes (C10), sesquiterpenes (C15), diterpenes (C20), etc. Terpenoids are classified into two groups: primary metabolites of the plant kingdom (carotenoids, terpenoid quinones, etc.); and secondary metabolites with highly species-dependent distribution and often undefined function. (DLP)

Further reading

Zweig, G. and Sherma, S. (1984) Introduction. In: Coscia, C.J. (ed.) *Handbook of Chromatography. Terpenoids,* Vol. I. CRC Press, Boca Raton, Florida, pp. 1–3.

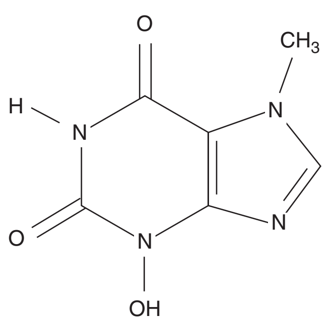
Testa Also called the seed coat, the hard outer layer of tissue surrounding the seed of flowering plants. Also involved in the control of seed dormancy. (ED)

Tetany, grass A hypomagnesaemic disorder of cattle in early lactation when magnesium requirement is increased by the demands of lactation. Grass tetany is usually associated with the consumption of lush, high-quality pasture that is low in magnesium or contains high concentrations of potassium, nitrogen or tricarbaryllic acids (which interfere with the absorption of magnesium across the rumen). As a result, magnesium concentrations in plasma, and especially cerebral spinal fluid, decrease and can reach levels that no longer support normal nerve function. In affected cows the plasma magnesium concentration often falls from a normal value of 1–1.1 mM magnesium to less than 0.5 mM. Animals become hyperexcitable and can go into uncontrolled muscle spasms (tetany) and convulsion leading to death. The syndrome is often accompanied by hypocalcaemia secondary to the low blood magnesium concentration. Treatment of animals with convulsions

consists of intravenous administration of magnesium and calcium salt solutions, though the results are often disappointing. In mild cases, the animals can be treated with oral drenches containing magnesium salts. In housed animals, prevention is easily achieved by feeding higher amounts of magnesium (adding 20–30 g magnesium in a mineral form each day to the diet) but it can be difficult to ensure that grazing animals get sufficient supplemental magnesium. (JPG)
See also: Hypomagnesaemia

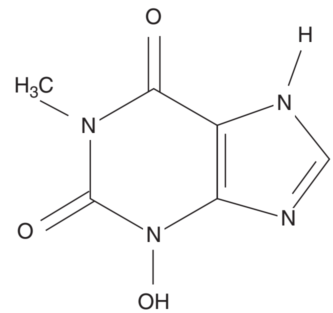
Tetrahydrofolate 5,6,7,8-Tetrahydropteroyl-glutamic acid, the fully reduced form of the water-soluble B vitamin, folic acid. In foods, folic acid is found as more than ten separate species, including folic acid, dihydrofolate and tetrahydrofolate. Tetrahydrofolate is involved in one-carbon metabolism and is found as the 5- or 10-formyl, 5-formimino, 5-methyl, 5,10-methenyl or 5,10-methylene forms and as a number of polyglutamates, the most prevalent form being the pentaglutamate. In metabolism, these one-carbon intermediates are critical to the *de novo* synthesis of nucleic acids. (NJB)

Theobromine A xanthine alkaloid (3,7-dimethylxanthine; $C_7H_8N_4O_2$, molecular weight 180) similar to caffeine. It is either extracted from the dried ripe seed of *Theobroma cacao* or made synthetically. Theobromine is a diuretic and a smooth muscle relaxant. It has little stimulant activity on the central nervous system and hence is preferred over caffeine in the treatment of certain cardiac ailments.



(KEP)

Theophylline A caffeine-like alkaloid (1,3-dimethylxanthine; $C_7H_8N_4O_2$, molecular weight 180), isomeric with theobromine and first isolated from tea (*Camellia sinensis*) in 1885. It is synthesized from caffeine or other xanthine derivatives. Theophylline is used in many prescription drugs and causes smooth muscle relaxation and possesses diuretic properties.



(KEP)

Thermogenesis The generation of heat in the body in the course of metabolism. (JAMcL)
See also: Heat production; Non-shivering thermogenesis

Thermoregulation Thermoregulation in warm-blooded animals (homeotherms) is brought about by involuntary (reflex) and voluntary (behavioural) actions. The principal reflex actions are as follows.

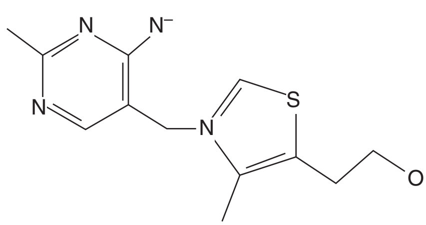
- Vasodilation or vasoconstriction of capillary vessels alters blood flow in the skin and subdermal regions. This effectively alters the insulation of the body.
- Piloerection: piloerector muscles in the dermis cause fluffing up of the fur or feathers, trapping a greater depth of still air, which is a good thermal insulator.
- Sweating makes liquid water available at the skin surface for evaporation, which is a very effective method of cooling because every gram of water vaporized absorbs some 2.2 kJ of energy (heat) from the evaporating surface.

- Panting increases the airflow over moist internal surfaces in the respiratory tract. The humidity and temperature of air respired are raised from the levels in ambient air to saturation at deep-body temperature. It follows that respiratory evaporative heat loss increases in proportion to the volume of air breathed in and out.
- Shivering is a form of increased heat production resulting from involuntary muscular activity that occurs in the cold.
- Behavioural actions include seeking shelter, huddling and curling up, which all limit heat loss. Standing in the wind promotes both convective and evaporative heat losses. The heat load of direct solar radiation may be avoided by seeking shade.

(JAMcL)

See also: Climate; Environmental temperature; Evaporative heat loss

Thiamine Vitamin B_1, one of the water-soluble B vitamins. Thiamine is a coenzyme intimately associated with metabolism of carbohydrates, fatty acids and some amino acids and with two metabolites in the tricarboxylic acid cycle. It is widely distributed in nature and found in numerous animal and plant foods. It is also produced commercially and sold as thiamine hydrochloride ($C_{12}H_{18}Cl_2N_4OS$) and as thiamine mononitrate ($C_{12}H_{17}N_5O_4S$).



Although thiamine is produced by bacteria in the intestine, the site of microbial synthesis is distal to the site where the vitamin is digested and absorbed so thiamine is required in the diet of all non-ruminant animals. Requirements are in the range of mg kg^{-1} diet. In ruminants, microbial synthesis in the rumen provides an adequate supply. Thiamine is absorbed by an energy- and sodium-dependent process. It is found in four distinct forms in cells: thiamine (T), thiamine monophosphate (TMP), thiamine diphosphate (TDP) and thiamine triphosphate (TTP). One enzyme, thiamine pyrophosphokinase, is involved in using ATP in each phosphorylation step T → TMP → TDP. Independent phosphatases are involved in dephosphorylating TTP, TDP and TMP. In tissues, T makes up about 3%, TMP 8%, TDP 88% and TTP 1% of the total thiamine. In blood serum, T and TMP are found in approximately equal amounts but only traces of TDP and TTP are seen.

The vitamin co-factor form of the vitamin is TDP. Thiamine as TDP is a co-factor for the enzyme pyruvic dehydrogenase, which is involved in the decarboxylation of pyruvic acid to acetyl-CoA and CO_2. TDP is the co-factor in the decarboxylation reactions involving α-ketoglutarate to form succinyl-CoA, and the decarboxylation of the ketoacids of the branched-chain amino acids leucine, isoleucine and valine to form the CoA forms of their decarboxylated keto acids. Additionally, TDP is thought to be a co-factor in the decarboxylation reaction of the keto acid of methionine, and α-ketobutyrate which is derived from both methionine and threonine.

A deficiency of thiamine can be assessed by an oral glucose load and measuring blood concentrations of lactic and pyruvic acids. As a metabolic deficiency progresses, the amounts of these products appearing in blood and excreted in the urine increase. Another approach to identifying a deficiency of thiamine is by measuring the activity of the erythrocyte enzyme transketolase, which requires TDP as a co-factor. This assay is most meaningful when it is tested with and without the addition of the enzyme co-factor TDP. As a deficiency progresses, the amount of cellular TDP available to support the activity of the enzyme decreases and the activity of the enzyme declines. In the laboratory test, direct addition of the co-factor (TDP) to the *in vitro* test results in a greater stimulation or recovery of enzyme activity, which is an indication of a deficiency. (NJB)

Thickeners and gelling agents The following thickeners and gelling agents are listed in the Feedingstuffs (UK) Regulations 2000.

Alginic acid	E400
Sodium alginate	E401
Potassium alginate	E402
Calcium alginate	E404
Propylene glycol alginate	E405
Agar	E406
Carrageenan	E407
Locust bean gum	E410
Tamarind seed flour	E411
Guar gum	E412
Tragacanth	E413
Acacia	E414
Xanthan gum	E415
Pectins	E440
Microcrystalline cellulose	E460
Cellulose powder	E460(ii)
Methylcellulose	E461
Ethylcellulose	E462
Hydroxypropylmethylcellulose	E464
Ethylmethylcellulose	E465
Carboxymethylcellulose	E466

(MG)

Thioctic acid 6,8 Thioctic acid, α-lipoic acid, $HOOC{\cdot}(CH_2)_4{\cdot}CH{\cdot}CH_2{\cdot}CH_2$ acts

| |
S–––––S

as a coenzyme. As lipoamide it receives the two-carbon acetyl unit from α-hydroxyethyl thiamine diphosphate, producing acetyl-lipoamide, an intermediate of the pyruvate dehydrogenase complex by which pyruvate is converted to acetyl-CoA. In the reaction, the disulphide form or lipoamide is converted to the disulphydryl form dihydrolipoamide, which must be oxidized to lipoamide by FAD bound to a protein which is part of the pyruvate dehydrogenase complex. Thioctic acid (lipoic acid) participates in other dehydrogenase reactions such as the α-ketoglutarate dehydrogenase complex. (NJB)

Thiocyanates Metabolic and detoxification products of glucosinolates and cyanogenic glycosides. Poisoning occurs when free cyanide (HCN) is liberated from the glycoside. Thiocyanates and isothiocyanates inhibit iodine uptake by the thyroid gland, which becomes enlarged (goitre). This can be prevented by increasing the level of dietary iodine. Cyanide is readily detoxified and so acute toxicity occurs only if the detoxification rate is exceeded. All animal tissues contain an enzyme called rhodanase, which catalyses the conversion of cyanide to thiocyanate, which is subsequently excreted in the urine. This reaction is significant in the treatment of cyanide poisoning by injection of sodium thiosulphate and sodium nitrate (intravenously). Sodium thiosulphate reacts with cyanide and produces a sulphate product and the less toxic thiocyanate, while the nitrate converts haemoglobin to methaemoglobin, which has a greater affinity for cyanide than does cytochrome oxidase (the biochemical target for cyanide toxicity). Therefore, the methaemoglobin participates in stripping the cyanide from the enzyme. Treatment is usually impractical in farm situations because of the acute nature of cyanide poisoning. Chronic cyanide poisoning from moderate exposure to cyanogenic glycosides has occurred in some human populations. In tropical Africa where cassava and other foods containing cyanogens are dietary staples, a condition called tropical ataxic neuropathy occurs. Symptoms are lesions of optic, auditory and peripheral nerves, elevated blood levels of thiocyanates and an increase in goitre. Vitamin B_{12} and sulphur amino acids such as methionine supplementation have beneficial effects. Similar neurological disorders have been observed in livestock consuming chronic levels of cyanogenic forages. (KEP)

Thioglucosidase: *see* Glucosidase

Thiomolybdates The thiomolybdates are sulphur- and molybdenum-containing compounds that occur naturally in many farm animal feedstuffs. They have the chemical forms MoO_3S^{2-}, $MoO_2S_2^{2-}$, $MoOS_3^{2-}$ and MoS_4^{2-}. The tri- and tetramolybdate forms readily bind copper and render it unavailable for absorption from the gut. This is a special problem in ruminant animals, where copper complexes can be formed with naturally occurring sulphur and molybdenum compounds in feed during ruminal digestion.

(PGR)

See also: Copper; Molybdenum

Further reading

Suttle, N.F. (1991) The interactions between copper, molybdenum, and sulphur in ruminant nutrition. In: Olsen, R.E., Bier, D.M. and

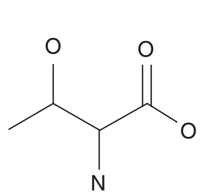
McCormick, D.B. (eds) *Annual Review of Nutrition.* Annual Reviews Inc., Palo Alto, California, pp. 121–140.

Thiosulphates In biological systems, thiosulphate ($S_2O_3^{2-}$) is a by-product of the metabolism of the amino acids cysteine and cystine. The salts of thiosulphate, such as sodium thiosulphate, are often used as treatment for copper or cyanide poisoning in animals. Thiosulphate plus molybdenum forms thiomolybdate, which will complex with copper and reduce its availability for absorption. (PGR)

See also: Copper; Molybdenum; Thiomolybdates

Thirst: *see* Water deprivation; Water intake

Threonine An essential amino acid ($CH_3 \cdot CHOH \cdot CHNH_2 \cdot COOH$, molecular weight 119.1) found in protein. Because threonine contains a hydroxyl group on the β-carbon atom, it, along with serine, is often referred to as a hydroxy amino acid. Threonine is sometimes a limiting amino acid in practical diets for growing animals. It is the second-limiting amino acid in soybean meal (after methionine) and in most cereal grains (after lysine). The endogenous proteins that enter the gut have a high concentration of threonine and may account for as much as one-half of the total dietary requirement for threonine. Threonine in the body does not enter into transamination reactions. Instead, three different enzymes are involved in the initial reaction of threonine catabolism (a dehydrogenase, a dehydratase and an aldolase) and glycine is produced as a product in two of these three pathways.



(DHB)

See also: Essential amino acids

Thrombosis The formation of a thrombus (a blood clot) in a blood vessel. Thrombosis is a relatively common condition in cattle. The usual site is the caudal vena cava but the cranial vena cava is sometimes involved. The thrombi often arise from liver abscesses, caused by rumenitis following rumen acidosis after feeding on large amounts of starchy feeds, e.g. rolled barley. Vena cava thrombosis commonly leads to pulmonary abscesses, which can cause fresh blood to be seen in the nose. This sequence of events was more frequent when ‘barley beef’ cattle were reared on diets consisting largely of ground barley. The condition is often fatal, the animal drowning in blood, but some live for several days or weeks after signs first appear. Treatment is of no avail, and cattle showing fresh frothy blood at the nose may be slaughtered. (WRW)

Thromboxanes Lipid compounds biosynthesized by addition of oxygen at C-9, C-11 and C-15 of arachidonic acid, a 20-carbon unsaturated (T6, 20:4 $\Delta^{5, 8, 11, 14}$) fatty acid derived from linoleic acid (18:2 $\Delta^{9, 12}$). Cats cannot convert linoleic acid to arachidonic acid and so it is an essential dietary component. For thromboxane biosynthesis, arachidonic acid precursors must be located on the *sn*-2 position of glycerol in phospholipids of cell membranes. The 20-carbon thromboxanes are synthesized in platelets via a cyclooxygenase-dependent pathway and upon release cause vasoconstriction and platelet aggregation. Their synthesis is specifically inhibited by aspirin, indomethacin, ibuprofen and other non-steroidal anti-inflammatory drugs. (TDC)

Thymine A pyrimidine base, 5-methyluracil, $C_5H_6N_2O_2$, found in DNA as the nucleoside thymidine. It is not found in RNA. (NJB)

Thyroid A two-lobed endocrine gland located in the anterior neck that synthesizes and releases mainly 3,5,3′,5′-tetraiodothyronine, also called thyroxine or T_4. Although 90% of total secretion is composed of T_4, 10% of secretions also contain 3,5,3′-triiodothyronine or T_3. Less than 1% of secretion is made up of 3,3′,5′-triiodothyronine or reverse T_3. Iodine plays a central role in thyroid hormone synthesis, which involves the coupling of two iodinated tyrosine molecules. Hormone release is regulated by the hypothalamic–pituitary axis. Thyrotropin-releasing hormone (TRH) from the hypothalamus stimulates release of thyroid-stimulating hormone (TSH) from the anterior pituitary, which in turn causes the release of T_4 and T_3. Release of TRH in animals is decreased by a reduction in caloric intake and increased by exposure to cold. T_4 and T_3 also exhibit strong negative feedback inhibition on TSH release. More than 99.5% of T_4 and T_3 is bound to thyroid-binding globulin in plasma, and only free forms of the hormones are active. T_4 functions mainly as a prohormone for the production of T_3, which exhibits most of the physiological effects. Activation of the thyroid hormone receptor in cells specifically regulates gene transcription, causing a multitude of metabolic effects. The major effects of thyroid hormones are to increase metabolic rate, heart rate, cardiac output, ventilation and total body heat production. (GG)

Thyroid antagonists Compounds that interfere with the ability of the thyroid gland to produce thyroid hormones, which can ultimately result in thyroid hormone deficiency. Such compounds are called goitrogens; ultimately they can cause the thyroid to enlarge, a condition called goitre. (JPG)
See also: Goitrogen

Thyroid diseases Metabolic disorders arising from either the overproduction of thyroid hormones (hyperthyroidism), leading to excessive metabolic rates, or inadequate thyroid hormone production (hypothyroidism), resulting in reduced metabolic rates. Hypothyroidism is often due to iodine deficiency or the presence of goitrogens in the diet. (JPG)
See also: Goitre; Goitrogen; Hypothyroidism; Iodine

Thyroxine: *see* Thyroid

Tilapia Freshwater finfish belonging to the family Cichlidae. Tilapias or tilapiine fish are grouped into three genera: *Tilapia*, *Sarotherodon* and *Oreochromis*, characterized by both their feeding and their reproductive habits. In general, tilapia of the genera *Sarotherodon* and *Oreochromis* are primarily omnivorous, feeding on phytoplankton, periphyton or detritus, whilst members of the *Tilapia* genus tend to take coarser food, including macrophytes. *Tilapia* are substrate spawners whereas *Oreochromis* are maternal mouthbrooders and *Sarotherodon* are biparental mouthbrooders.

Tilapias originated exclusively from the African continent (excluding Madagascar) and from Palestine (Jordan valley and coastal rivers) but they have been introduced into different habitats in various countries throughout the tropics. Tilapia culture, whether extensive, semi-intensive or intensive, has expanded worldwide and represents nearly 5% of farmed finfish; Nile tilapia (*Oreochromis niloticus*) account for nearly 75% of this volume. Most *Oreochromis* species are euryhaline and offer an advantage in culture. Commonly cultured tilapia species are very adaptable and hardy, and are considered an ideal fish for culture in the tropics.

The highest protein digestibility in tilapia occurs at 25°C and the optimum dietary protein:energy ratio for *O. niloticus* juveniles is approximately 18 g DP MJ^{-1} DE. *O. niloticus* benefit from several daily feedings, with four or more feedings a day resulting in better growth than two. (RMG)

Key references

Jauncey, K. (1998) *Tilapia Feeds and Feeding*. Pisces Press, Stirling, UK.

Pullin, R.S.V. and Lowe-McConnell, R.H. (eds) (1982) *The Biology and Culture of Tilapias*. ICLARM Conference Proceedings 7, ICLARM, Manila, Philippines.

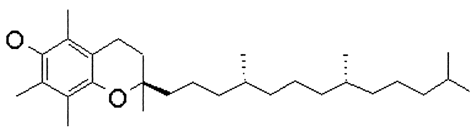
Titanium dioxide One of several indigestible markers that may be added to diets for the measurement of digestibility or the rate of passage of digesta. (MFF)

Toasting The application of dry (usually radiant) heat to feed materials to improve either their chemical structure or their nutritional value. (MG)

Tocopherols A group of compounds, each of which possesses vitamin E activity.

They have a phenolic functional group at carbon 6 on a chroman ring (substituted six-member heterocyclic double rings) with either a 16-carbon phytanyl (tocopherols) or isoprenoid (tocotrienols) chain attached to C-2 of the chroman ring. In addition to the hydroxyl group on carbon 6, either a CH_3 or H is attached to C-5, C-7 or C-8, leading to a total of four tocopherols and four tocotrienols.

Tocopherols	*C-5*	*C-6*	*C-7*	*C-8*	*Tocotrienols*
α-tocopherol	CH_3	OH	CH_3	CH_3	α-tocotrienol
β-tocopherol	CH_3	OH	H	CH_3	β-tocotrienol
γ-tocopherol	H	OH	CH_3	CH_3	γ-tocotrienol
δ-tocopherol	H	OH	H	CH_3	δ-tocotrienol



Structure of α-tocopherol.

The 16-carbon phytanyl chain in tocopherols is saturated and has three chiral carbons (C-2, C-4′ and C-8′) leading to a racemic mixture of eight stereoisomers in chemically synthesized tocopherols. In the case of α-tocopherol, this mixture is called all-racemic (all-rac-) α-tocopherol. Variation in vitamin E activity of tocopherols depends on the orientation (*R* or *S*) at the chiral carbons and the number and position of methyl groups on the chroman ring. The table lists the relative biological effectiveness of the four tocopherols and two of the four tocotrienes, in two different bioassays.

Relative vitamin E activity of homologues of tocopherols and tocotrienes in rats.

Form	Gestation/resorption	Haemolysis
α-Tocopherol	100	100
β-Tocopherol	25–40	15–25
γ-Tocopherol	8–19	3–18
δ-Tocopherol	~ 1	~ 1
α-Tocotrienol	21	17
β-Tocotrienol	4	1–4

α-Tocopherol is a slightly viscous, pale yellow oil with a melting point of 2.5–3.5°C and a boiling point of 200–220°C. It fluoresces when exposed to a wavelength of 296 nm, emitting light at 325 nm. The ultraviolet absorption maximum is at 294 nm. α-Tocopherol is soluble in organic solvents but poorly soluble in water. It is stable to heat and alkalis in the absence of oxygen, but slowly oxidizes upon exposure to atmospheric oxygen and rapidly oxidizes in the presence of ferric salts. Feed handling methods can result in loss of natural α-tocopherol. Drying forages in sunlight, treatment of maize with propionic acid and ensiling of high-moisture maize have been shown to result in substantial loss of α-tocopherol. In order to stabilize α-tocopherol, the C-6 phenolic hydroxyl group is shrouded by esterification to acetate. During extraction of tocopherols from plant or animal tissue, it is common to amend the extraction medium with a cation chelator and a reductant to protect the tocopherols, as they may come into contact with oxygen during sample preparation. A common approach for quantifying α-tocopherol involves liquid chromatography with UV or fluorescence detection. α-Tocopherol is considered to be the most important natural antioxidant in cell membranes. Physicochemical studies have demonstrated that the polarity and structure of α-tocopherol account for the chroman group being located at the surface of a lipid bilayer membrane with the phytanyl tail serving to anchor the molecule in the interior, lipophilic region of the membrane. The protective activities of α-tocopherol are related to oxidative damage which is attributed to the presence of molecular oxygen in aerobic organisms and its solubility in tissues. Specific chemical species known as reactive oxygen species have been implicated in cells as strong pro-oxidants that participate in fatty acid oxidation reactions. Prominent reactive oxygen species are superoxide anion/radical ($O_2\cdot^-$), hydrogen peroxide (H_2O_2), and hydroxyl radical (HO·). During oxidation of unsaturated fatty acids, peroxyl and alkoxyl radicals arise and propagate fatty acid oxidation. α-Tocopherol quenches free-radical-mediated fatty acid oxidation by donating a proton and an electron from its C-6 hydroxyl group to radical species, thus converting them to less oxidative, stable species. In the process, α-tocopherol becomes α-tocopheroxyl radical, but this radical is much less reactive than the radicals that have been quenched. Since α-tocopherol is located in membranes and membranes are composed of predominantly unsaturated fatty acids that are inherently prone to oxidation, α-tocopherol's role as a premier tissue antioxidant is very logical. α-Tocopherol can be regenerated from α-tocopheroxyl radical by reductions involving, for example, ascorbic acid, glutathione and ubiquinone. Providing high levels of α-tocopheryl acetate to livestock has not produced evidence of toxicity. (DMS)

Key reference

Brubacher, G.A. and Wiss, O. (1972) Vitamin E active compounds, synergists and antagonists. In: Sebrell, W.H. Jr and Harris, R.S. (eds) *The Vitamins. Chemistry, Physiology, Pathology, Methods*, 2nd edn, Vol. 5. Academic Press, New York, pp. 255–258.

Tocotrienols A group of compounds with a phenolic functional group at carbon 6 on a chroman ring (substituted 6-member heterocyclic double rings) with a 16-carbon isoprenoid chain attached to C-2 of the chroman ring. The number and location of methyl groups on the chroman ring determine the identity of α, β, γ and δ tocotrienols (*see* **Tocopherols**). Since the isoprenoid chain of tocotrienols has three C-C double bonds, there is only one chiral carbon (C-2). While the biological activity of the tocopherols varies from 1.49 IU mg^{-1} (for D-α-tocopherol, 2*R*, 4′*R*, 8′*R*) to 0.85 IU mg^{-1} (for 2*R*, 4′*S*, 8′*R*), the tocotrienols are about one-fifth as biologically active. (DMS)

Tolerance, immune: *see* Immune tolerance

Tomato By-products of commercial tomato (*Solanum lycopersicum* L.) production and processing include waste fruit and tomato pomace (the residue of juice extraction), which may be pressed and dried. These materials have limited use for non-ruminants. Tomato cannery waste can be used as a feed ingredient in low-energy poultry diets, i.e. broiler, breeder and laying hen rations, at < 20% of total diet. Tomato products may be fed to ruminants with no specific limitations. (JKM)

Tooth disease The buccal cavity, as the point of entry of air, food and water into the body, is particularly exposed to diseases. These are often manifested in the periodontal region, due to its exposure to ambient conditions. Three main types of disease prevail: infections, mineral disorders of the teeth and physical damage. Infections favour this site of colonization of the body because of the ability to transmit the disease during communal feeding; however, the bacteriostatic properties of salivary antibodies and other compounds, such as agglutinins, help to prevent disease. Foot-and-mouth disease is one example of a disease readily transmitted between grazing animals. The gums, with their exposed state, are also prone to inflammation, as in gingivitis, and vascular disorders, such as the localized hypoxia that accompanies lead poisoning and is manifested as a blue coloration or 'lead line'. Mineral disorders commonly affect the teeth, due to their mineralized nature, and the status of many minerals in animals can be assessed by chemical analysis of teeth. Fluorine toxicity, or fluorosis, is accompanied by a yellowing of the teeth and is common near aluminium smelters. Physical damage is mainly to the teeth, and tooth loss (a temporary problem in young cattle progressing from milk teeth to permanent teeth) is a common source of morbidity in sheep grazing stony pastures. Sheep grazing short mountain pastures suffer excessive tooth wear and become

Nutrient composition of tomato products (g kg^{-1} dry matter).

		Nutrient composition (g kg^{-1} DM)						
	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Skin and seeds, dried	933	248	276	66	220	190	1.8	2.6
Oil cake	–	370	283	74	68	205	1.6	5.9

NFE, nitrogen-free extract.

'broken-mouthed', at which time they can only satisfactorily graze on lush lowland pastures, where they are unlikely to consume small stones that will further damage their teeth. Free-range pigs can also suffer tooth damage when stone chewing.

The periodontal region is subject to a number of abnormalities, such as over- or undershot jaws, a problem (particularly in ruminants) where the lower jaw fails to meet the hard pad in the upper jaw. (CJCP)

Total body water The sum of extracellular and intracellular water. Total body water (TBW) is usually measured by the dilution of isotopically labelled water. The label may be deuterium (^{2}H), tritium (^{3}H) or ^{18}O. Each of these gives a slight overestimate (up to 5%) of total body water because there is some exchange of isotope with substances other than water. (MFF)

Total digestible nutrients (TDN) The total digestible nutrient value of a feed is calculated as: digestible crude protein + digestible crude fibre + digestible nitrogen-free extract + 2.25 × digestible ether extract. In contrast to digestible energy (DE), which is based on energy values of nutrients, TDN is based on mass with a correction factor for lipids. (JvanM)

See also: Efficiency of energy utilization; Energy systems

Toxins: *see* Poisoning

See also: Aflatoxins; Algal toxins; Alkaloids; Aspergillosis; Botulism; Bracken fern; Carcinogens; etc.

Trace elements Trace elements are the metallic elements required in the diet in trace amounts (between 1 and 100 mg kg^{-1} diet) for growth and maintenance. They include copper, iron, manganese and zinc. Other trace elements that show beneficial effects in some animal species include silicon, chromium and fluorine. Dietary elements required in concentrations of < 1 mg kg^{-1} diet are generally referred to as ultra-trace elements. (PGR)

See also: Chromium; Copper; Fluorine; Iron; Manganese; Silicon; Ultra-trace elements; Zinc

***Trans* fatty acids** Unsaturated fatty acids in which one or more double bonds are in the *trans* configuration, in contrast to the all-*cis* configuration that predominates in nature. They are formed naturally from dietary unsaturated fatty acids by ruminal bacteria, thus occurring in small amounts (< 5%) in ruminant fats. Diverse *trans* fatty acids are formed by the industrial hydrogenation of unsaturated vegetable oils. *Trans* unsaturation increases the melting point compared with the *cis* analogue. (DLP)

Transamination The process whereby the α-amino nitrogen (X·CHNH$_2$·COOH) of many amino acids can be removed and then transferred to the α-keto acid (X·CO·COOH) precursor of an amino acid to form the amino acid. The transamination reaction is dependent on the vitamin B$_6$ (**pyridoxine**) co-factor pyridoxal 5′-phosphate and forms pyridoxamine 5′-phosphate, which is the nitrogen-carrying intermediate in transamination reactions. By transamination an inappropriate pattern of amino acids from the diet can be modified to produce an amino acid pattern that more closely meets its metabolic needs. Nitrogen supplied in a simple compound such as ammonium citrate can be taken up as glutamate and used as a source of α-amino nitrogen for dispensable amino acid biosynthesis. This biosynthesis of dispensable amino acids is dependent on the production of the α-keto acid precursors of the amino acids (i.e. pyruvate, α-ketoglutarate, oxaloacetate, etc.) which are usually derived from the catabolism of carbohydrates such as glucose and glycerol. Transamination is also, for many amino acids, the first step in the process of catabolism. (NJB)

Transferrin A glycoprotein that provides the primary means for inter-organ transport of non-haem iron, binding up to two iron atoms in the +3 (ferric) oxidation state. It is present in blood in the diferric, monoferric and apo- or iron-free forms. In adult animals the majority of serum transferrin is iron-free (about 70%), helping to prevent the accumulation of toxic (not protein-bound) iron. Diferric transferrin binds to cell-surface transferrin receptors and is internalized into cells by receptor-mediated endocytosis. (RSE)

Transferrin receptor A glycoprotein present in the membrane of many cell types that is required for the internalization of transferrin (Tf) iron. The transferrin receptor (TfR) is a 90,000 dalton glycoprotein that dimerizes: each TfR monomer binds one Tf molecule. Iron-loaded Tf binds much more tightly to the TfR than does the iron-free form of Tf, thus assuring iron uptake. TfR is brought into the cell (endocytosed) in membrane-bound vesicles called endosomes. The endosomes containing TfR with Tf bound to it become acidified; this is required for release of iron from Tf and its delivery to the cytosol. Under these conditions of low pH the iron-free Tf binds well to TfR and is brought back to the cell surface and released to find more iron. Iron-deficient cells increase their expression of TfR to acquire more iron: conversely, in iron overload, TfR expression is reduced. Cells can contain from several thousand TfR to several million, as on immature red blood cells that are actively making the iron protein, haemoglobin. Genetic inactivation of the TfR gene is lethal to the embryo in part because TfR represents the only way to deliver iron into immature red blood cells. As red cells mature they lose their TfR, leading to the formation of a serum form of TfR which is thought to be a good indicator of body iron status. High serum TfR suggests iron deficiency. Recently a second TfR, TfR2, was discovered. TfR2 also allows for internalization of iron. TfR2 is highly expressed in liver and the inability to reduce its expression in iron overload may lead to damage to tissues such as liver. (RSE)

Transit time Transit time is a measure of the time required for a dietary component to pass through the whole digestive tract or a part of it. The transit time through the stomach is strongly influenced by feed composition, in particular the physical structure, because particles above a certain size cannot pass through the pylorus. Furthermore, gastric emptying rate is under nervous and hormonal control and is regulated to allow adequate digestion of food material in the upper part of the small intestine before more material enters. Thus, non-absorbed lipids trigger the release of cholecystokinin (CCK) from receptors in the duodenum and also of gastric inhibitory polypeptide from receptors in the jejunum; both hormones inhibit gastric emptying.

In the small intestine, digesta are propelled by peristaltic contractions associated with the migration of myoelectric complexes from duodenum to ileum. These complexes are composed of a quiescent phase whose duration varies according to feeding and time of day, a phase of irregular spiking activity lasting 50–80 min and a phase of regular spiking activity lasting 3–5 min. The myoelectric complexes migrate at a decelerating speed from about 20–30 cm min^{-1} in the first part of the small intestine to about 5 cm min^{-1} in the distal parts.

Transit processes in the large intestine are less well documented. The caecum acts more or less as a mixing reservoir, and the slow transit through the colon is based on peristaltic waves.

Dietary fibre reduces transit time in the stomach and small intestine but increases transit time in the large intestine, resulting in a general increase throughout the whole digestive tract.

The transit time or passage rate can be studied by the use of markers. Chromic oxide or rare-earth minerals which bind strongly to fibre compounds that are not degraded are commonly used. Also native dietary fibre compounds such as lignin or insoluble ash can be used. Simultaneous electromyographic and radiological observations are also useful methods.

The transit time varies between species and generally increases with complexity of the digestive tract. In chicken and turkey, markers appear in the faeces 2–2.5 h after ingestion and are almost completely excreted after 24 h. In pigs, average transit time throughout the digestive tract is about 24 h. In ruminants, the transit time is considerably higher due to a retention time in the rumen of typically 50–80 h when foods are highly lignified, or 30–50 h for more readily digested foods such as immature pasture herbage or concentrates. (SB)

See also: Gastric emptying; Motility

Trehalase A glycolytic enzyme (α,α-trehalose glucohydrolase; EC 3.2.1.28) that hydrolyses the disaccharide trehalose (abundant in algae and fungi as well as in the haemolymph of insects) into its constituent, glucose. Trehalase is attached to the brush border of epithelial cells in the small intestine. (SB)

See also: Carbohydrates

Trehalose A disaccharide, $C_{12} H_{22}O_{11}$, molecular weight 342, of two glucopyranose residues joined at their anomeric carbons (carbon 1). It is an important reserve carbohydrate in yeasts, lichens and algae. It also occurs in insect eggs, larvae and pupae and is the major blood sugar in some mature insects. (JAM)

See also: Carbohydrates

Triacylglycerol lipase An enzyme that hydrolyses triacylglycerols to free fatty acids and glycerol. In the digestion of dietary fats, triacylglycerol lipases are secreted from the tongue (specific for medium-chain triacylglycerols), the stomach and the pancreas. In adipocytes, triacylglycerol is hydrolysed to glycerol and fatty acids by a hormone-sensitive lipase. In blood, triacylglycerols in chylomicrons and very-low-density lipoproteins are converted to glycerol and fatty acids by lipoprotein lipase. (NJB)

Triacylglycerols Esters of glycerol and fatty acids, also called triglycerides. The alcohol groups on a single glycerol of most naturally occurring triacylglycerols do not contain the same fatty acid residue and thus are mixed acylglycerols. They are the main form of fat in feedstuffs and the major energy reserve in higher animals. (JAM)

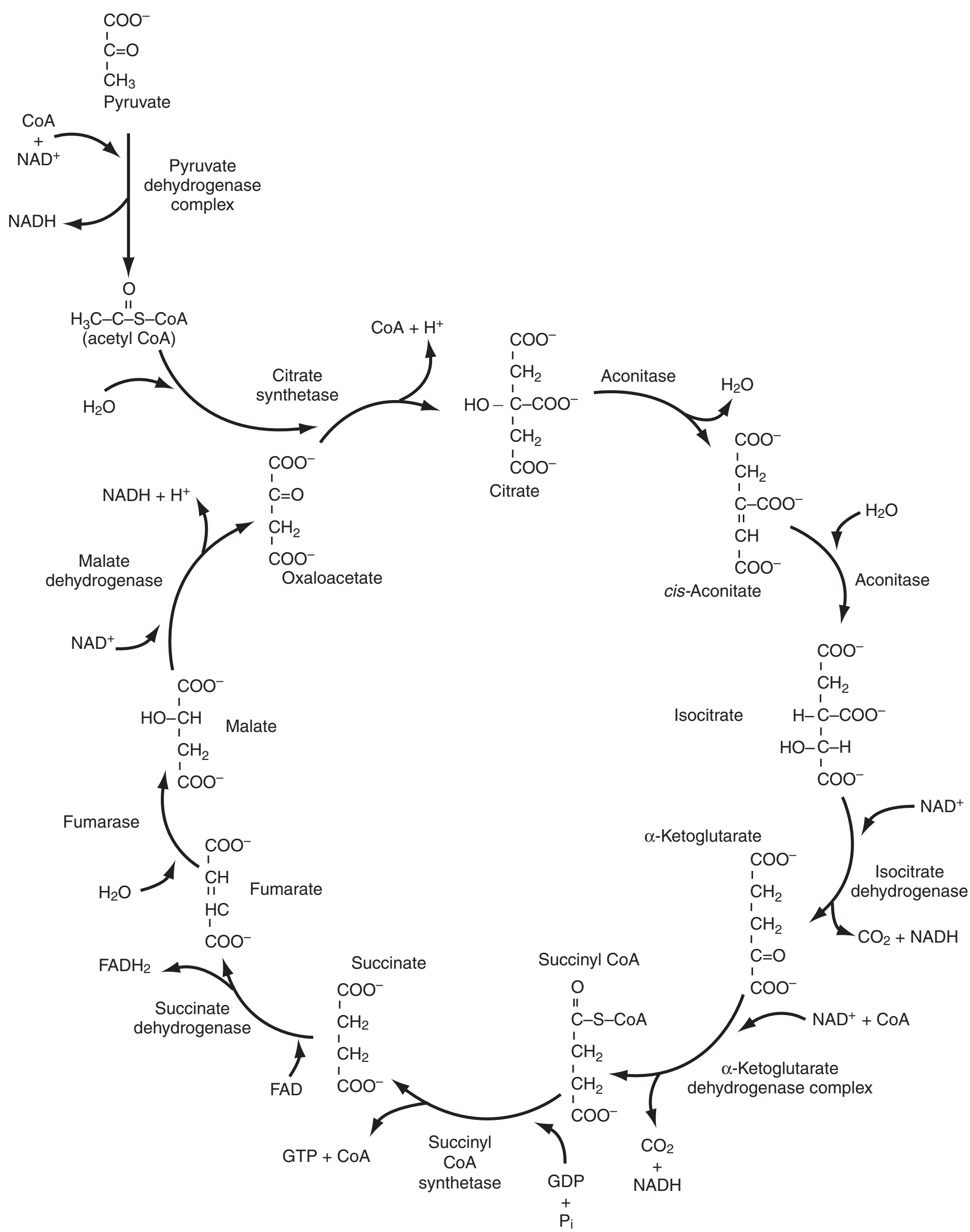
See also: Fats

Tricarballylate A metabolite of trans-aconitic acid, an organic acid of lush, growing plants. Tricarballylate, produced in the rumen, can bind magnesium and other cations to form a stable complex preventing absorption of the bound cations. Tricarballylate may be a cause of hypomagnesaemia in grazing ruminants. (JPG)

See: Hypomagnesaemia; Tetany, grass

Tricarboxylic acid (TCA) cycle Also called the Krebs cycle or the citric acid cycle, a series of reactions in which the carbon of citric acid is converted to CO_2. This metabolic pathway is especially associated with the cristae in the matrix of the mitochondrion. In summarizing an assortment of experiments in 1937, H.A. Krebs, Professor of Biochemistry at Oxford, proposed a series of reactions to account for the catalytic effect of added citrate on increased oxygen consumption in a pigeon breast muscle preparation. These reactions form a cycle because in the first step of the catabolism of acetyl-CoA, acetyl-CoA combines with oxaloacetic acid to form citric acid. In the ensuing nine steps in the breakdown of citric acid two moles of CO_2 are produced and in the last step in the TCA cycle, oxaloacetic acid is produced. The catabolism of acetyl-CoA produces 2 CO_2 and 12 ATP. The following is the sequence of reactions that comprise the TCA cycle: oxaloacetate + acetyl-CoA → citrate → *cis*-aconitate → isocitrate* → CO_2 + α-ketoglutarate* → + CO_2 + succinyl-CoA → CoASH + ATP + succinate** → fumarate → malate* → oxaloacetate. In steps marked *, NAD → NADH + H^+, and in steps marked **, FAD → $FADH_2$. The energy trapped in the reduced co-factors is recovered as ATP when the reduced co-factors are oxidized by the electron transport chain. In the electron transport chain, the electrons carried by the reduced co-factors NADH and $FADH_2$ are used to reduce O_2 to H_2O in a process whereby the energy in the reduced co-factors is used to synthesize ATP from ADP + P. The catabolism of acetyl-CoA in the TCA cycle results in 3 NAD → 3 NADH + 3 H^+, 1 FAD → $FADH_2$ and the equivalent of one ATP produced in a single substrate → product reaction. Each NADH is equivalent to three ATPs and each $FADH_2$ equivalent to two ATPs for a total of 12 ATPs ($3 \times 3 = 9, + 2 + 1 = 12$).

The reactions of the TCA cycle participate in both catabolism and anabolism. In catabolism, CO_2 is produced from the carbon in the substrates and the energy in the substrates is captured ultimately as ATP. In anabolism, non-glucose carbon can be converted to glucose carbon in a process called **gluconeogenesis** and non-amino acid carbon can be converted to dispensable amino acid carbon. In catabolism, the TCA cycle is the metabolic pathway by which the acetyl-CoA produced from the catabolism of fatty acids and some



amino acids, or the acetyl-CoA produced from glucose or amino acids via pyruvate, is converted to CO_2. The TCA cycle is also the pathway by which carbon from amino acids which produce oxaloacetate, α-ketoglutarate, fumarate or succinate in their catabolism is converted to CO_2.

The role of the TCA cycle in anabolism is in gluconeogenesis and in lipogenesis. In gluconeogenesis, compounds that become intermediates in the TCA cycle (i.e. oxaloacetate, fumarate, succinate and α-ketoglutarate) can be converted into glucose carbon. Thus, aspartate, glutamate and parts of arginine, histidine, glutamine, proline, isoleucine, methionine, valine, tyrosine, phenylalanine, threonine and propionate are carbon sources for the synthesis of glucose. Because pyruvate can be converted to oxaloacetate, parts of amino acids that are converted to pyruvate are also gluconeogenic. Thus, alanine, cysteine, glycine, serine and threonine are sources of glucose carbon. In lipogenesis, citrate leaves the mitochondrion and is converted into acetyl-CoA which is the two-carbon precursor used in the biosynthesis of long-chain fatty acids. Thus, aspartate, glutamate and parts of arginine, histidine, glutamine, proline, isoleucine, methionine, valine, tyrosine, phenylalanine, threonine and propionate are carbon sources for the synthesis of long-chain fatty acids and cholesterol. (NJB)

Key reference

Mayes, P.A. (2000) The citric acid cycle: the catabolism of acetyl-CoA. In: Murray, R.K., Granner, D.K., Mayes, P.A. and Rodwell, V.W. (eds) *Harper's Biochemistry*, 25th edn. Appleton and Lange, Stamford, Connecticut, pp. 182–189.

Trichothecenes Mycotoxins produced by several species of *Fusarium* fungi. More than 100 trichothecenes are known; the most important are T-2 toxin, HT-2 toxin, diacetoxyscirpenol (DAS), 15-monoacetoxyscirpenol (15-MAS) and vomitoxin (deoxynivalenol or DON). The name trichothecene derives from the fungus *Trichothecium roseum*, from which the compounds were first isolated. Trichothecenes have neurotoxic, cytotoxic and immunotoxic effects. They are potent inhibitors of protein synthesis. Cytotoxic effects include inflammation and necrosis of epithelial tissue, especially of the oral and gastrointestinal tracts. Feed refusal and vomiting, especially with DON, are common signs. Neurotoxic effects include posterior paralysis (swine) and incoordination. Thymic involution and impaired antibody production are immunotoxic effects. Specific trichothecene-induced disorders include mouldy corn toxicosis in cattle (T-2), alimentary toxic aleukia in humans (T-2), bean hull poisoning in horses, and stachybotryotoxicosis. The production of trichothecenes in grains is stimulated by low environmental temperatures. (PC)

Triglycerides: *see* Triacylglycerols

Triiodothyronine Also called T_3, 3,5,3′-triiodothyronine, $HO{\cdot}C_6H_3I{\cdot}O{\cdot}C_6H_2I_2{\cdot}CH_2{\cdot}CH(NH_2){\cdot}COOH$, is a thyroid hormone derived from thyroxine (T_4,3,5,3′,5′-tetraiodothyronine, $HO{\cdot}C_6H_3I_2{\cdot}O{\cdot}C_6H_2I_2{\cdot}CH_2{\cdot}CH(NH_2){\cdot}COOH$). These hormones are produced in the thyroid gland and are unique in that they contain iodine. They are transported in the blood bound to thyroxine-binding protein. T_3 has its effect by binding to receptors on target cells. These hormones are required for growth and normal development and to maintain the basal metabolic rate. (NJB)

Trimethylamine A colourless liquid, $(CH_3)_3{\cdot}N$, with a fishy ammoniacal odour. In animals it is a product of the microbial degradation of choline $(CH_3)_3{\cdot}N^+{\cdot}CH_2{\cdot}COH$ and betaine $(CH_3)_3{\cdot}N{\cdot}CH_2{\cdot}COOH$. (NJB)

Trimethyllysine $(CH_3)_3{\cdot}N{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$. Trimethyllysine is produced by methylation of protein-bound lysine by *S*-adenosylmethionine. When protein is degraded, trimethyllysine is released and becomes available for the synthesis of carnitine. (NJB)

Tripeptidase A peptidase that specifically hydrolyses tripeptides. Tripeptidases are located together with dipeptidases and aminopeptidases in the epithelial cells in the small intestine, mainly in the jejunum. (SB)
See also: Protein digestion

Triticale A hybrid cereal derived from wheat (*Triticum* spp.) and rye (*Secale* spp.). It combines the desirable characteristics of wheat (grain quality, productivity, baking properties, disease resistance) with those of rye (vigour, hardiness). Triticale is grown commercially mainly for animal feeding in Central and Northern Europe and North and South America. Spring varieties are an alternative source of forage to oats and barley; winter varieties are grown mainly as a spring pasture for ensiling or harvesting for grain. Winter triticale may also be planted in mixtures with barley or oats to produce a high quality silage crop with late-season grazing.

By-products include triticale meal, rolled triticale, quick triticale flakes and triticale bits. Recent varieties of triticale are comparable to wheat in terms of protein content but there is a high degree of variability (110–185 g kg^{-1} dry matter) among varieties. Protein quality is higher than in wheat, due to the higher concentration of lysine and sulphur-containing amino acids, but triticale is deficient in tryptophan. Triticale contains antinutritional factors (trypsin inhibitors, alkyl resorcinols) which have been implicated in poor palatability and performance in pigs. Triticale should not contribute more than half the total grain fed in the diet of farm animals. (ED)

Further reading

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D. and Morgan, C.A. (1995) *Animal Nutrition*, 5th edn. Longman, Harlow, UK, 607 pp.

Trough: *see* Drinker; Feed trough

Trout A term most commonly used to denote any of several species of Salmonidae in the genera *Salmo* (e.g. brown trout, *Salmo trutta*), *Salvelinus* (e.g. brook trout, *Salvelinus fontinalis*) and *Oncorhynchus* (e.g. rainbow trout, *Oncorhynchus mykiss*). The term has also been applied to fishes other than Salmonidae, such as the Australian family Galaxiidae, and certain Sciaenidae (drums) of the genus *Cynoscion* ('seatrouts'). (RHP)
See also: Rainbow trout

True digestibility A calculated value for the digestibility of a dietary component after correction of the determined apparent digestibility for endogenous losses. For example, the digestibility of amino acids is based on the collection of ileal digesta, which contain not only undigested proteins (amino acids) but also unreabsorbed endogenous amino acids. Part of this endogenous loss can be regarded as a basal (minimal) loss; part is induced by the diet. After correction for the estimated basal loss of amino acids the 'true' digestibility is obtained. True protein digestibility is now often referred to as 'standardized digestibility'. (SB)

True metabolizable energy True metabolizable energy, often abbreviated to TME, is used to characterize the energy values of feeds for poultry. Apparent metabolizable energy (AME) is measured directly as the difference between ingested and excreted energy. Because the excreta contain uric acid, the measured value is higher in a bird that retains more of the dietary nitrogen than in one that retains less and excretes more. TME is calculated by subtracting from AME the energy that would have been expended if all the dietary N had been excreted as uric acid (i.e. 34.4 kJ g^{-1} N), i.e. if no protein were deposited. TME is thus more independent than AME of the use to which dietary energy is put. (SB)
See also: Metabolizable energy

True protein The actual protein content of a material, exclusive of the non-protein nitrogenous compounds present in it that form part of the crude protein. Early workers in animal nutrition proposed methods for measuring true protein but none were acceptable and the distinction between true and crude protein now has little practical significance. Accurate measurement of true protein would entail extraction with a protein precipitant, such as 10% trichloroacetic acid, to remove non-protein N compounds, followed by an amino acid analysis of the residue. The true protein content of the material could then be obtained from the sum of the component amino acids – provided that allowance is made for water lost when amino acids combine in peptide linkage. Note that N analysis of the extracted material would not provide a measure of true protein as, without knowing its amino acid composition, the percentage of N in the protein is not precisely known. (CBC)
See also: Crude protein

Trypsin A pancreatic enzyme classified as an endopeptidase. It has a specificity for cleavage at the site of basic amino acids such as arginine and lysine. Trypsin is secreted as the inactive zymogen trypsinogen, which is activated by enterokinase. Trypsin in turn converts inactive chymotrypsinogen to chymotrypsin, its active form. Trypsin inhibitors are found in a number of plants, especially legume seeds. (NJB)

Trypsin inhibitors A widely distributed group of plant proteins that inactivate animal serine proteases. They can be classified into two groups. Those of the first group have either a single domain (single or double headed, *c*. 8 kDa, heat and pH stable) Bowman-Birk inhibitory structure (ranging from 14 amino acids in sunflowers to, more commonly, 60–70 amino acids as in some legumes and wheat), or two domains (e.g. barley and legumes), allowing simultaneous and independent binding of two trypsin molecules. A specific inhibitor threonine is highly conserved and provides optimal inhibition of trypsin. They increase pancreatic trypsin and chymotrypsin secretion. Those of the second group are Kunitz inhibitors (18–24 kDa, heat and pH labile; growth inhibition twice that of Bowman-Birk inhibitors) whose activity can vary 1000-fold. They increase pancreatic trypsin secretion. Inhibitors with similar *in vitro* inhibition patterns can have different *in vivo* effects. Dietary sources of trypsin inhibitors inhibit certain cancer cells, inhibit proteases from mammalian inflammation-mediating cells and can suppress superoxide anion radical secretion from immunocytes. Inhibitor-resistant duodenal pancreatic juice tryptic activity is evident after eating raw soybeans. Sources include *Leguminosae* (beans), *Poaceae* (cereals), *Chenopodiaceae* (spinach), *Solanaceae* (potatoes), *Convolvulaceae* (sweet potatoes), *Asteraceae* (lettuce, sunflowers), *Amaranthaceae* (amaranthus), *Brassicaceae* (radish) and *Cucurbitaceae* (squash). (JDO)
See also: Antinutritional factors

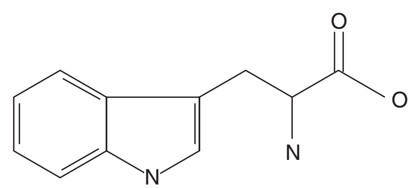
Trypsinogen The inactive precursor of trypsin, secreted from the pancreas via the pancreatic duct into the lumen of the duodenum, where it is activated by a specific cleavage of an N-terminal polypeptide, first by enterokinase and progressively by activated trypsin, which assures a rapid and complete activation. Spontaneous activation of trypsinogen in the pancreas is prevented by the presence of a potent trypsin inhibitor. (SB)
See also: Trypsin

Tryptamine, 5-hydroxy: *see* Serotonin

Tryptophan An essential amino acid ($C_8NH_6 \cdot CH_2 \cdot CHNH_2 \cdot COOH$, molecular weight 204.2) found in protein. Tryptophan is sometimes limiting in practical diets fed to non-ruminants. When evaluated in terms of g tryptophan per 16 g nitrogen (i.e. percentage of crude protein), maize and meat by-products are low in tryptophan whereas soybean meal is rich in this amino acid. Gelatin is virtually devoid of tryptophan.

The main catabolic pathway of tryptophan involves several oxidation reactions that result in the synthesis of 2-amino 3-carboxymuconate semialdehyde (ACS). This compound is primarily converted to acetoacetate and then CO_2, but some of the flux goes toward quinolinic acid which is a precursor for the synthesis of nicotinic acid mononucleotide, and ultimately NAD. Feline species have little capacity to make quinolinic acid from ACS, and therefore tryptophan does not reduce their niacin requirement.

An estimated 3% of the tryptophan catabolic flux involves hydroxylation followed by decarboxylation to form serotonin, a vasoactive amine. Serotonin synthesis occurs primarily in enterocytes and blood platelets, with a lesser quantity being synthesized in the brain. Some of the brain serotonin is converted to melatonin in the pineal gland.



(DHB)
See also: Essential amino acids; Niacin; Serotonin

Tube feeding: *see* Force feeding

Tubers: *see* Cassava; Jerusalem artichoke; Potato; Sweet potato, Yam

Turbot (*Scophthalmus maximus*) A highly valued flatfish. Landings of wild turbot have declined, generating an interest in commercial turbot cultivation. An industry emerged in the 1980s based on managed broodstocks which are manually stripped of gametes, with 10 days of hatchery incubation at about 10°C for the approximately 1 mm diameter eggs, larviculture using enriched rotifers and *Artemia* diets from about 3 days after hatching, and continuous illumination in large rearing tanks at the higher temperature of about 18°C. Time to market size depends on rearing temperature, nutrition and market demand, but may be 2–3 years. (KP)

Turkey

Origins of the domesticated turkey

The turkey (*Meleagris gallapavo*) was originally domesticated by the Native Americans. The wild turkey contains five sub-species. Its territory included all of Mexico except the extreme southern and western parts and all over the USA south of the Great Lakes and from the Atlantic coast west to Arizona.

The wild turkey is a poor flyer but it can run very fast and, once airborne, can sail for long distances. Settlers in North America consequently found them quite easy to shoot and decimated entire flocks. By 1900, only small populations of the once great flocks still existed. Since then, protective measures by the US Government have resulted in a population explosion to the extent that wild turkeys can now be found as far north as Canada.

Male turkeys destined for breeding should be fed so as to restrict their growth rate.

The domestication of the modern turkey owes much to European influence. It is thought that the first turkeys were brought to Europe by Spanish explorers early in the 16th century. A Yorkshireman, William Strickland, is credited with introducing the domesticated turkey to England. They soon became the favoured meat of royalty and nobility. The domesticated European turkey recrossed the Atlantic with the early European settlers. A further significant importation was of a broad-breasted strain imported from England in the 1920s.

The North American turkey industry proceeded to develop much faster than that of Europe, which suffered shortages of feedstuffs, during and after, the Second World War. Since the 1960s, there has been interchange of genetic material and the genetic stock is now very similar on both sides of the Atlantic.

Breeding programmes

The original domesticated turkeys were coloured bronze, the dominant feather colour being black with the tips of the feathers overlain with iridescent red-green bronzing and some feathers having terminal edging and barring in white.

Because of difficulty of removing all the small, developing black feathers, which then spoilt the appearance of the carcass, the white-feathered turkey now completely dominates the industrial market. However, alternative premium markets have been developed using black or bronze-feathered birds, using the black feathers to identify them as having a traditional farm-produced background.

The breeding programmes are based around breeding specialized lines selected strongly for reproduction to provide the parent female and crossing these with males from lines which have been selected strongly for growth rate and breast conformation. In all lines, fitness and mobility are of overriding concern because it is important for the birds to survive a full breeding season. The relative concentration on reproduction or growth rate differs according to the market for which the commercial cross offspring are destined.

Turkey nutrition

Different breeds have been developed for different markets, with different speeds of growth. The males grow considerably faster than the females. However, it is not normal to formulate different feeds for different breeds or sexes. Instead, the age schedule for feeding the different diets is modified, with the slower-growing breeds going on to the lower-protein diets earlier than the fast-growing breeds. Similarly, the females will go on to lower-protein diets earlier than males. No difference has been demonstrated between the sexes in terms of diet requirements earlier than 8 weeks of age.

The turkey is a high-protein, low-fat animal and as such has a higher amino acid percentage requirement in its diet than the broiler chicken. The turkey's amino acid requirements reduce with increasing age. The closest fit to its requirements is obtained by the use of two feeds of different amino acid content being blended in different proportions each day. Alternatively, whole-grain wheat can be combined with a high-protein pelleted feed. The more normal system is to change the feed formulation every 3 or 4 weeks as age increases.

The nutrient density of the diet is a function of the nutrient proportions and the (metabolizable) energy concentration. The optimum density will depend on ingredient costs, primarily the ratio of the cost of protein-rich ingredients to energy-rich ingredients. Fat is particularly important to the latter category, being of higher energy value than protein or carbohydrate.

The recommended amino acid contents of diets advised by commercial breeding or feed companies are noticeably higher than indicated by published research work. The latter are obtained from work in small pens and at low stocking densities. Commercial recommendations allow for the adverse factors affecting food intake that are experienced by turkeys in commercial conditions. An example of commercial amino acid recommendations is shown in Table 1. The recommendations are expressed as grams amino acid per megajoule of metabolizable energy (ME) to allow for variations in desired nutrient density. The range of the most commonly used ME levels used is also shown.

With its rapid growth rate, it is important that the turkey consumes sufficient minerals for normal bone development. It is also prone to digestive upsets, resulting in wet droppings and subsequent wet litter problems. A potentiating factor can be the electrolyte balance in the feed. Table 2 shows typical mineral inclusion levels and electrolyte balance.

It is not necessary for future breeding stock to grow to maximum potential. It is normal to feed a lower-protein diet than for commercial birds during rearing. The nutrient recommendations given by a major primary breeder for turkey parent stock during rearing are shown in Tables 3a and 3b.

It is very desirable to grow future breeding males slowly after selection (which normally takes place when they are around 17–20 weeks of age). This is usually achieved by feeding a low-protein, high-energy diet *ad libitum* as shown in Table 3. However, some organizations will feed controlled quantities of a higher-protein diet, typically that being fed to hens at the same age, to control growth rate.

The turkey breeding hen has a high food consumption relative to its egg output. For this reason, the calcium content of its diet, which is necessary for shell quality, is lower than in chicken diets. The hen is sensitive to

Table 1. An example of amino acid:energy ratios for growing turkeys (g MJ^{-1} ME).

Age (weeks)	Lysine	Meth.	TSAA	Tryp.	Thr.	Arg.	Range of ME ($MJ\ kg^{-1}$)
0–4	1.57	0.57	1.02	0.27	1.00	1.69	11.7–12.2
4–8	1.34	0.53	0.94	0.23	0.86	1.46	11.9–12.8
8–12	1.10	0.46	0.83	0.19	0.75	1.21	12.1–13.4
12–16	0.89	0.40	0.71	0.15	0.58	1.02	12.2–13.6
16–20	0.75	0.36	0.64	0.13	0.48	0.88	12.3–14.0
20–24	0.65	0.32	0.57	0.11	0.42	0.80	12.5–14.0

ME, metabolizable energy.

Table 2. Typical mineral:energy ratios for growing turkeys (g MJ^{-1} ME) and electrolyte balances.

Age (weeks)	Calcium	Available phosphorus	Sodium	Chloride	Electrolyte balance (meq)
0–4	1.14	0.64	0.13	0.19	280
4–8	1.04	0.58	0.13	0.19	270
8–12	0.94	0.53	0.13	0.19	250
12–16	0.86	0.49	0.13	0.19	230
16–20	0.78	0.46	0.13	0.18	210
20–24	0.74	0.41	0.13	0.18	200

ME, metabolizable energy.

Table 3a. Typical turkey parent stock early-rearing diets.

Age (weeks): Males	0–4	4–8	8–14
Age (weeks): Females	0–4	4–8	8–12
Metabolizable energy (MJ kg^{-1})	11.8	12.0	12.1
Metabolizable energy (kcal kg^{-1})	2820	2860	2900
Crude protein (g kg^{-1})	260–285	230–250	180–205
Lysine (g kg^{-1})	15.7	12.1	10.0
Methionine (g kg^{-1})	6.0	4.8	4.1
TSAA (g kg^{-1})	10.2	8.5	7.2
Tryptophan (g kg^{-1})	2.7	2.2	1.7
Threonine (g kg^{-1})	10.1	7.9	6.5
Arginine (g kg^{-1})	17.0	13.1	11.5
Calcium (g kg^{-1})	13.0–13.5	12.0–12.5	11.0–11.5
Available P (g kg^{-1})	7.5	7.0	6.5
Essential fatty acids (g kg^{-1})	15.0	12.5	10.0

Table 3b. Typical turkey parent stock late-rearing diets.

Age (week): Males	14–17	–	17 to end of life
Age (week): Females	12–16	16–29	–
Metabolizable energy (MJ kg^{-1})	12.1	12.1	13.4
Metabolizable energy (kcal kg^{-1})	2900	2900	3200
Crude protein (g kg^{-1})	130–140	110–125	101
Lysine (g kg^{-1})	5.8	4.9	4.1
Methionine (g kg^{-1})	2.3	1.9	1.4
TSAA (g kg^{-1})	5.1	4.3	3.1
Tryptophan (g kg^{-1})			
Threonine (g kg^{-1})			
Arginine (g kg^{-1})			
Calcium (g kg^{-1})	9.0–9.5	9.0–9.5	9.5–10.5
Available P (g kg^{-1})	3.6	3.6	3.6
Essential fatty acids (g kg^{-1})	1.5	15	15

environmental temperature. High temperatures reduce food intake and increase the tendency of the hen to go broody. For this reason, it is normal to feed different turkey breeding diets according to the season of the year and the local climate. Typical breeding diets are shown in Table 4.

The added vitamin and trace-mineral levels are normally much higher than theoretical requirements, to allow for vitamin losses during processing and storage. Trace minerals are inexpensive. Typical supplements are shown in Table 5.

The use of drugs to prevent diseases and

Table 4. Typical turkey hen breeding diets according to seasonal temperature.

	Cool (mean temperature below 10°C)	Warm (mean temperature 10–25°C)	Hot (above 25°C)
Metabolizable energy (MJ kg^{-1})	12.0	12.1	12.3
Crude protein (g kg^{-1})	153	175	198
Lysine (g kg^{-1})	7.1	8.1	9.2
Methionine (g kg^{-1})	3.6	3.9	4.4
M + C (g kg^{-1})	6.1	6.5	7.3
Calcium (g kg^{-1})	24.5	28	31
Available P (g kg^{-1})	4.0	4.2	4.4
Sodium (g kg^{-1})	1.5	1.6	1.6
Chloride (g kg^{-1})	1.6	1.7	1.7
Essential fatty acids (g kg^{-1})	15.0	17.5	19.5

Table 5. Typical vitamin and mineral supplements (units added per kg feed) for turkey diets.

	Age in weeks			
Nutrient	0–4	4–12	12–29[a]	29–EOL[b]
Vitamin A (IU)	15,000	10,000	8,000	15,000
Vitamin D_3 (IU)	5,000	3,000	2,000	5,000
Vitamin E (mg)	100	40	30	100
Vitamin K (mg)	5	3	3	12
Folic acid (mg)	3	2	2	3
Nicotinic acid (mg)	75	50	40	70
Pantothenic acid (mg)	25	15	15	25
Riboflavin B_2 (mg)	8	6	6	20
Thiamine B_1 (mg)	5	1	1	2
Pyridoxine B_6 (mg)	7	5	3	5
Biotin (μg)	300	300	200	400
Choline chloride (mg)	400	150	100	450
Vitamin B_{12} (μg)	20	20	20	30
Molybdenum (mg)	–	–	–	0.5
Iodine (mg)	2	2	2	2
Selenium (μg)	200	200	200	200
Copper (mg)	50	20	20	20
Iron (mg)	50	20	20	50
Manganese (mg)	120	100	100	120
Zinc (mg)	100	70	70	100

[a] Age for breeders (for growers: 12 weeks to kill). For the pre-breeder diet from 16 weeks onwards, 80% of these levels in this third premix may be included.
[b] For hens in lay only.

the addition of antioxidants and other additives will vary according to local circumstances. To minimize the risk of digestive upsets, it is advised that changes in the ingredients used between diets or batches is kept to a minimum. Because good pellet quality is so important for turkeys, it is advised that a minimum of 15% wheat is included in all diets. Added fat levels should also be limited to the maximum that will allow good pellets to be produced. (CN)

Turkey feeding The day-old turkey (poult) should be given food in the form of crumbles or pellets not larger than 2 mm. Early food intake and growth are reduced if day-old turkeys are given food in meal form but this can be counteracted in part by increasing the nutrient density of the first diet. The age at which the young turkeys move on to pellets depends upon the size of the pellet being presented. If it is 3 mm cut short, i.e.

not much longer than 3 mm, it can be introduced as early as 14 days of age. The longer the pellet, the older the turkeys must be before it is introduced. The optimum changeover age is also influenced by the type of food on which the day-old poults were started. The changeover from meal to 4.5 mm pellets is difficult and may have to be delayed until 6 weeks of age. The optimum grist profile of the crumbles leaving the feed mill should approximate to 80% retained by 1.7 mm sieve and < 7% smaller than 1.18 mm.

It is important that the food is easily accessible to the very young turkey. For the first few days, in addition to food in tubular feeders, food should be presented either on paper or in trays so that the poults walk on the feed. This encourages them to learn to eat. The tubular feeders should not have a rim higher than a poult's shoulders and the level of the food should be kept high to enable the poult to see and reach it easily.

It is important that the poult learns to drink soon after arrival at the farm. Some managers provide only water to the poults on arrival and then introduce the feed an hour or so after arrival. To encourage early drinking the lights should be bright, in order to create a sparkling effect on the water surface, which induces the poult to peck at it and so learn to drink.

It is good practice to turn the lights out 3 h after placement. This prevents overeating, which is thought to be a factor in poults losing their balance and coordination and can result in death from overheating under the brooders. A programme of alternate periods of 3 h light and 3 h dark is recommended for at least the first 36 h, and preferably for a week or longer, to improve liveability and early growth rates.

The food intake of turkeys is sensitive to the pellet quality, i.e. the percentage of broken pellets and dust. Pellet quality is the responsibility of the feed mill but it can be exacerbated by the feed delivery system both to the feed bins and to the feeders within the house. If older turkeys are given feed in meal form, feed intake is markedly reduced, resulting in reduced growth rates and also excessive feed wastage as the turkeys will flick the meal out while looking for larger particles. The drinkers will also contain more feed material, resulting from the meal sticking to beaks during eating. There is circumstantial evidence that meal feeding increases the number of turkeys suffering from pendulous crops.

As the turkeys grow, the feeders and drinkers should be raised accordingly with access being at around shoulder height. The type of feeder and drinker should enable the turkey to eat or drink standing at right angles to the feeder. The bird should not have to resort to feeding at an acute angle to obtain food or water. To prevent wastage by the older turkeys, particularly the males, while the food should have a depth of at least 3 cm, the distance between the food level and the rim of the feeder should be great enough to prevent the birds from flicking the food out and wasting it. The minimum feeder and drinker space increases with age and is greater for males than females. As an indication, for large males, one tube feeder or 120 cm of linear trough space is required for 40 males. Less drinker space is required: one bell-type drinker or 100 cm of linear trough space is required for 100 birds. Breeding birds have similar requirements. If breeding males are being fed controlled quantities per day, they require more feeder space, probably double that recommended for commercial males.

Specially designed feed supplements for feeding the poults during transit and even in the hatchery have been developed with the aim of reducing early mortality. The use of whole-wheat feeding has become more common in recent years and there are several systems for feeding it. One system adds the wheat on top of the pellet feed in the vehicle at the feed mill prior to delivery. By the time it is delivered to the birds, it is mixed with the pellets. The quantity of wheat added is calculated from the feed formulation. If the feed formulation is using 50% wheat, 15% wheat is left in the formulation that is pelleted, to aid pellet quality, and the remaining 35% wheat is added as whole grain. Other systems require two bulk bins: one for the pellets, the other for the wheat. There may be two separate feed bins within the house to allow the birds free choice of wheat or pellets. The better system involves weighing out prescribed quantities of each into a central hopper from which the mixture is delivered into the house. The quantities of wheat can be pre-determined or, in the most sophisticated system, calculated by computer according to the flock weight and the target intake of lysine for that weight. Whole-wheat feeding results in better litter quality and is reported to give a fitter bird. There is a clear cost saving resulting from the wheat not incurring milling charges. (CN)

Turnip *Brassica rapa*, a temperate root crop widely grown for feeding cattle and sheep. It may be used from July to December to provide green feed when grass growth or quality is declining. Root turnips are usually grown in more northerly areas of Europe and take 8 weeks from sowing to feeding, yielding grey-white fleshy tubers, which are very palatable but have laxative properties when fed at high levels. Turnips are usually fed by strip grazing. Intakes by cattle should be restricted to 30–35 kg day^{-1}. Turnips can be included in the diets of dairy and beef cattle at < 50% of the total diet, calves at < 20%, lambs at 25% and ewes at 75%. The dry matter (DM) content of turnips is 105 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is crude protein 115, crude fibre 105, ether extract 10, digestible crude protein 85, neutral detergent fibre 254, ash 65, starch 7 and sugar 550, with MER 12.5 MJ kg^{-1}. (JKM)

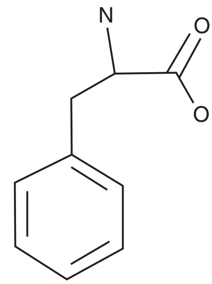
Turnover A concept used to describe dynamic aspects of metabolism. It represents the molecular flow or flux of a metabolite, and has units of mol min^{-1}. Turnover describes the continuous synthesis and breakdown of an individual metabolite such as acetyl-CoA or of polymers such as proteins, fats and glycogen. Measurement of turnover is facilitated by the use of isotopic tracers. The rate of entry of a tracer into a molecular pool such as glucose or protein can be measured and from this the turnover rate can be calculated and expressed as the fractional turnover rate (i.e. % day^{-1}). If the size of the pool is also measured, an absolute turnover rate (i.e. mol min^{-1}) can be calculated. (NJB)

Twin lamb disease A form of ketosis, so called because ewes in late pregnancy with more than one fetus are particularly susceptible, although it can occur in single-bearing ewes and non-pregnant sheep, including rams. It is due to the toxic effects of ketones produced in excessive quantities during rapid mobilization of adipose tissue when food supply is short and energy requirements are high. An affected animal staggers, collapses and if not treated dies within a few hours. It is also known as snow-blindness, because heavy snow prevents grazing and the early symptoms include apparent blindness in affected animals. Treatment is by rapid supply of energy-yielding substrates, the most common method being oral administration of glycerol by gavage. Over-fat animals are particularly susceptible. (JMF)

Twinning The production of two offspring by the same female at the same time. Often defined at their birth, but strictly refers to the conception of two individuals when an embryo splits after fertilization, giving rise to identical twins, or when two ova are fertilized. The incidence of twinning in dairy cattle is approximately 2% and in beef cattle approximately 0.5%. Twinning is the norm in goats and is common in sheep, with a large variation between breeds. Twinning is unusual in horses and twin pregnancies tend not to be carried to term. (PJHB)

Tyramine A pressor amine, $C_8H_{11}NO$, molecular weight 137, produced from tyrosine by L-aromatic amino acid decarboxylase, primarily by bacterial action. It is metabolized in gut tissue and liver by monoamine oxidase to the corresponding aldehyde and NH_3. Its biological actions are somewhat similar to those of adrenaline. If monoamine oxidase action is blocked or insufficient, tyramine accumulation in the organism can elevate blood pressure to dangerous levels. Tyramine production is increased during acute rumen acidosis and tyramine accumulation may play a role in the pathogenesis of the acidosis. (JAM)

Tyrosine An aromatic amino acid ($HO{\cdot}C_6H_4{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$, molecular weight 181.2) found in protein. It is synthesized from phenylalanine. The hydroxylation of phenylalanine to form tyrosine is an irreversible reaction. Both phenylalanine and tyrosine are required for protein synthesis, but excess phenylalanine can meet the physiological need for tyrosine. Of the total requirement for aromatic amino acids (Phe + Tyr), about half is for phenylalanine and half is for tyrosine. Tyrosine is catabolized primarily through homogentisic acid to fumarate and acetoacetate. A smaller portion of tyrosine is metabolized to thyroxine, norepinephrine, epinephrine and melanin.



(DHB)

See also: Epinephrine; Norepinephrine; Phenylalanine; Thyroid consist of calcium phosphate, calcium oxalate and magnesium ammonium phosphate but uric acid and other crystals may also be found. Urinary infection with an organism capable of hydrolysing urea, e.g. *Proteus* spp., favours the formation of an alkaline urine and crystals of magnesium ammonium phosphate. In some dry areas, e.g. South Australia, renal calculi of silica may be formed by grazing ruminants as a result of a low intake of water and the absorption of micro crystals of silica from the intestinal contents. Excessive urinary excretion of calcium and phosphate in primary hyperparathyroidism is associated with the incidence of renal calculi containing calcium phosphate. In housed lambs fed a high-concentrate diet at more than 1.5% body weight, urolithiasis begins. This is especially true when the diet is high in magnesium. The ingestion of relatively large quantities of oxalate and a high dietary intake of phosphate are also factors that may be involved in the incidence of urolithiasis. Depressed water intake, resulting in increased concentrations of the precipitating salts in the urine, is a major underlying cause of the condition. Another is the formation of a nucleating centre of desquamated epithelial cells which favours the deposition of crystals about itself. A deficiency of vitamin A or an excess of oestrogen may both exacerbate this phenomenon. (ADC)

Uronans Polysaccharides in which the main sugar residue is uronic acid. The primary uronic acids are glucuronic acid in animals and galacturonic acid in plants. (JAM)
See also: Carbohydrates; Dietary fibre; Galactouronans; Glucuronic acid; Pectic substances; Rhamnogalactouronans; Uronic acids

Uronic acids The most important type of acidic sugars, occurring almost exclusively as hexuronic acids. Oxidation of the terminal alcohol group or non-reducing end of a sugar gives rise to a uronic acid. In biosynthetic sequences, hexuronic acids are intermediates in the conversion of hexoses into pentoses via oxidation and decarboxylation. In animal metabolism, D-glucuronic acid is conjugated with a wide variety of compounds, e.g. steroids, phenols, aromatic carboxylic acids and pharmaceutical agents, increasing their solubility and thus promoting their urinary excretion. D-Glucuronic and D-galacturonic acids are also found in plant gums and bacterial cell walls. As the major sugar residue in uronans and pectic substances, galacturonic acid is widely distributed in the plant world, functioning as a structural polysaccharide, frequently in close association with cellulose, and as a storage polysaccharide. D-Mannuronic and L-glucoronic acids are found in algae, D-glucuronic acid is a component of proteoglycans and L-iduronic acids are components of two of the glycosaminoglycans, dermatan sulphate and heparin. D-Glucuronic acid is also a component of heparin. Uronic acids are difficult to isolate from natural sources; the strong acidic conditions necessary to break glycosidic linkages cause decarboxylation and elimination reactions. (JAM)
See also: Carbohydrates; Dietary fibre; Galactouronans; Galacturonic acid; Glucuronic acid; Pectic substances; Uronans

Utilization, energy: *see* Energy utilization

Utilization, protein: *see* Protein utilization

Ultrasound Sound with frequency above the audible range (20 kHz to 1000 MHz). Ultrasound is widely used in biology and medicine for measuring and imaging body tissues. Simple ultrasound reflectance machines are used to measure the thickness of fat and muscle in meat animals. Ultrasonic scanning is used to provide detailed images of body tissues, especially when X-rays would be damaging. Ultrasound is transmitted into the body by the scanner and the reflected ultrasound waves from the internal tissues are detected and displayed as a real-time image on a screen. Ultrasound has a number of other applications in industry, biology and medicine, based on its diverse effects on gases, liquids and solids. (SPL)

Undegradable dietary protein (UDP) Protein that is resistant to, or escapes, hydrolysis and degradation by rumen microorganisms. In ruminants, metabolizable protein (MP) requirements are met by a combination of effective rumen degradable protein (ERDP), which microorganisms use to produce microbial crude protein (MCP), and UDP. MCP synthesis alone may not be sufficient to meet the MP requirements of productive animals, and in such situations UDP levels must be sufficient to make up the requirement. UDP can be maximized by including protein food sources resistant to microbial degradation, such as fish meal or artificially protected soybean. However, the ERDP (and thus UDP) of feeds in the rumen is not constant. ERDP is affected by the rate at which feed passes through the rumen. Increasing the feed intake by increasing the proportion of highly digestible food increases the rate at which it passes through the rumen. This reduces the length of exposure of the food to rumen microorganisms and therefore its degree of digestion.

For the most effective use of protein-containing feeds there is a need to classify feedstuffs by the rumen degradability of their protein, but there are no simple reliable methods for measuring this. It can be determined directly *in vivo* in fistulated animals, or estimated by incubating test samples of food in dacron bags within the rumen (the *in sacco* method). *In vitro* methods using isolated enzymes, microorganisms, or infrared reflectance spectroscopy are being developed. (JKM)

Underfeeding: *see* Undernutrition

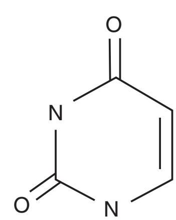
Undernutrition A general lack of all nutrients due to insufficient intake of food and failure to achieve the potential appetite. Short-term or moderate undernutrition due to temporary lack of food is not detrimental to production, except in young animals in which the tissues growing most rapidly at the time of undernutrition are most affected, sometimes permanently. Body tissues may be mobilized to compensate for particular deficiencies, particularly in energy intake. Long-term undernutrition and inanition leads to starvation and eventual death. (JMF, CJCP)

See also: Malnutrition; Stunting

Unsaturated fatty acids Fatty acids with one or more double bonds C=C making up the fatty acid chain. Unsaturated fatty acids can be monounsaturated (having one double bond) such as oleic acid (18:1) or polyunsaturated (having two or more double bonds) such as arachidonic acid (20:4). (NJB)

Uptake: *see* Absorption

Uracil A pyrimidine base, $C_4H_4N_2O_2$, found in RNA as the nucleoside uridine. It is not found in DNA.



(NJB)

Urea A nitrogenous end-product of amino acid catabolism, $CO{\cdot}(NH_2)_2$, excreted in urine. Variable proportions of the total production of urea are excreted into the intestinal tract in both ruminants and non-ruminants. In ruminant animals, urea secreted into the rumen via saliva is used as a nitrogen source by rumen bacteria and under conditions of limited dietary nitrogen intake can add substantially to the nitrogen economy of the animal. In some cases the microbial nitrogen outflow from the rumen can exceed the dietary nitrogen intake. In non-ruminants, most of the amino acid synthesis by intestinal microflora occurs distal to the site of amino acid absorption and so microbial protein is not a major source of nitrogen for body functions, because most is excreted in the faeces. Urea is synthesized in the liver by enzymes of the urea cycle: the immediate nitrogen precursors are ammonium and aspartate. (NJB)

Urea cycle A sequence of reactions in which nitrogen, from ammonium and aspartate-N (from amino acid-N), is converted to urea, the main end-product of nitrogen metabolism in mammals. The urea cycle is the main process for the detoxification of ammonia. In the synthesis of urea, NH_4, CO_2 and N from aspartate and four ATP equivalents are used in the reaction sequences shown at the bottom of the page.

The complete urea cycle is found only in liver, and analysis of the subcellular distribution of the urea cycle enzymes shows that some are housed in the matrix of the mitochondrion while the remainder are found in the cytoplasm. The mitochondrion has two membranes. The inner is less permeable than the outer and requires a transporter for many metabolites to enter or exit from the matrix. A source of ammonium nitrogen into the matrix (probably glutamate or glutamine and transport-dependent) as well as ornithine and citrulline must also be transported across the inner mitochondrial membrane.

The first step in urea biosynthesis occurs in the matrix of the mitochondrion. In this step 1 mol ammonia combines with 1 mol CO_2 to form carbamyl phosphate. This reaction, $NH_4 + CO_2 + 2ATP \rightarrow$ carbamyl phosphate + 2ADP, is carried out by carbamyl phosphate synthetase-1. The next step is the combination of carbamyl phosphate with ornithine to form citrulline. This step is carried out by the enzyme ornithine transcarbamoylase. The second transport requirement for urea biosynthesis is the transport or ornithine into the mitochondrial matrix followed by its conversion to citrulline and the transport of citrulline out of the matrix. The next step in the cycle is the synthesis of arginosuccinate carried out by argininosuccinate synthetase. The reaction, citrulline + ATP + aspartate $\rightarrow$ argininosuccinate + AMP + P~P, utilizes two ATP equivalents and the second nitrogen for urea comes from aspartate. The third reaction of the cycle is carried out by argininosuccinate lyase, which cleaves argininosuccinate to arginine and fumarate. Fumarate is reduced to malate, which requires a transporter to enter the mitochondrion and be converted into aspartate for the synthesis of the next molecule of urea. The movement of aspartate out of the matrix is yet another transport step. To complete the cycle arginine is cleaved by arginase to yield urea and ornithine which, once it is transported into the matrix, can again be used to form citrulline. (NJB)

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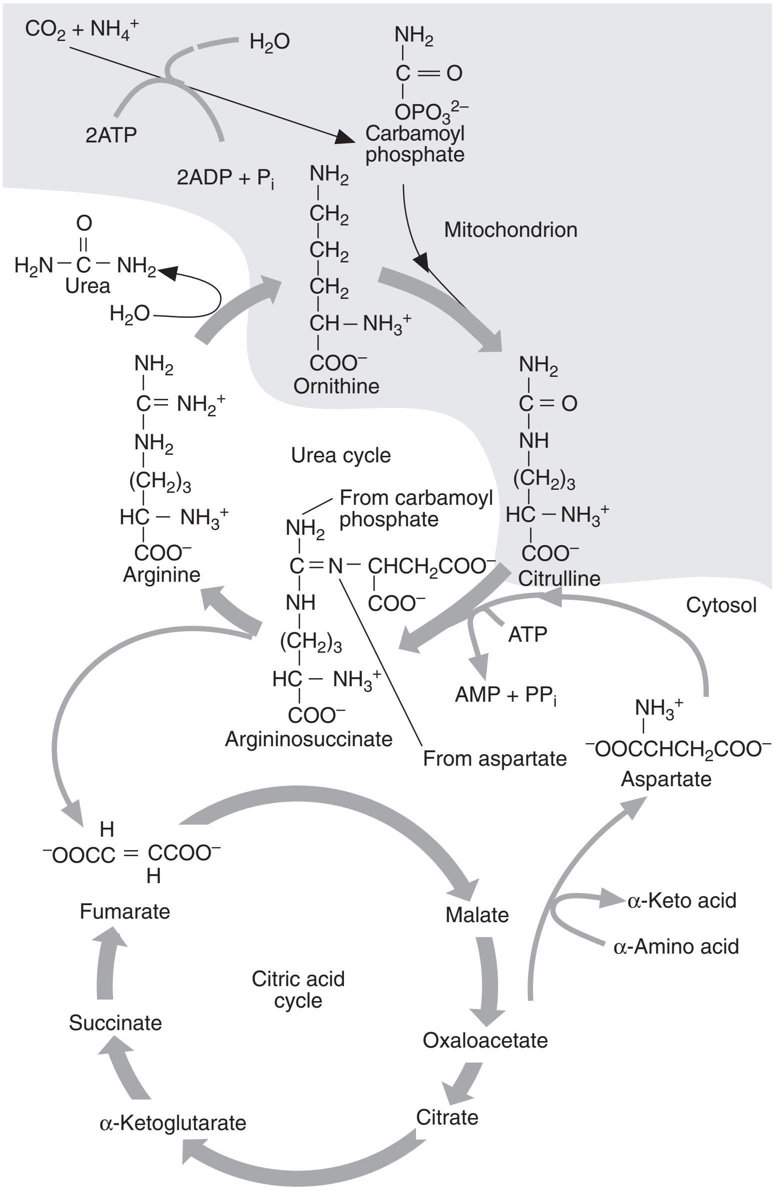
Urease An enzyme that catalyses the conversion urea to ammonium and bicarbonate ($CH_4N_2O + 2H_2O + H^+ \rightarrow 2NH_4^+ +$

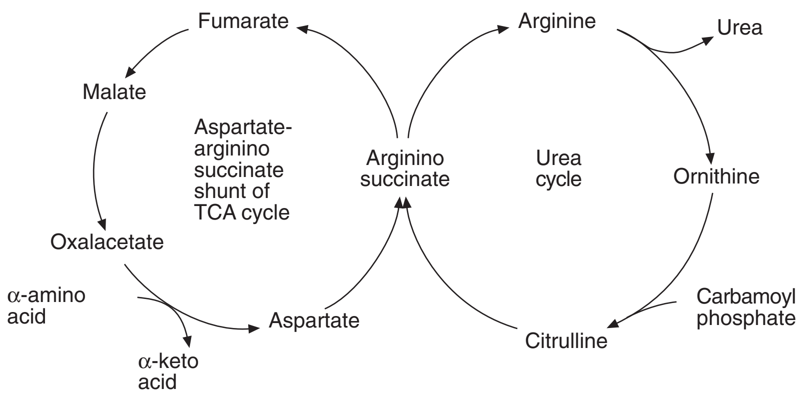
$NH_4 + CO_2 + 2ATP \rightarrow$ carbamyl phosphate + 2ADP
Carbamyl phosphate + ornithine $\rightarrow$ citrulline
Citrulline + ATP + aspartate $\rightarrow$ argininosuccinate + AMP + P~P
Argininosuccinate $\rightarrow$ arginine + fumarate
Arginine $\rightarrow$ urea + ornithine.



The urea cycle.

HCO_3^-). It is found in legume seeds such as soybean and jackbeans. Urease is not produced by higher animals but is produced by certain intestinal bacteria and is found throughout the digestive tract. Microbial urease is critical to the recycling of nitrogen, especially in ruminants, because it makes urea-N available for microbial use. (NJB)

Uric acid A nitrogenous end-product of amino acid and purine catabolism, $C_5H_4N_4O_3$. It is the main end-product of nitrogen metabolism in birds, in which it is excreted in combination with the faeces, but is also found in the urine of mammals. In the production of uric acid, one molecule of glycine provides two carbon atoms (C) and



The relationship of the urea cycle to the TCA cycle.

one nitrogen atom (N), aspartate one N, glutamine two N, carbon dioxide one C and the folate system two C. Because this form of nitrogen excretion draws on the folate one-carbon system it increases the demand for folate carbon, leading to a potential shortage of methyl groups for other processes such as nucleic acid biosynthesis. (NJB)

Urinary tract diseases Cystitis is an inflammatory condition of the bladder which is usually caused by a bacterial infection. It is accompanied by frequent, painful urination. It is commonly associated with calculi within the bladder and also with stagnation of the urine so that bacteria ascending via the urethra can invade damaged mucosa. The urine may contain blood. Rupture of the bladder occurs most commonly in castrated male ruminants because of obstruction of the urethra by calculi (*see* **Urolithiasis**). The diameter of the urethra may be reduced by a high level of dietary oestrogens, e.g. from grazing subterranean clover. After rupture, abdominal distension soon becomes apparent and death follows within 2–3 days. (ADC)

Urine A pale yellow fluid derived from blood filtered by the kidney. Filtration takes place in the glomerulus of the kidney nephron. The glomerular filtrate passes through the nephron to the collecting duct and is then stored in the bladder until it is discharged. The volume of urine produced per day is dependent on the amount of fluid consumed and the rate of evaporative water loss. With a constant fluid intake, more evaporative water loss results in less urine being produced. Urine is a complex fluid, its composition changing with the metabolic state of the animal. It contains nitrogenous compounds such as protein, urea, ammonium, creatine, creatinine, uric acid, allantoin and amino acids. Ketone bodies, citric acid and volatiles such as phenols are also found, as well as sulphate, carbonate and the mineral elements chloride, potassium, sodium, calcium, copper, magnesium, iron, etc. Methylated and sulphated detoxification products are also excreted in the urine. The pH of urine can range from acid (pH 4–5) to basic (pH 8–9), depending on the diet and other factors. (NJB)

Urolithiasis The formation of urinary calculi. Urine is normally supersaturated with regard to calcium, magnesium and phosphate and, in some species, also oxalate and urate. The solubility of calcium and magnesium is increased by chelation with organic acids, e.g. citrate, but the potential for this chelation to take place decreases in acid urine. There are specific inhibitors of crystallization in urine, such as pyrophosphate. The latter is increased during increased dietary intake of orthophosphate but its urinary concentration is insufficient to account for all the inhibition of crystallization noted in normal urine. The identity of the other inhibitors is unknown. Renal stones commonly consist of calcium phosphate, calcium oxalate and magnesium ammonium phosphate but uric acid and other crystals may also be found. Urinary infection with an organism capable of hydrolysing urea, e.g. *Proteus* spp., favours the formation of an alkaline urine and crystals of magnesium ammonium phosphate. In some dry areas, e.g. South Australia, renal calculi of silica may be formed by grazing ruminants as a result of a low intake of water and the absorption of micro crystals of silica from the intestinal contents. Excessive urinary excretion of calcium and phosphate in primary hyperparathyroidism is associated with the incidence of renal calculi containing calcium phosphate. In housed lambs fed a high-concentrate diet at more than 1.5% body weight, urolithiasis begins. This is especially true when the diet is high in magnesium. The ingestion of relatively large quantities of oxalate and a high dietary intake of phosphate are also factors that may be involved in the incidence of urolithiasis. Depressed water intake, resulting in increased concentrations of the precipitating salts in the urine, is a major underlying cause of the condition. Another is the formation of a nucleating centre of desquamated epithelial cells which favours the deposition of crystals about itself. A deficiency of vitamin A or an excess of oestrogen may both exacerbate this phenomenon. (ADC)

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Utilization, energy: *see* Energy utilization

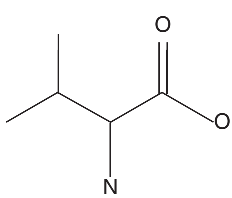
Utilization, protein: *see* Protein utilization

V

Valeric acid Pentanoic acid, an odd-chain saturated short-chain fatty acid, $CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COOH$, molecular weight 102.13. It may be produced by fermentation during digestion or from partial degradation of longer odd-chain fatty acids. (NJB)

Valine An essential amino acid $(CH_3)_2{\cdot}CH{\cdot}CHNH_2{\cdot}COOH$, molecular weight 117.2) found in protein. Valine is one of the three branched-chain amino acids (with leucine and isoleucine). It is purely gluconeogenic, yielding propionate as an end-product of catabolism. The first two enzymatic reactions involved in valine catabolism use the same enzymes that catabolize leucine and isoleucine. The first reaction involves transamination, primarily in muscle. This produces the keto analogue, ketoisovaleric acid. This is then oxidatively decarboxylated, primarily in liver, by branched-chain keto acid dehydrogenase to the CoA derivative.

After lysine, which is first limiting in low-protein maize–soybean meal diets, valine is among the next limiting amino acids (along with one or more of tryptophan, threonine and methionine) for young pigs, chickens and turkeys.



(DHB)

See also: Essential amino acids

Vanadium Vanadium (V) is a mineral element with a molecular mass of 50.9415. It exists in nature in four valency states of +2, +3, +4 and +5. It exists in biological systems primarily in the metavanadate (VO_3^-) or the orthovanadate ($(HO)_2VO_2^-$) configurations. The concentrations of V in animal organs and tissues range from 10 to 200 μg kg^{-1} fresh sample (muscle to testes, respectively). This low concentration is perhaps caused by the fact that both the natural intake of V and the rate of absorption are very low. Estimates of V absorption show that < 1% of the intake is transferred from the intestinal tract to the body.

Initial studies suggested that V was an essential nutrient for animals. Less than 10 μg V kg^{-1} diet seemed to retard feather growth and body weight in chicks when compared with higher dietary amounts. The addition of 100 μg V kg^{-1} diet increased growth in laboratory animals previously fed a low-V diet. Although these studies seemed to suggest that V was a positive factor in the diets of animals, the results have not been confirmed. The effects may arise from a pharmacological response, because vanadate can act as insulin mimetic that stimulates glucose metabolism in insulin-responsive organs. This attribute of V is so effective that it has been tested recently as a supplement in the management of human diabetes mellitus.

Because of the questionable and variable nature of the responses of animals to V supplements, this element is not considered to be an essential nutrient by the US National Research Council, which has therefore not provided a recommended dietary requirement level for V for any of the farm species. Vanadium is a very toxic element and the maximal recommended intake for many species of animals is around 20 mg kg^{-1} diet. (PGR)

See also: Ultra-trace elements

Further reading

Nielsen, F.H. (1997) Vanadium. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements.* Marcel Dekker, New York, pp. 619–630.

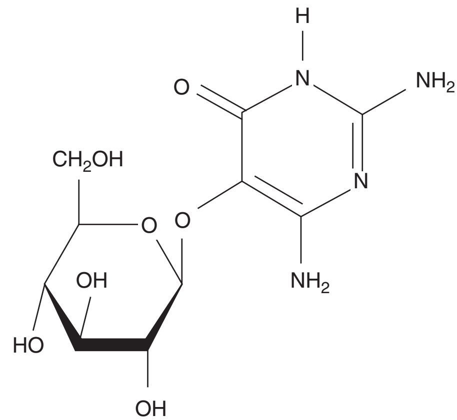
Vasoactive intestinal peptide Vasoactive intestinal peptide (VIP) is a 28 amino acid polypeptide that is released from nerve endings, primarily throughout the gastrointestinal tract. This neurocrine substance acts through a cyclic-adenosine monophosphate (cAMP)-mediated intracellular pathway to cause the relaxation of smooth muscle in both intestine and blood vessels. VIP regulates intestinal motility and blood flow, and may also stimulate pancreatic and intestinal secretions. (GG)

Veal calves: *see* Calf

Verbascose An oligosaccharide of five sugar residues, three galactoses and one glucose, all 1→6-linked, and fructose, linked to the glucose via 1→2 linkage, molecular weight 828. Verbascose is present in small amounts in the tubers, rhizomes and seeds of certain plants, where its accumulation during maturation and disappearance during germination suggests it is a reserve carbohydrate. The classic source is mullein (*Verbascum thapsus*) root. (JAM)
See also: Carbohydrates; Oligosaccharides

Very low-density lipoproteins (VLDL) A plasma triacylglycerol-rich (> 60%) lipoprotein of density < 1.006 synthesized in the liver of non-ruminants. The predominant apoprotein is apoB100. (DLP)

Vicine A gluco-alkaloid ($C_{10}H_{16}N_4O_7$, molecular weight 304) isolated from the seed of *Vicia sativa* and *V. faba*, both legume vetches. Poisoning in livestock has been reported from these plants as well as *V. villosa* (hairy vetch). Ingestion of hairy vetch seeds caused death in chicken and turkey poults. In a survey of 23 herds of cattle, ingestion of hairy vetch apparently caused dermatitis, conjunctivitis and diarrhoea, with 6–8% morbidity and 50% mortality among those affected. Abortion was reported occasionally among the herds affected.



(KEP)

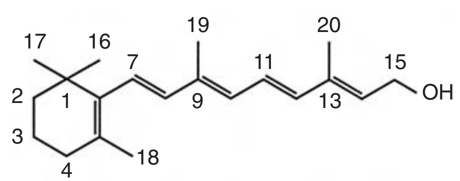
Villi (singular: villus) Fingerlike projections of the epithelial cell layer of the small intestine which increase the surface area for absorption tenfold. (SB)
See also: Gastrointestinal tract

Vinasse The residue from alcoholic fermentations, especially those based on beet sugar. A rich source of phosphorus, it is used in livestock feeding and as a fertilizer. (MFF)

Viscosity The frictional resistance of a fluid, which reduces its ability to flow freely. Certain non-starch polysaccharides (NSPs), such as β-glucans from barley, often increase the viscosity of digesta through the water-holding capacity of their large hydrophilic molecules. These NSPs can reduce nutrient absorption, increase water consumption and alter the gastrointestinal microflora. They also cause wet and sticky excreta and litter, which may increase the incidence of ill health, dirty animals and dirty products such as eggs. (TA)

Vitamin A Vitamin A is a descriptor for all compounds (other than carotenoids) that possess the biological activity of all-*trans* retinol. Retinol supports all known functions of the vitamin. The term provitamin A is used to describe carotenoids that give rise to vitamin A activity. Quantitatively, the most important carotenoid is all-*trans*-β-carotene. Most farm animals obtain their vitamin A in the form of carotenoids, unless their diets are supplemented artificially. The Committee on Animal Nutrition of the National Academy of Sciences–National Research Council periodically updates the requirements for provitamin A carotenoids and vitamin A for most domestic animals (http://www.nap.edu/index.html).

Retinol consists of a non-aromatic ring structure, an isoprenoid side chain and an alcohol functional end group (see figure). Retinol exists predominantly in the all-*trans* configuration. Retinol is sensitive to destruction by oxidation and isomerization by ultraviolet light. Vitamin A must be obtained in the diet of all farm mammals and birds and is required for normal growth and cellular differentiation, reproduction and vision. Retinol exists in animal products almost exclusively in the form of retinyl ester (primarily as the palmitate ester), whereas in plants, carotenoids serve as the retinol precursor. The major natural sources of provitamin A for livestock are green pasture, silage and hay. Most other common feeds, except yellow maize, contain little provitamin A activity. Lucerne meal has been used as a source of supplemental provitamin A activity. In addition, synthetic vitamin A can be fed as a component of a mixed ration or included in vitamin/mineral mixtures. Retinyl esters, often in conjunction with an antioxidant, are most commonly used for this purpose.



Retinyl esters are hydrolysed in the intestinal lumen to retinol by the action of a pancreatic retinyl ester hydrolase and absorbed as the free alcohol. In contrast, carotenoids are absorbed as such and metabolized to retinol once inside the intestinal enterocyte. There, retinol is re-esterified with palmitic or stearic acid, incorporated into chylomicrons and secreted into the lymphatic system. The majority of retinyl ester is taken up by the liver, with much of that remaining taken up by bone marrow cells. In the parenchymal cells of the liver the retinyl ester is hydrolysed to retinol, which is then re-esterified and stored in the liver stellate cell or exported for delivery to the peripheral target tissues. Retinol is the primary vitamin A metabolite found in the blood and it circulates bound to a serum retinol-binding protein (RBP), which is also bound to transthyretin (prealbumin).

Vitamin A deficiency can be demonstrated in nearly all farm animals. The signs of vitamin A deficiency in mammals include night blindness, abnormal keratinization of mucus-secreting epithelial tissues (for example, trachea and vagina), poor growth, reproductive abnormalities in both the male and female and fetal anomalies. For example, in pregnant cows, deficiency of the vitamin can lead to the birth of dead, uncoordinated or blind calves. In the chicken, hypovitaminosis A leads to poor growth, loss of vision, ataxia, epithelial abnormalities, kidney lesions and a fall in egg production.

The vitamin A metabolite, retinaldehyde, plays an essential role in vision. In the pigmented epithelium of the retina, esterified all-*trans* retinol is hydrolysed and isomerized to 11-*cis* retinol and further oxidized to 11-*cis* retinaldehyde, which is shuttled to the rod outer segment of the eye to combine with opsin to form rhodopsin. It is this form of the vitamin that plays a key role in enabling vision in dim light. 11-*cis* Retinaldehyde also serves as a light-absorbing pigment in the cone cells of the retina which are responsible for vision in daylight.

Retinaldehyde can be further oxidized to another active vitamin A metabolite, retinoic acid. The all-*trans* configuration of retinoic acid is the most abundant form. All-*trans* retinoic acid acts by binding to nuclear retinoic acid receptors (RARs) to satisfy the growth and differentiative functions of the vitamin. There are three subtypes of RAR (α, β and γ) encoded by three separate genes, and multiple isoforms are produced by alternative splicing or differential promoter use. These receptors serve as ligand-activated transcription factors which regulate the state of activity of retinoid-responsive genes. The RARs bind to specific sequences of DNA called retinoic acid response elements. In conjunction with other proteins, including the heterodimeric retinoid-X receptor (RXR) partner and other co-modulator proteins, the ligand-bound RAR regulates transcription by derepressing higher order chromatin structure and by facilitating transcriptional initiation (in the case of positively regulated genes). The mechanistic details of transcriptional repression are less well understood. The changes in gene expression elicited by all-*trans* retinoic acid are cell-type specific and result ultimately in changes in cell activity or differentiation. Additional retinoic acid isomers (9-*cis* retinoic acid, 13-*cis* retinoic acid, 9,13-*cis* retinoic acid) and oxidation products (4-hydroxy-all-*trans* retinoic acid, 4-oxo-all-*trans* retinoic acid, 18-hydroxy-all-*trans* retinoic acid and 4-oxo-13-*cis* retinoic acid) have been described but the importance of these metabolites in normal physiology remains to be resolved. The 9-*cis* isomer of retinoic acid has been shown to bind to the RXR which serves as a heterodimeric partner for many nuclear receptor proteins, including the RAR. However, the necessity for RXR ligand in vitamin A signalling has not been proven. Oxidized metabolites of retinoic acid are believed to represent retinoic acid catabolites, although a number of these have been shown to retain some biological activity. Additional vitamin A metabolites have been described (14-hydroxy-4,14-retro-retinol, 4-hydroxy-retinol and 4-oxo-retinol) but their physiological importance remains to be established.

Animals made deficient in vitamin A and then fed all-*trans* retinoic acid appear normal with the exception of night blindness, thus questioning the biological importance of the aforementioned retinol metabolites. In the chicken 3,4-didehydroretinoic acid is present in addition to all-*trans* RA, and these metabolites appear to be equipotent in RAR binding and gene expression. Both retinol and retinoic acid are subject to glucuronidation. (MC-D)

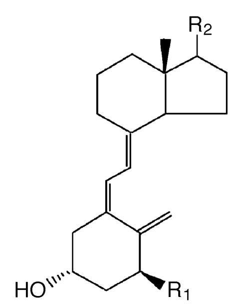
See also: Carotenoids; Retinyl palmitate

Vitamin A excess Vitamin A and its metabolites given in excess can be toxic. Toxicity can result from acute exposure or chronic administration of retinyl esters or exposure of embryos to vitamin A or its metabolites at critical times in development. In both animals and humans, toxicity can also result from the pharmacological administration of retinoic acids or active retinoid analogues. Lesions include mucous cell formation in keratinized membranes, scaly or thickened skin, bone softening and fracture, haemorrhage and fetal resorption or congenital abnormalities. An upper limit for safe intake of retinyl ester in cattle has been set by the National Academy of Sciences USA at 16–30 times the daily requirement. In contrast, carotenoids do not appear to be toxic, even in large amounts. (MC-D)

See also: Carotenoids; Retinoids; Retinyl acetate; Retinyl palmitate; Vitamin A

Vitamin B complex: *see* B-complex vitamins

Vitamin D Vitamin D is a general term to describe compounds that act in preventing the disease rickets in the young and osteomalacia in the adult. It functions by its conversion first in the liver to 25-hydroxyvitamin D and in the kidney to 1,25-dihydroxyvitamin D. This hormonal form of vitamin D then stimulates the intestine to absorb calcium and phosphorus, stimulates osteoblasts and osteoclasts of bone to mobilize calcium from bone, and stimulates renal reabsorption of calcium together with the parathyroid hormone. The elevation of these mineral nutrients in blood results in the mineralization of the skeleton and the prevention of hypocalcaemic tetany, a disease of convulsions resulting from low blood calcium. The vitamin D hormone, i.e. 1,25-dihydroxyvitamin D, functions by interacting with a nuclear receptor that forms a transcription complex on target genes with specific DNA elements called vitamin D responsive elements. Vitamin D has the general structure:



where R_1 is H or OH and R_2 is a hydrocarbon side chain. (HFDeL)

Vitamin deficiencies Vitamin deficiencies may occur due to inadequate concentrations in the diet, to storage or processing losses, or to inadequate absorption. The requirements are low in comparison with other nutrients and in some cases the gut microflora can synthesize adequate quantities for their host. For ruminants this usually provides adequate supplies, but for non-ruminants the caecal and large intestine fermentation may occur after the site of absorption, leading to low levels of absorption unless the animal is coprophagous. The table overleaf gives the most common symptoms of deficiency of all the vitamins and pseudovitamins. (CJCP)

Vitamin E One of the four fat-soluble vitamins. All of the compounds with E activity are 6-hydroxychromanes (substituted 6-member heterocyclic double rings) with 16-carbon phytanyl or isoprenoid side chains. The homologue (also called a vitamer) with greatest vitamin E activity is α-tocopherol ($C_{29}H_{50}O_2$, molecular weight 430.69). The four naturally occurring tocopherols, i.e. α, β, γ and δ (*see* **Tocopherols**), each contain three asymmetric carbons at C-2, C-4′ and C-8′. Each has the potential for the *R* or *S* configuration. All of the natural tocopherols have the *R* configuration at C-2, C-4′ and C-8′, are designated by the prefix '*RRR*' and exist in plants in the active, unesterified form. Chemical synthesis of a tocopherol results in random assembly at each of the asymmetric carbons. Thus, a total of eight stereoisomers (2^3) results when a specific tocopherol is chemically synthesized. The mixture of stereoisomers resulting from chemical synthesis of a tocopherol is designated by the prefix 'all racemic' or 'all-rac'.

Vitamin E is biosynthesized in leaf chloroplasts and found in the lipid-rich areas of plant cells, such as membranes and in oil droplets. Hence, vegetable oils are good sources of vitamin E, which occurs principally as α, γ and δ tocopherol. Vitamin E activity was first associated with the ability of lettuce leaves to prevent fetal resorption in animals fed rancid lard. Later, α-tocopherol was isolated from wheatgerm oil. Tocopherols in feeds are released from their *in vivo* locations in plants during digestion. Likewise, commercially prepared α-tocopheryl esters are hydrolysed by esterases in intestinal contents to α-tocopherol. Absorption of the alcoholic forms is concurrent with and facilitated by other fats in the diet, but they must be solubilized by bile acids in order to interact with the surface of enterocytes where vitamin E is absorbed by a non-saturable, non-carrier-mediated, passive diffusion process. Tocopherols may also gain access to enterocytes as part of micelles. In the enterocyte, they are incorporated into chylomicrons, which are transported to the lymphatics, thence to the thoracic duct and into the bloodstream. The efficiency of absorption is relatively low (20–40%). Diseases or conditions that affect lipid absorption are likely to result in diminished absorption of the tocopherols and hence can lead to a deficiency of vitamin E.

The liver discriminates among the various forms that arrive in the chylomicrons. α-Tocopherol is preferred, as are those stereoisomers with the 2*R* configuration. The selectivity is believed to be imposed by the hepatic tocopherol transfer protein which facilitates α-tocopherol incorporation into VLDL for delivery to tissues. α-Tocopherol is stored in cellular lipophilic locations such as cell membranes and adipocytes. Tissues that accumulate the greatest concentrations of α-tocopherol are adipose tissue and adrenal gland. The turnover of α-tocopherol varies greatly between tissues. In rats fed *RRR*-α-tocopheryl acetate, the half-life of α-tocopherol was less than 11 days for plasma, liver and small intestine; 11–15 days for erythrocytes, heart and skeletal muscle; and 29–77 days for brain, testes, adipose tissue and spinal cord.

The biological effectiveness of the eight stereoisomers of α-tocopherol produced in the chemical synthesis of the vitamin have been evaluated using the rat resorption–gestation assay (*International Journal of Vitamin Research* 52, 351–372, 1982). The relative values of the four isomers of α-tocopherol with C-2 in the *R* form are (in IU mg^{-1}) 1.49 (4*R*, 8*R*), 1.34 (4*R*, 8*S*), 1.09 (4*S*, 8*S*) and 0.85 (4*S*, 8*R*). Values for the C-2 *S* series of α-tocopherol are roughly one-third of their *R* counterpart. One international unit (IU) is

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
A (retinol)	Eye disorders and xerophthalmia in extreme cases, skin disorders, low milk yields and rebreeding difficulties in cattle	Rare except in cattle fed a diet low in β-carotene	Ruminant diet lacking green forage
Biotin	Epidermal tissue disorders, scaly skin, foot lesions, soft keratinized tissues (hoof, beak, horn)	Largely unknown, especially in ruminants	Low availability in wheat and barley
B_1 (thiamine)	Reduced energy availability, muscle weakness and cramps, head bent back (star-gazing), heart defects	Rare due to ubiquitous presence of thiamine in food and synthesis by micro-organisms	Fish products containing thiaminase
B_2 (riboflavin)	Slow growth and various species-specific disorders, e.g. clubbed down and curly toe in chicks, nerve degeneration in pigs	Rare in ruminants	Riboflavin-barring gene in some strains of poultry
B_3 (niacin)	Inappetence, scaly dermatitis, intestinal ulcers, chondrodystrophy in chickens, pellagra in pigs	Rare, but occurs in poultry and pigs	Reduced availability in cereals, high leucine content of diet
B_5 (pantothenic acid)	Ill-thrift, crusted skin around eyes or mouth, goose-stepping in pigs, depigmentation or hair/feather loss	Occurs in pigs and poultry on high cereal diets	Low folic acid and biotin, high cereal diet
B_6 (pyridoxine)	Ill-thrift, hyperkeratosis, diarrhoea	Clinical symptoms rare due to wide distribution of vitamin and synthesis by microbes	None
B_{12} (cyanocobalamin)	Nervous disorders, rough coats, ill-thrift, pine	Occurs in pre-ruminant calves	Inadequate Co in diet
C (ascorbic acid)	Swelling and bleeding gums, weak and aching bones	Rare, but occasionally occurs in very young animals	Stress, infections, overcrowding
Carnitine	None under practical conditions	Non-existent	None
Choline	Reduced growth rate, leg weaknesses (perosis in poultry, possibly splayleg in pigs)	Rare, due to ubiquitous nature in feed and ability to synthesize	Low folic acid, B_{12} or methionine status
D	Rickets in young growing animals, thin-shelled eggs in poultry and (less commonly) osteoporosis in adult animals	Can occur in ruminants at end of winter and in young, growing non-ruminants if not supplemented	Low dietary Ca, lack of exposure to sunlight
E	Myopathy, white muscle disease in calves, heart failure, encephalomalacia and exudative diathesis in chicks, weak immunity	Common in all farm animals	Diet high in polyunsaturated fatty acids, stress, low Se in diet, mycotoxins
Folic acid	Anaemia, low growth rate	Rare	Low vegetable diets, B_{12} or iron deficiency
Inositol	Never observed in farm animals, but rodents develop alopecia	Non-existent	None
K	Poor blood coagulation	Rare (gut synthesis in ruminants, horses and pigs), supplementation required in poultry	Animals that have consumed anticoagulants

equivalent to the activity of 1 mg of all-rac α-tocopheryl acetate, the chemically synthesized form of the vitamin with eight potential stereoisomers.

Many of the effects of a vitamin E deficiency are made more striking by a selenium deficiency. Selenium is a component of the enzyme glutathione peroxidase, which provides a protective role due to destruction of H_2O_2. A deficiency of vitamin E is generally accompanied by an increase in lipid peroxidation as identified by visible tissue damage such as altered tissue architecture and by an increase in measurable blood and tissue malondialdehyde, or exhaled ethane or pentane. These products are the result of fatty acid oxidation. Adverse consequences of vitamin E and selenium deficiencies are mulberry heart disease in pigs, nutritional muscular dystrophy (also known as 'white muscle disease') in many animals, stiff lamb disease in newborn lambs, exudative diathesis in chickens and pigs, testicular degeneration, atrophy of ovaries, and sterility and resorption of fetuses in all farm animals. These symptoms all relate to a loss of cellular integrity.

Placental transfer of vitamin E is inefficient. The latest estimates of requirements for vitamin E for beef cattle (15–60 IU kg^{-1} diet for calves), dairy cattle (calves 15, lactating cows 25 IU kg^{-1} diet), fish (25–100 mg kg^{-1} diet), horses (~80–100 IU kg^{-1} diet), laboratory animals (rat 27, mouse 32 IU kg^{-1} diet), poultry (~5–10 IU kg^{-1} diet), sheep (lambs 20, adults 15 IU kg^{-1} diet) and swine (44 IU kg^{-1} diet) can be found in the Nutrient Requirement series published by National Academy Press in Washington, DC.

Hypervitaminosis E has been studied in rats, chicks and humans. Available data indicate maximum tolerable levels to be in the range of 1000–2000 IU kg^{-1} diet. A tentative presumed upper safe use level is suggested to be 75 IU kg^{-1} body weight day^{-1}.

The classical approach for assessing dietary vitamin E requirements has been to use growth or reproduction as response variables. Recent research has shown that mammary gland health in dairy cows, beef colour and immune system efficacy are also important. Supplementation of 1000 IU day^{-1} during the dry period and 500 IU day^{-1} to lactating cows has reduced the incidence of clinical mastitis. Supplementation of 500 IU day^{-1} for the last 100 days of the finishing period results in fresh beef products that have a colour display life that is about 100% longer than products from unsupplemented cattle. Blood neutrophils obtained from cows fed 500 IU day^{-1} had greater ability to kill bacterial pathogens than neutrophils from cows fed no supplemental vitamin E. (DMS)

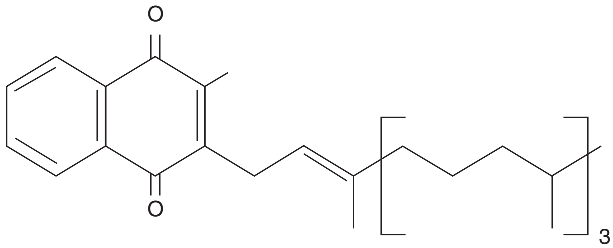
Key references

Bowman, B.A. and Russell, R.M. (2001) *Present Knowledge in Nutrition*, 8th edn. ILSI Press, Washington, DC.

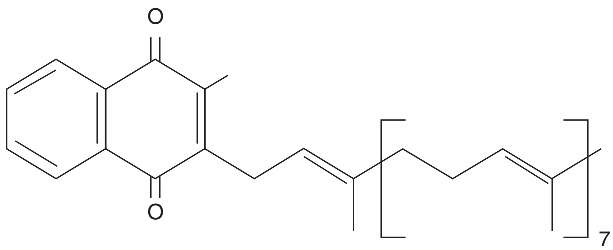
Ziegler, E.E. and Filer, L.J. Jr (1996) *Present Knowledge in Nutrition*, 7th edn. ILSI Press, Washington, DC.

Vitamin E acetate α-Tocopheryl acetate, $C_{31}H_{52}O_3$, molecular weight 472.73. All-racemic (all-rac) α-tocopheryl acetate is the commonly used form of supplemental vitamin E for dietary fortification. The antioxidant reactivity of α-tocopherol is dependent on a functional alcohol group attached to carbon 6 of the chroman ring system. The acetate ester at C-6 stabilizes α-tocopherol against oxidation prior to consumption. Intestinal tract esterases hydrolyse the acetate ester, resulting in all-rac α-tocopherol which is freely available for absorption and restored in its vitamin E activity. One international unit (1 IU) of vitamin E activity is defined as the activity produced by 1 mg of all-rac α-tocopheryl acetate. (DMS)

Vitamin K Compounds with vitamin K activity are 2-methyl-1,4-naphthoquinones with a hydrophobic polyprenyl substituent at the 3-position (Fig. 1). Phylloquinone (vitamin K_1), the form isolated from green plants, has a phytyl group, while the bacterially synthesized forms of the vitamin (menaquinones) have an unsaturated multiprenyl group at this position. A wide range of menaquinones are synthesized by different bacteria, but menaquinones with six to ten isoprenoid groups in a side chain (MK-6 to MK-10) are the most common. Although their activity differs



Phylloquinone



Menaquinone-8

Fig. 1. Structure of phylloquinone and a common menaquinone.

somewhat, all of the menaquinones will satisfy the vitamin K requirement of animals. In non-ruminant animals, menaquinones are synthesized in the lower bowel but are absorbed very poorly. Ruminants can satisfy their vitamin K requirement from menaquinones synthesized by rumen microorganisms. The synthetic compound menadione (2-methyl-1,4-naphthoquinone) is commonly used as a source of vitamin K in animal feeds; it is alkylated to MK-4 in the liver. Menaquinone-4 is also formed in animal tissues from phylloquinone by a mechanism that is not yet understood. It may have additional metabolic roles.

Vitamin K was shown to be a required dietary factor in the 1930s when Henrich Dam demonstrated that chicks fed a fat-free diet developed a haemorrhagic syndrome. This condition was cured by the addition of lucerne meal or lipid extracts of green plants to the diet. The concentration of the plasma procoagulant prothrombin (factor II) was decreased in deficient chicks, and later the concentrations of clotting factors VII, IX and X were also shown to be decreased in a vitamin K deficiency. The active factor in green plants was soon isolated and characterized but little progress in determining the metabolic role of vitamin K was made until the mid 1960s. At that time, a number of lines of evidence suggested that a post-translational modification of proteins was involved and administration of a vitamin K antagonist, warfarin, was found to result in secretion into the plasma of an inactive form of prothrombin.

Characterization of the bovine form of this abnormal prothrombin revealed that it lacked the specific calcium-binding sites present in normal prothrombin and that it did not demonstrate a calcium-dependent association with phospholipid surfaces. This calcium dependence was subsequently shown to be due to the presence of α-carboxyglutamic acid (Gla), a previously unrecognized acidic amino acid, in prothrombin. By the mid 1970s it was demonstrated that vitamin K was a substrate for a microsomal enzyme that converted inactive hepatic precursors of the vitamin K-dependent proteins to their active forms by the α-carboxylation of specific glutamyl residues.

Plasma clotting factors VII, IX and X also depend on vitamin K for their synthesis and contain Gla residues. The amino-terminal regions of these proteins are very homologous, and the multiple Gla residues occupy essentially the same position in all of these clotting factors. Two more homologous Gla-containing plasma proteins, protein C and protein S, play an anticoagulant rather than a procoagulant role in normal haemostasis, and a final Gla-containing plasma protein (protein Z) appears to have a procoagulant role. Osteocalcin, a low-molecular-weight protein synthesized by bone cells, and a structurally related protein, matrix Gla protein, which is synthesized in a number of tissues containing Gla residues, appear to regulate bone and soft tissue calcification. Another protein containing Gla residues, gas-6, is involved in growth control, and two other Gla-containing proteins, PRGP-1 and PRGP-2, are possibly involved in signal transduction. Vitamin K-dependent carboxylase activity can be demonstrated in most tissues and it is likely that other vitamin K-dependent proteins will be found.

The carboxylase does not require ATP and biotin is not involved. The substrates for the enzyme are a glutamic acid (Glu) residue, O_2, CO_2 and the reduced (hydronaphthoquinone) form of the vitamin. The co-product of the reaction is vitamin K 2,3-epoxide. The energy needed to drive the carboxylation is derived from the oxidation of reduced vitamin K to its epoxide. The role of vitamin K is to remove the very non-acidic γ-hydrogen from the glutamyl residue, leaving a species equivalent to a carbanion. The reaction is completed by attack of CO_2 at this position to produce the α-carboxylated product.

Efficient carboxylation of the vitamin K-dependent proteins appears to involve more than the normal enzyme/substrate interactions. Their primary gene products contain a very homologous 'propeptide' between the amino terminus of the mature protein and the signal peptide which acts as a 'docking' or 'recognition site' for the enzyme. This domain is approximately 18 residues in length, and three residues (Leu at −6, Ala at −10 and Phe at −16) have been shown to be critical for a high affinity interaction between the enzyme and its substrate. This region also acts as an allosteric activator of the enzyme by increasing the affinity of the Glu site substrate. The multiple Gla residues of the vitamin K-dependent plasma proteins are present in a homologous amino terminal domain. Under normal conditions, all of the Glu residues in this domain are carboxylated, suggesting a high degree of processivity to the reaction. Current *in vitro* studies of the enzyme also support a processive reaction and are consistent with the substrate protein remaining tethered to the enzyme as individual Glu residues are carboxylated to Glas. Whether this efficient mechanism is mediated only by an interaction between the substrate and the active site or whether some unidentified chaperone protein or other co-factor is required is not known.

The commonly prescribed anticoagulant, warfarin (coumadin^R) and other 4-hydroxycoumarins are effective antagonists of vitamin K action *in vivo*. They interfere with the ability of tissues to recycle the co-product of the carboxylase reaction, vitamin K 2,3-epoxide, to the enzymatically active reduced form. This microsomal enzyme, the vitamin K epoxide reductase, has the ability to reduce the epoxide to the quinone, and the quinone to the hydroquinone form of the vitamin. This activity is driven *in vitro* by a reduced dithiol but the physiologically important reductant has not been identified. Both reduction steps are inhibited by warfarin, resulting in a decrease in the concentration of the hydroquinone form of vitamin K and decreased carboxylase activity. As there are other cellular quinone reductases that are not warfarin-sensitive, administration of vitamin K can overcome a warfarin inhibition of vitamin K action. Chloro-K (2-chloro-3-phytyl-1,4-naphthoquinone) is an effective inhibitor of the carboxylase, and the reduced form of this analogue has been shown to be competitive vs. the reduced vitamin site. Substitution of a trifluoromethyl group, a hydroxymethyl group or a methoxymethyl group at the 2-position of the naphthoquinone ring also results in inhibitory compounds. Tetrachloropyridinol and other polychlorinated phenols also directly inhibit the carboxylase. The general metabolic conversion of vitamin K and the site of action of the various inhibitors of this important post-translational modification are shown in Fig. 2.

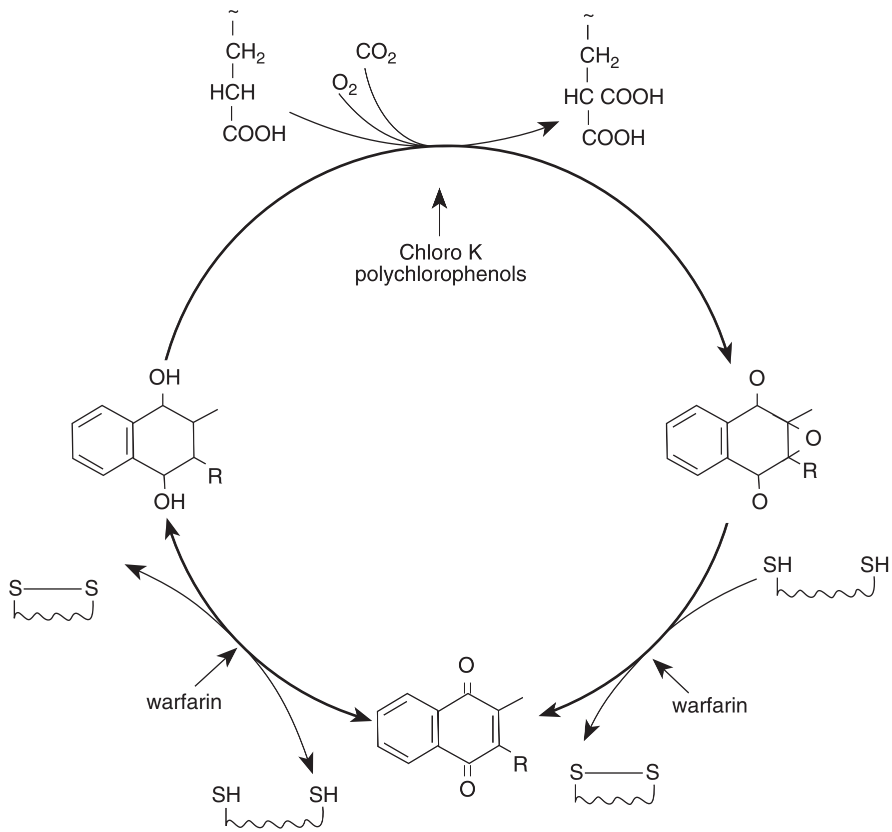


Fig. 2. Metabolism of vitamin K by the vitamin K-dependent carboxylase and the epoxide reductase. Sites of inhibition are indicated.

The dietary requirement of most animals for vitamin K is low (< 10 μg kg^{-1} day^{-1}) and not well defined for most animal species. Requirements for poultry are higher. Diets for pigs and poultry are routinely supplemented with menadione. (JWS)

Further reading

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Vitamin nomenclature Nomenclature of vitamins involves two main classes: the fat-soluble vitamins, A, D, E and K; and the water-soluble vitamins, thiamine, riboflavin, pantothenic acid, pyridoxine, biotin, nicotinic acid, folic acid, vitamin B_{12} and ascorbic acid (vitamin C). Not all vitamins need to be part of the diet for all animals. For example, vitamin D may be produced in the skin by exposure to sunlight. The water-soluble vitamins can be produced by intestinal tract microorganisms and be absorbed into the body. In ruminant animals, ruminal contents flow to the small intestine and the vitamins can be absorbed there. In non-ruminant animals that practice coprophagy (consumption of dung), vitamins produced by microorganisms in the large intestine can be absorbed and utilized when night faeces are consumed and digested. (NJB)

Vitamin premix A mixture of purified fat-soluble and water-soluble vitamins usually in a carrier (glucose, sucrose, starch or lactose) to dilute the concentration of the vitamins to facilitate a more uniform distribution of them in a mixed diet or supplement. The concentration of each vitamin in the premix is adjusted to meet the requirement of the animals consuming the diet, taking into account the vitamin content of the unsupplemented diet. (NJB)

Vitamin supplement: *see* Mineral and vitamin supplements

Vitamins Complex organic compounds found in foods and required by animals. They include the fat-soluble vitamins, A, D, E and K, the water-soluble vitamin C and the eight vitamins of the B-complex: thiamine, riboflavin, pyridoxine, niacin, folic acid, biotin, pantothenic acid and vitamin B_{12}. Vitamins are intimately involved as coenzymes or co-substrates or they facilitate reactions in cellular metabolism. A deficiency of any vitamin over sufficient time results in somewhat repeatable symptoms and may lead to death. Not all foods have all vitamins and not all foods have the same concentration of vitamins in the edible portion of the food. With the exception of vitamin C, all vitamins are required in the diets of non-ruminant animals. Primates and guinea pigs and a few other animals require a dietary source of vitamin C. Because of fermentative digestion, the microorganisms in the rumen of ruminant animals produce the B vitamins and therefore little attention is given to the B vitamin content of their diets. The fat-soluble vitamins, however, must be supplied. Vitamins are also produced commercially and are commonly added to mixed diets for all farm animals. (NJB)
See also: Water-soluble vitamins

Volatile fatty acids (VFAs) Weak organic acids with short chain lengths, most commonly acetic, propionic and butyric acids. These are monocarboxylic, alkanoic acids with the characteristics shown in the table.

	Molecular weight	Boiling point (°C)	pKa
Acetic	60	118	4.76
Propionic	74	141	4.87
Butyric	88	163.5	4.83

These acids produce readily detectable odours that range from pungent to rancid. In the 1940s steam distillation was used to extract them from the digesta and blood of ruminants in order to gain insight into their metabolic importance. In ruminants, the VFAs account for 50–85% of the metabolizable energy; in non-ruminants, their contribution ranges from negligible to substantial depending upon the intake of forages or other fermentable constituents, and upon the adaptation of the animal.

VFAs are produced by microbial fermentations (*see* **Fermentation**) in a wide variety of anoxic habitats in addition to the digestive tracts of the animals. In livestock operations, these habitats include high-moisture forage and grain stored in air-tight structures, manure storage containers and manure lagoons. A wide variety of fermentative organisms degrade carbohydrates, proteins, lipids and other classes of degradable organic compounds to the VFAs and possibly lactic acid. Where residence times of the organic matter are relatively long, i.e. 5 days or longer, and there are no inhibitory factors, such as acidic pH, the VFAs are completely metabolized to CO_2 and CH_4. This complete decomposition of organic matter is possible because of the syntrophic association of VFA-catabolizing and methane-producing bacteria. The VFA-catabolizing bacteria have slow growth rates, hence the requirement for long residence time. These organisms would be present in lagoon sediment and in manure digestion systems designed to convert manure-carbon to methane. Feed particles in livestock digestive tracts have residence times of typically 2 days or less and so the VFA-catabolizing bacteria are not able to proliferate; VFAs accumulate in the digestive tract and are available for absorption.

Silage fermentations are unique because bacterial fermentation is inhibited by low pH. Following ensilage of feedstuffs that have readily degradable carbohydrate fractions, aerobic metabolism depletes available oxygen to make the environment anaerobic. The most water-soluble carbohydrate fraction is rapidly fermented to lactic acid and acetic acid. The pH of the fermenting feeds falls to 3.5, causing microbial fermentation to cease. Consequently, lactic acid is not converted to VFAs, nor are VFA-catabolizing bacteria able to grow. Hence, the silage is stabilized against spoilage and further fermentation.

In the digestive tract, bacteria, protozoa and anaerobic fungi accomplish the conversion of carbohydrates (and amino acids) to VFAs. The microbes use glycolysis to catabolize carbohydrates to pyruvate and then certain enzymes of the citric acid cycle to yield the VFAs. The profile of the VFAs produced is a function of microbial enzymatic abilities, growth rate, pattern of acids that allows the organism to maximize its ATP yield, substrate-product carbon balance, and substrate-product oxidation–reduction balance. VFAs are readily absorbed from the digestive tract via a pH- and concentration-dependent VFA/bicarbonate antiportal mechanism. Absorption rate is increased at lower pH. The absorption rate depends on chain length, ranked as butyrate > propionate > acetate. VFA absorption is associated with bicarbonate appearance in the gut lumen. VFAs are metabolized as energy sources by the mucosal epithelium, and butyrate is most stimulatory for mucosal cell growth. Butyric acid is oxidized to β-hydroxy butyric acid and released into the portal circulation by the rumen epithelium. VFAs are carried by the portal vein to the liver, where absorbed propionate is quantitatively cleared. In ruminants, propionate is the primary precursor for glucose synthesis (providing 40–60% of the total glucose synthesized). Little acetate is taken up by the liver, but it is used extensively as an energy source (25–30% of total CO_2 output) and is the primary carbon source for *de novo* fatty acid synthesis. In ruminants, acetate is also an important source of NADPH for fatty acid synthesis, via oxidation and the cytosolic isocitrate dehydrogenase. Acetate turnover in ruminants is rapid, with a half-time of 3–13 minutes; utilization by most tissues is insulin dependent, but uptake of both glucose and acetate by the mammary gland is independent of insulin. Oxidation of propionate, both directly and indirectly (via glucose), totals about 20% of the total CO_2 output. β-Hydroxybutyrate is a primer of fatty acid synthesis and is incorporated as an intact 4-carbon unit into the methyl-terminal end of fatty acids synthesized *de novo*, and otherwise is quantitatively oxidized. (DMS)

Voluntary food intake The food intake of animals allowed continuous unrestricted access to feed (*ad libitum* feeding). It is usually expressed as the weight of food eaten per 24 h.

Control by food and animal factors

The voluntary food intake of individual animals tends to be consistent from day to day as long as diet, physiological requirements and environment (including day length) remain unchanged. In the long term, voluntary food intake is dependent on both food and animal factors. The principal food factor determining intake is the rate at which it is digested. Slowly digested feeds remain longer in the rumen, or the non-ruminant stomach, than rapidly digested materials, allowing an increased intake. If the nutrient supply is in excess of the animal's requirements, an increase in digestibility, and in particular the energy value of the food, may decrease voluntary food intake as the animal consumes only sufficient food to supply the amount of energy it requires. Voluntary food intake may be stimulated by psychological factors, such as providing a mixture of feeds, and the physical presentation of the food. More natural presentation methods (e.g. from the floor rather than a raised rack or bunk) may promote greater intakes.

The most important animal factor influencing voluntary food intake is an animal's physiological state. Increased requirements, e.g. the energy demands of peak lactation, are associated with increased intake. Body composition is also important: fat livestock tend to have reduced intakes. However, despite increased requirements, animals in late pregnancy have reduced intakes, due to the presence of the fetus. After periods of forced feeding or food deprivation, animals adjust their intake in such a way as to return to their original body weight, or their original rate of weight change. There are also social factors, with isolated livestock or those that are bullied in a small confined space having low intake, particularly in the case of social animal species, such as sheep.

It is often said that animals 'eat for calories' and, indeed, that is frequently observed. For example, when the energy concentration of food is increased, voluntary intake is reduced in order, apparently, to maintain a constant intake of energy. Equally, increased energy demands, as during lactation or exposure to cold, are compensated for by increased food intake. However, the concept of caloric control is not sufficient to explain many observed changes in food intake in response to changes in the animal's demand for nutrients, changes in the environment and in the composition of the food.

Hunger and satiety

Motivation to eat is initiated by hunger and terminated by satiety. Hunger may be either for a specific nutrient, e.g. sodium, in which case it is termed euphagia, or may be generalized to evoke a variety of satiety responses. In the short term, voluntary food intake is dependent on the perception of food, as determined by the senses (taste, smell, vision and tactile), as well as feedback on distension of digestive organs and post-digestion chemosensory feedback. The different aspects of perception of food combine to provide feedback on the acceptability of different foods, sometimes referred to as palatability. The principal taste sensations influencing intake are sweet, sour, salt and bitter, which provide information on the carbohydrate content, ion balance, sodium content and the presence of toxins, respectively. Flavours (*see* **Flavour compounds**) interact and aversive flavours, such as bitterness, can be masked by pleasurable flavours, such as sweeteners. Most flavours are aversive at high concentrations and pleasurable or neutral at low concentrations, but experience is important in modifying an animal's response to taste stimuli. Some flavours interact, or modify the perceived intensity of another flavour, e.g. thaumatin and bitter flavours. Food perception is also influenced by tactile senses, hence the physical form of the food can be important – particularly in the case of sheep and goats, whose mouthparts are more sensitive than those of cattle. For example, forage leaves that are excessively hairy or waxy can reduce intake, and the presence of thorns can damage sensitive mouthparts. Cereals that are excessively comminuted, such as by grinding, are often dusty and unpalatable.

Such evidence implies homeostatic control of voluntary food intake and body weight, and various theories (energo-, lipo-, gluco-, amino-, thermo- and ponderostatic) have been proposed to account for this control but no single theory can account for observed levels of intake in all situations. Voluntary control of food intake in any animal depends on integration of feedback from a wide variety of neural and chemical signals, involving brain, eyes, mouth, alimentary tract, liver, and circulating metabolites and hormones. Control mechanisms may operate in the short or longer term and these are considered here in the categories of alimentary, metabolic and central controls.

Alimentary control

Some physical limitations to intake include a very slow rate of eating (e.g. due to very sparse food availability, preventing the animal from reaching its potential intake in the time available) or limited capacity of the stomach(s), especially where the food must remain in the stomach for a long time in order to be digested (this is especially true in ruminant animals which have developed blind stomachs in order to sequester food for long periods to be digested by symbiotic microorganisms and which can only be emptied when a certain degree of digestion has taken place). In cattle and sheep, the capacity to store food in the rumen and to remasticate the food later during **rumination** is a valuable means of concentrating grazing into the daylight hours with rumination continuing (while lying) into the period of darkness.

As an animal eats, its stomach wall becomes stretched, and this is sensed by mechanoreceptors and transmitted to the central nervous system (CNS), where it contributes to satiation. Digestion proper commences rapidly: breakdown of food constituents into molecules to be absorbed begins, and the bulk of the food begins to be reduced by absorption and passage along the digestive tract; these factors reduce the volume of material in the stomach. An early theory of food intake control was based on the simple concept of stomach fill and this is still particularly relevant for ruminants. However, most animals take many meals each day and the size of any one meal is not large, in relation to stomach capacity, suggesting that stomach fill is not the only factor controlling voluntary food intake.

Evidence of an association between meal initiation (hunger) and gut emptying in simple-stomached animals comes from experiments in which differences in rate of food passage, attributable to manipulation of diet nutrient density, ambient temperature or the vagus nerve, were reflected in differences in the ratio of mean meal size to mean meal length plus mean interval length. In ruminants, the intake of fibrous foods increases when the foods are ground into small particles before feeding, due to their faster exit from the rumen. An association between meal termination (satiety) and gut filling is seen in experiments in which differences in meal length, attributable to variation in particle size, reflected the time taken to consume the same weight of food, but not to absorb the same amount of nutrients.

Several peptides are released in the alimentary tract in response to passage of digesta, and some of these also occur in nervous tissue. Two that have been proposed as satiety agents are bombesin and cholecystokinin and it is likely that the combined effects of several peptides, together with other factors, might be sufficient to explain normal satiety.

The wall of the digestive tract is sensitive to chemicals as well as physical stimulation. The rumen wall receptors are sensitive to pH and specifically to the volatile fatty acids, especially acetate.

Metabolic control

There are short-term fluctuations in the supply of nutrients from the digestive tract which are involved in the control of meal frequency and size. Although the early glucostatic theory of intake control is no longer thought to be valid on its own, there is nevertheless a sensing of the supply of oxidizable substances to the liver which is transmitted to the CNS to play a part in the overall control of intake. In many animals on starchy diets, glucose is likely to be the main contributor to this route of satiation. In ruminants, where little glucose is absorbed, the satiating agent at the level of the liver is its precursor, propionate, produced by the microbial population of the rumen.

In the longer term, blood levels and receptor sensitivities for metabolites, such as long-chain fatty acids, and hormones, such as insulin and leptin, are involved in the control of food intake. Leptin has the properties of a negative feedback mechanism for maintaining the stability of body fat content. It is produced by fat cells in proportion to their fat content, circulates in the blood and influences feeding via CNS receptors.

Central control

Although blood composition is monitored in both brain and liver, and effects of vagal denervation on feeding responses to intraportal infusions of nutrients indicate that the liver does have a part to play, ultimately all components of feeding behaviour are coordinated in the brain. The ‘dual control’ system, based on a hunger centre in the lateral hypothalamus and a satiety centre in the ventromedial hypothalamus, is no longer considered valid.

Central neuropeptides and monoamine transmitters that have been implicated in feeding control in laboratory animals have also been shown to be active in farm mammals and, to some extent, in birds. Neuropeptide Y in the brain is probably the most potent known stimulator of food intake in mammals and birds and leptin exerts its intake-moderating activity via this peptide. Finally, feeding, drinking and other behaviours are implicated with central release of opioid peptides, and it seems likely that they may be at least partly responsible for positive reinforcement of any activity of a repetitive nature.

Integrated control

As indicated above, no single alimentary or metabolic signal to the CNS can explain how food intake is controlled. It is proposed that numerous factors are involved and that animals learn to minimize the imbalance between the various factors causing hunger and those causing satiety. In different situations, even in the same animal, the relative importance of the various factors is different, making it very difficult to propose a simple hypothesis of the control of voluntary food intake. Nevertheless, the prediction of voluntary food intake is an important aspect of designing diets and feeding strategies for all classes of livestock.

(JMF, CJCP, JSav)

Vomiting Vomiting (emesis) is a complex reflex activity coordinated in the brain stem. Vomiting is associated with a number of actions, including the contraction of the abdominal musculature, which increases intra-abdominal pressure, an expansion of the chest cavity and opening of the upper oesophageal sphincter. Vomiting is a protective mechanism to help to prevent absorption of noxious substances. Pigs vomit easily. In ruminants, vomiting occurs as an injection of abomasal contents into the forestomach.

The stimulation of the vomiting reflex comes from a large number of receptors, e.g. mechanoreceptors in the pharynx, and tension and chemoreceptors in the gastric and duodenal mucosae. Offending stimuli from the gastrointestinal mucosa can result in vomiting. Vomiting is not always an indication of a primary gastrointestinal problem. Similar stimuli can arise from numerous other organs and a chemoreceptor trigger zone, which is sensitive to the presence of toxins and drugs in the blood, can also cause vomiting. (SB)

Vomitoxin Vomitoxin (deoxynivalenol or DON) is a trichothecene mycotoxin, produced by *Fusarium* fungi. Vomitoxin causes feed refusal and vomiting in pigs. Pigs, dogs, cats and ducklings are the most sensitive animals. As little as 5% infected grain kernels or 10 ppm DON in feed causes feed refusal in pigs. Chickens may tolerate as much as 100 ppm in the feed. Emetic effects may involve effects on brain neurotransmitters. (PC)

W

Wafering Common name for pressing or the formation of pellets by compressing meal through a die, with or without heat.

(MG)

See also: Pelleting

Water A colourless, odourless, tasteless liquid, H_2O, required by all organic life forms. Together with CO_2, water is a major end-product of cellular oxidative metabolism, e.g. for carbohydrates $C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2$. Water is taken up in biosynthetic reactions such as the conversion of carbohydrate to fat and is thus a required substrate for cellular metabolism. Finally, much of the oxygen consumed is recovered in cellular water as a result of cellular oxidation of foodstuffs. (NJB)

Water buffalo There are 169 million water buffaloes (*Bubalus bubalis*) in the world, compared with a cattle population of 1350 million. There are two main types. The swamp buffalo has large curved horns and is used primarily as a working animal; it is found in the Philippines (where it is often called the carabao), in India and in other countries of South-East Asia. The river buffalo is found in India, Egypt, Europe, the Caribbean and South America; it has lightly coiled or drooping straight horns. River buffaloes supply both draught power and milk; 35% of India's milk animals, other than goats, are river buffaloes and they produce almost 70% of India's milk.

Buffaloes have been used in India for 5000 years and in China for 4000 years but for only 1000 years in Europe. Most buffaloes are located in Asia but there are 3 million in Egypt, > 1.5 million in Brazil (imported during the last 80 years) and small numbers in Trinidad and other countries of the Caribbean and South America. Buffaloes have a quiet temperament, unlike the wild African buffalo *Syncerus caffer*, which has a reputation for being very dangerous and unreliable.

Water buffalo supply both draught power and milk.

Water buffaloes can live in temperate climates but can overheat in hot climates, especially when used for work, because they have a limited ability to lose heat by sweating compared with cattle. Buffaloes produce good lean meat and provide rich milk. The butterfat from buffalo milk is the major source of cooking oil (ghee) in India. Buffalo milk contains twice as much butterfat as that produced by dairy cows. Mozzarella cheese is made from buffalo milk. In Hindu countries such as India and Nepal, where cows cannot be killed, the slaughter of buffaloes is permitted and their meat can be eaten.

There are no distinct breeds of swamp buffalo but they do vary in size from area to area. For example, swamp buffaloes in Thailand average 450–500 kg, whereas in Burma they average 300 kg. There are 18 breeds of river buffalo in India and Pakistan, classified by area of origin: Murrah, Gujarat, Uttar Pradesh, Central India and South India breeds. The swamp buffalo is reported to have 48 chromosomes and the river buffalo 50 but this may not be true, because they contain similar chromosomal material and produce fertile offspring when crossbred. Cattle have 60 chromosomes and will mate with buffalo but offspring are infertile.

When adequately fed, both males and females reach puberty at 18 months of age. Oestrus lasts for 24 h (range 11–72 h) with a 21-day cycle. Buffalo show few outward signs of heat and often mate at night. Conception may be as high as 80%. The semen can be frozen. The gestation period (310 days) is longer than that of cattle (*c*. 280 days). The first calf is normally born before the dam is 3 years of age. Buffaloes will return to heat 40 days after calving, but normally produce only two calves every 3 years.

Buffaloes are lean animals with killing-out percentages ranging from 53 to 56%. They tend to be highly muscular, because they have been developed for draught purposes. Buffalo meat and beef are similar but the meat of buffalo is darker and the fat is always white. There is no evidence to indicate that the meat is tougher than that of cattle of a similar age.

Five per cent of the world's milk is produced from buffaloes. In countries such as Egypt, the milk yield of buffaloes is generally higher (680–800 kg) than that of local cattle (360–500 kg). The highest yield comes from Murrah buffalo (1800 kg per lactation). Calves of some types of buffalo are about the same size as a Holstein calf. They grow very quickly, because of the quality of buffalo milk, and can weigh 360 kg at 1 year old. However, many calves die in India and Egypt because the milk is used for human consumption and not enough is left for the calf. Buffalo udders are very variable in shape, making machine milking difficult. The presence of the calf is not normally needed to stimulate milk let-down as is the case of many zebu cattle.

Buffalo milk contains 16% total solids compared with 12–14% for cows. Butterfat percentage is 6–8%, compared with 3–5% in cows. Buffalo milk lacks the yellow pigment, carotene, and is therefore white. It can be processed in a similar way to cow's milk. To produce 1 kg cheese requires 8 kg cow's milk but only 5 kg buffalo milk; 1 kg of butter requires 14 kg cow's milk but only 10 kg buffalo milk.

Buffaloes are reputed to provide 20–30% of the farm power in South-East Asia. They are said to move easily through mud, because they have large boxy hooves, but are no better at working under paddy field conditions than cattle. Because of their limited ability to sweat, buffalo are not suitable for working under dry land conditions. They need to wallow after 2 h work to get rid of excess heat produced during work. They can walk 3 km h^{-1}, and can work for 5 h day^{-1}. At this rate of work they may take 6–10 days to plough, harrow and prepare 1 ha of rice paddy.

The domestic buffalo is a ruminant and the general structure of its rumen, reticulum and omasum is very similar to that of cattle. Therefore the nutrition of the buffalo is broadly similar to that of *Bos taurus* and *Bos indicus* animals. In most trials, buffalo have grown faster than native cattle (range 0.25–1.25 kg day^{-1}). This is probably because they have a larger mature body size. Some experiments have shown that buffalo digest cellulose more efficiently than cattle (e.g. straw fibre 80% vs. 65%). They may have different microorganisms, or proportions of them, in the rumen. However, other experiments show that cattle are more efficient than buffalo. They are often fed mainly on rice straw, maize stover or other similarly low-quality feeds. Lack of adequate nutrition, in both quality and quantity, is the main reason why buffalo are unproductive. For all practical purposes, knowledge of the nutrition of cattle can be applied to water buffalo, provided that differences in body weight and in the composition of the milk are taken into account.

(AJS)

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Water content: *see* Dry matter

Water deprivation When the intake of water, either as liquid or as part of the food before or after metabolism, is insufficient to maintain the insensible losses of water through the skin, lungs and obligatory urine production by the kidneys there is a decrease in circulatory volume which in turn leads to a fall in blood pressure, a rise in heart rate, circulatory collapse, renal failure and death. Thirst is the main regulator of water balance, reinforced by angiotensin II. Observation of skin turgor in some species provides a useful guide to the necessity for fluid replacement therapy (*see* **Dehydration, body**).

If more water than sodium is lost, as in pigs (which lack sweat glands) when exposed to a high environmental temperature and lack of adequate water, a condition of salt poisoning develops. This is associated with raised plasma sodium concentration and marked cellular dehydration, which may have fatal consequences. Diets fed to pigs should not contain more than 1% salt. (ADC)

Water excretion Water is lost from the body in two forms: as a liquid, mainly in sweat and urine; and as a gas by evaporation. Loss of water from the body in liquid form is required because water is the major solvent of the cellular and extracellular environment and the medium in which excretory products are carried to the site of excretion, whether urine, skin or lung. These include not only end-products of metabolism but also toxic or detoxified substances made water-soluble by metabolic modification. Water loss from an animal occurs via evaporation (sweat and respiratory) and as liquid water in milk, eggs, saliva, urine and faeces. Evaporative water loss is increased (~ 50%) as the environmental temperature increases through the thermoneutral zone. Evaporation is increased with higher air speed but reduced by high humidity. Because of the high heat of vaporization of water (~ 2.4 MJ g^{-1} at 30°C), evaporative cooling is critical to the regulation of body temperature in homeothermic animals (those that maintain body temperature). At high environmental temperatures evaporative cooling, whether by sweating, panting or wallowing, becomes the major route of heat loss. (NJB)

Water-holding capacity The ability to absorb and retain free water. The water-holding capacity of a feedstuff is primarily governed by the types of non-structural carbohydrate (often described as fibre) in the feedstuff. Feedstuffs with high water-holding capacities are sugarbeet pulp, linseed meal, lupin seeds and other pulses as well as certain varieties of barley, wheat and other cereals. Increased intake of non-starch polysaccharides (with a consequent increase in water-holding capacity) often increases the transit time of feed in the gastrointestinal tract. Although this gives a longer time for digestive enzymes and microorganisms to function, increased viscosity of the digesta tends to reduce nutrient mobility and thus reduce digestibility. In pigs and poultry, feedstuffs with high water-holding capacity tend to increase endogenous losses of nutrients from the gut. Nutrient availability in poultry is negatively correlated with the water-holding capacity of the feed. Increased water intake and digesta viscosity lead to wet and sticky faeces, increasing the risk of health problems and encouraging the colonization of the gastrointestinal tract by pathogens. Finally, the gastrointestinal tract of animals is larger (and proportionately heavier) when they are fed diets with a high water-holding capacity. (TA)

Water intake In order to maintain water balance, water intake must exactly counterbalance the water lost from the body as well as water stored in new growth. Water intake is achieved by direct consumption of water or as part of food consumed, or it is produced by metabolism. Water produced by metabolism is called metabolic water. For example, cellular oxidation of 100 g of protein, carbohydrate or fat yield *c.* 40 g, 60 g or 109 g of metabolic water, respectively. Water intake is usually 1.5 to 3 times the dry matter consumed but increases with the salt content of the diet. Specific estimates of water consumption can be found for pigs and dairy cattle in US National Research Council reports. For pigs, water intake (l day^{-1}) = 0.149 + (3.053 × kg daily dry feed intake). For dairy cattle water intake (kg day^{-1}) = 15.99 + ((1.58 ± 0.271) × (kg dry matter intake day^{-1})) + ((0.90 ± 0.157) × (kg milk production day^{-1})) + ((0.05 ± 0.023) × (g sodium intake day^{-1})) + ((1.20 ± 0.106) × (minimum daily temperature, °C)). The type and intensity of animal performance increases water needs. Water consumption increases with environmental temperature, milk production and the intensity and duration of exercise. (NJB)

Key reference

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Water melon: *see* Melon

Water requirements: *see* Water intake

Water-soluble vitamins A term embracing the B-complex vitamins and vitamin C. It thus includes thiamine, riboflavin, pyridoxine, niacin, folic acid, biotin, pantothenic acid, vitamin B_{12} and ascorbic acid (vitamin C). (NJB)

Water temperature Most aquatic animals are poikilotherms (body temperature conforms to water temperature) and their metabolic rate increases with water temperature. Growth is usually faster at higher temperatures but water temperatures outside the optimal range of a species will negatively affect its physiology, leading to reduced growth and feed consumption. At higher temperatures, increased production of metabolic wastes (ammonia and carbon dioxide) combined with lower dissolved oxygen levels may reduce water quality. Water temperature tolerance varies significantly among fish species and other aquatic animals. (DAN)

See also: Freezing; Fresh water; Sea water

Waxes Fatty acid esters of long-chain primary alcohols. Alcohol chains of 8 to > 40 carbons have been identified in both plants and animals. Some secondary alcohols occur and monoenoic alcohols are found in cetaceans. The ester linkage of waxes is hydrolysed with great difficulty. (DLP)

Further reading

Deuel, H.J. Jr (1951) *The Lipids. Their Chemistry and Biochemistry* (Ch. IV. Waxes, higher alcohols including steroils, triterpenes, glyceryl esters, colored fats and hydrocarbons). Interscience Publishers, New York.

Weaning The natural process by which young mammals gradually replace their mother's milk with other sources of nutrients. In

The ability of young animals to survive and grow on solid food alone is more closely linked to their age than their weight.

some production systems weaning has become an abrupt event. Examples are the weaning of piglets at 3 weeks and of lambs at 4 or 5 weeks, both done to reduce the interval to rebreeding. The ability of young animals to survive and grow on solid food alone is more closely linked to their age than their weight. Young fast-growing animals receiving copious amounts of their mother's milk are usually slower in developing their enzyme systems for the digestion of solid food than their slower-growing contemporaries that have been forced to augment their mother's milk with solid food. (JJR)

Weende analysis Analysis of carbohydrates was, for many decades, accomplished by proximate analysis procedures developed at the Weende Experiment Station in Germany over 100 years ago and hence frequently referred to as Weende analysis. The procedure divided carbohydrates into soluble (nitrogen-free extract) and insoluble (crude fibre) fractions, the former being the digestible portion and the latter the less digestible portion. Crude fibre was determined by boiling the sample in weak acid and then in weak alkali. The residue so obtained was dried and the loss from it, upon ignition, was the crude fibre. Nitrogen-free extract was determined by difference, being the weight of material remaining after subtracting from the weight of starting material the values previously obtained for crude fibre, crude protein, ether extract and ash. Consequently, Weende analysis entailed a proximate analysis of the sample under test. Weende analysis served nutritionists well for over a century in that it enabled feeds to be separated into broad categories such as roughages with high crude fibre and concentrates with low crude fibre. However, the digestibility of crude fibre may sometimes be higher than that of nitrogen-free extract. Consequently, crude fibre does not separate carbohydrates into readily digestible and less readily digestible portions. A more recent method uses detergent extraction to separate carbohydrate fractions. (CBC)
See also: Acid detergent fibre; Crude fibre; Neutral-detergent fibre; Nitrogen-free extractives; Proximate analysis of foods

Weir formula A formula for calculating heat production from respiratory exchange data, mainly used in human studies:

Heat output (kcal) = 3.9% l O_2 produced + 1.1% l CO_2 consumed

For farm animals the Brouwer formula is more appropriate. (JAMcL)
See also: Brouwer formula; Indirect calorimetry

Wet feeding: *see* Liquid diets

Wet season In many parts of the world, especially in the tropics and subtropics, defined wet and dry seasons are normal. In most regions wet seasons occur in the warmer months, resulting in optimum conditions for plant growth. In equatorial regions two rainy seasons per year are not uncommon.

In the wet season, where grazing is available livestock generally have sufficient natural vegetation, which is high in protein and low in fibre, for their current needs and recovery from dry-season underfeeding. Where grazing is not available, animals are often stall-fed or tethered during the rains, to protect cropping areas. Because demands for labour are high at this time, cut-and-carry is often inadequate. For animals in these conditions, wet-season feeding stress is possible. The start of the rains is followed by ploughing and planting. Where land pressure is high and rainfall adequate, two arable crops are needed every year (e.g. wheat; rice). In the arid and semi-arid regions rainfall tends to be variable, in both amount and pattern of distribution, often threatening production of stable foods. When available, irrigation expands the growing season. (TS)
See also: Rainy season

Wheat Wheat is one of the oldest and most important members of the *Gramineae* (grass) family cultivated for its grain. On a worldwide basis, a greater area is devoted to growing wheat than to any other food crop. The world's largest producer is China, with an estimated annual yield of almost 100 million tonnes. Other leading producers include the USA, Russia, India, Ukraine, France, Canada, Kazakhstan and Turkey.

The wheat plant has long, slender leaves, generally hollow stems and heads with varying numbers of flowers, ranging from 20 to 100. The flowers are grouped together in spikelets, each having two to six flowers. In most spikelets, two or three of the flowers become fertilized, producing grains.

Of the thousands of known varieties of wheat the most important are: *Triticum aestivum*, used to make bread; *T. durum*, used in making pasta; and *T. compactum*, also known as club wheat, a softer type, used for cake baking, crackers, biscuits, pastries and flours. Though grown under a wide range of climates and soil types, wheat is best adapted to temperate regions with rainfall between 30 and 90 cm. Both winter and spring wheat varieties are available, with the severity of the winter determining whether a winter or spring variety is cultivated. Winter wheat is always sown in the autumn while spring wheat, though generally sown in the spring, can be sown in autumn where winters are mild.

The wheat grain is composed of the seed and the pericarp or seed coat. The protective layers or glumes that surround the seed are associated only loosely with the grain and are easily separated during grain threshing. This is different from barley, where the glumes fuse with the outer coating of the developing seed and thereby produce a covered or closed grain. The starch-rich endosperm represents the largest proportion of the wheat grain (about 82%), with the bran or seed coat (15%) and the germ (3%) making up the remainder. The crude protein (CP) concentration ranges from 60 to 220 g kg^{-1} dry matter (DM) but is normally between 100 and 170 g kg^{-1} DM. The amount and quality of the proteins present in wheat are very important since they determine the suitability of the flour for bread making. The mixture of proteins present in the endosperm, collectively referred to as 'gluten', have elastic properties and comprise two main proteins: prolamin (gliadin) and glutelin (glutenin). The main amino acids present in wheat gluten are glutamic acid (330 g kg^{-1}) and proline (120 g kg^{-1}) and the proportion of essential amino acids is similar to that of other cereals, with lysine being the first limiting amino acid for pigs and poultry. The grains also contain 256 to 636 g starch kg^{-1} DM, 5–40 g ether extract kg^{-1} DM and 133–366 g neutral detergent fibre kg^{-1} DM.

Although used predominantly for human food purposes, wheat is also an important feed resource for livestock. Wheat grains are commonly processed by coarsely grinding or crushing prior to being fed to cattle, pigs and horses. The whole grains can be fed to sheep. Wheat can comprise about 25% of the concentrate ration for young ruminants (calves and lambs) and about 40% for dairy cows and beef cattle. Wheat can be included up to about 50% of the concentrate ration for different classes of pigs and 60% for poultry, excluding chicks (about 50% of concentrate).

Owing to the gluten content of the grains, fine grinding can result in a sticky dough following ingestion and lead to a reduction in digestibility. It can also lead to stomach ulcers. For ruminants, processing increases the rate and extent of starch degradation in the rumen and decreases the amount of starch digested post-ruminally. Fine grinding may be detrimental since the rapid fermentation of starch depresses rumen pH, inhibits cellulolysis and ultimately decreases intake. For ruminant feeding, in place of rolling or grinding, whole wheat grains are commonly treated with sodium hydroxide in order to rupture the seed coat and improve digestibility. In certain countries cooked wheat is fed to horses as a partial substitute for oats.

In North America and Europe, wheat is also grown as forage and used to provide a first cut of forage in the spring or harvested and ensiled when the grains are at the waxy stage. Wheat forage is generally harvested for hay while the leaves are still green (milk stage). Wheat can also be preserved following treatment with urea (urea-treated whole-crop wheat). Wheat forage, as with crops from other members of the *Gramineae* family, has a low protein content and requires further protein supplementation with fresh or conserved forage legumes or protein concentrates. Because of its low protein content, wheat may be grown in a bi-crop system with other protein-rich crops (e.g. peas, beans).

The processing of wheat (milling) for flour manufacture results in the production of a number of by-products for use as livestock feeds. Milling grain for flour is carried out in order to separate the endosperm from the bran and germ. Cleaned grains are passed through a series of rollers; these firstly release the bran coat from the endosperm and gradually break up the kernels. At the end of each stage the flour is removed by sieving. The proportion of

Chemical composition of wheat grain and wheat by-products (as g kg^{-1} DM unless otherwise stated). (Source: MAFF, 1990, *UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs*.)

	DM (g kg^{-1})	CP	EE	Starch	Crude fibre	NDF	GE (MJ kg^{-1} DM)
Wheat grain (all seasons)	857	128	17.3	674	21.2	124	18.4
Wheat grain (spring)	864	146	24.1	625	21.3	145	18.8
Wheat grain (winter)	857	127	17.0	676	21.2	123	18.4
Wheat germ	900	140–180	180–260		30–70		
Wheat bran	892	174	39.4	196	104	475	18.9
Wheat feed	890	179	43.4	277	81.0	364	19.1
Wheat middlings	879	175	39.3	306	71.3	–	19.2
Wheat offals	878	185	46.9	329	70.3	354	19.1
Wheat straw (all seasons, untreated)	872	38.9	11.9	11.6	424	809	18.2
Wheat straw (all seasons, ammonia treated)	869	68.4	13.3	1.2	434	773	18.6
Wheat straw (winter, sodium hydroxide treated)	842	36.1	8.7	8.7	439	689	17.2

CP, crude protein; DM, dry matter; EE, ether extract; GE, gross energy; NDF, neutral-detergent fibre.

flour obtained from the original grain is defined as 'extraction rate' and in practice a rate of 0.75 represents the limit of white flour extraction. Higher extraction rates imply the addition of bran and germ to the flour.

Modern flour milling gives rise to three main residues or 'offals' as by-products: germ, fine wheat feed (also called shorts in the USA or pollards in Australia) and coarse wheat feed or bran. Wheat bran consists largely of fragments of the outer skins and grain particles from which the majority of the endosperm has been removed. Although low in energy and starch content, it can be utilized for animal feeding and can be included, for example, at about 20% in the concentrate portion of dairy concentrates. For ruminants, the digestibility of the organic matter and protein reach values of 0.70–0.75 and 0.75–0.80, respectively, while values for pigs are lower (0.65 and 0.75 for organic matter and protein, respectively). Digestibility values for horses are also modest and are even lower for poultry. The use of wheat bran in pig diets is usually confined to sows (10% and 20% of concentrate).

Wheat germ is an excellent supplement for livestock because of its high protein content (up to 380 g kg^{-1} DM basis), the protein having a better amino acid composition than that of the whole grain. Wheat germ is included in mixtures for growing animals in general and high-yielding dairy cows. (ED)

Further reading

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Piccioni, M. (1989) *Dizionario degli Alimenti per il Bestiame*, 5th edn. Edagricole, Bologna, Italy, 1039 pp.

Wheatfeed: *see* Milling by-products

Whey Whey is a by-product of cheese manufacture after the curds have been removed from milk. Whey contains approximately 93% water, 5% lactose, 1% protein, 0.6% ash and 0.4% fat. Whey can be fed in liquid form to pigs, or dried for manufacture of milk substitutes. (PCG)

See also: Dried whey; Milk substitute

Whey protein Whey protein consists of the albumins and globulins found in milk, but not the casein, which is removed during cheese manufacture. Whey proteins may be concentrated by ultrafiltration to produce whey concentrate (12% protein), or the lactose, minerals or both may be removed to produce demineralized, delactosed whey (30% protein). (PCG)

Whole-crop silage Silage made from cereals in which the seeds have begun to form but are not yet ripe. The entire plant is ensiled. Crops used for this purpose are barley, wheat, triticale, oats, sorghum, rye, rice

Nutrient composition of whole-crop silage.

	Whole-crop wheat silage	Whole-crop maize silage	Grass silage
Dry matter (g kg^{-1})	350–500	300	200–250
Metabolizable energy (MJ kg^{-1} DM)	9.5–11.5	11–12	10.5–12
Digestibility (g kg^{-1} DM)	60–70	70–75	65–75
Crude protein (g kg^{-1} DM)	90–110	80–100	120–180
pH	3.8–4.8	3.5–4.5	3.7–4.2
Starch (g kg^{-1} DM)	150–300	250–350	0
Ammonia (g kg^{-1} TN)	30–70	40–70	10–100

and maize. Worldwide, maize is the most popular cereal crop for conservation as silage (see table). The advantage of whole-crop over grass silage is that grain formation in whole-crop gives the silage a high starch content and thus provides more rapidly available energy, but conversely whole-crop has a lower crude protein content than grass silage. However, urea treatment or mixing with forage legumes can alleviate this problem. Typical chemical analyses are outlined in the table.

Like grasses, whole-crop cereals contain soluble sugars as the main non-structural carbohydrate, but unlike grasses their digestibility does not fall during maturation as formation of starch in the seed offsets decreased digestibility of other plant parts. In areas where maize will not grow, barley and wheat (in temperate regions) and sorghum (in arid and semi-arid areas) are used. The optimal harvesting stage for whole-crop silage is between the milky and late mealy-ripe stages. Corn crackers are fitted to forage harvesters for maize to crack the grain, so reducing the passage of undigested grain through the ruminant gut without digestion. Whole-crop is easy to ensile because it has a high dry matter, low buffering capacity and ample sugar for a good fermentation. However, at feed-out these silages are more prone to aerobic spoilage, partly due to the high dry matter content, which makes compaction more difficult and can allow the survival of larger yeast populations during the fermentation phase. (DD)

Wilting A method of reducing the moisture content of crops in the field, using natural resources of wind and solar energy. Wilting of herbage crops for silage requires the herbage to be cut with a mower and left in the field for varying periods prior to lifting and ensiling. In poor weather conditions, dry matter (DM) content of crops will increase only slightly and in extended wilting periods soluble sugars and protein content will be reduced. In contrast, during good weather conditions wilting will be rapid with minimum losses of soluble sugars and protein content. Under these conditions the dry matter content of the crop may exceed 350 g kg^{-1}. Ensiling of wilted herbage can result in the fermentation process being inhibited with high pH (> 4.5) and high residual sugar content of > 50 g kg^{-1} DM. Wilting may also reduce undesirable microorganism activity such as clostridia and result in silage free of butyric acid. Wilting of crops to > 300 g kg^{-1} will almost eliminate silage effluent production. Rapid wilting of grass crops has been shown to give improved nutritive quality with higher dry matter intakes and animal production responses. (RJ)

Winemaking residues Winemaking residues, or winery pomace, are by-products of grape juice production. Winery waste pressed with the stalks consists of 30% stalks, 30% seeds and 40% skin and pulp. Its nutritional value is similar to that of straw (see table). Pomace without stalks may be fed to dairy cattle (up to 6.5 kg day^{-1}), providing a good feed when supplemented with concentrates and hay. Grape seed may be separated from the pomace and pressed for its oil. The energy required to digest the residual grape seed meal, due to its high fibre and tannic acid contents, is so great that realistically it is only usable as a carrier for feed ingredients such as molasses. Grape marc, the deseeded pomace, The nutrient composition of winemaking residues.

	Dry matter ($g\ kg^{-1}$)	Nutrient composition ($g\ kg^{-1}$ DM)				
		Crude protein	Crude fibre	Ash	Ether extract	NFE
Fresh leaves	300	158	92	86	134	530
Seeds	930	96	457	42	152	256
Oil cake (hydraulic press)	885	136	440	52	85	287
Pomace (stalk, skin, seed)	406	117	255	77	99	452
Pomace (stalk and skin)	465–881	137–149	236–358	89–128	50–70	429
Pomace (skin)	889	140–190	220–320	63–80	66–80	350–387

Amended from FAO (2002) Feed resources information service
http://www.fao.org/ag/AGA/AGAP/FRG/AFRIS/Data/19.HTM
NFE, nitrogen-free extract.

has a lower fibre content than pomace and can be fed to horses at < 10% of total diet. Pulp and seeds are good sources of calcium but poor sources of phosphorus, magnesium and sodium and have a copper level capable of causing hypercupraemia in some species. Winery by-products are generally only usable in diets for ruminants and horses. (JKM)

Withdrawal feed A feed given in the final period before slaughter, used when the diets of animals destined for meat include antibiotics or other drugs that cannot be allowed into human food. These substances are omitted from the withdrawal feed, allowing time for their residues to be cleared from the animal's body. (MFF)

Wood residues Wood contains a high percentage of potentially digestible carbohydrates but is largely indigestible when fed in the form of untreated sawdust or chips. Wood by-products include treated and untreated wood, cellulose and paper. Exposing the cellulose from the protecting lignin, rendering it more accessible to cellulose-splitting enzymes, can increase digestibility. The most promising treatments are chemical, ball milling, steam, muka (heating at 210°C followed by milling) and solid fermentation using fungi. Lignocellulose can be released from lignin and hemicellulose by chemical treatment to produce cellulose, which has a high energy value for ruminants, and it is also digestible by horses and adult pigs. In adult pigs the digestibility of the organic matter in average cellulose is 53%. Ground cellulose is 90% digestible by sheep but cellulose in the form of torn sheets is only 79% digestible. (JKM)

Wool Wool growth is determined principally by the sheep's genotype. Within any breed or strain, however, the annual weight of wool produced and the quality of that wool are both influenced to a large extent by feeding. Seasonal changes in wool growth, which can be very large (more than fourfold in some breeds), are due in part to circa-annual

The nutrient composition of wood residues.

	Dry matter ($g\ kg^{-1}$)	Nutrient composition ($g\ kg^{-1}$ DM)						
		Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Untreated pinewood	–	10	698	5	4	283	–	–
Treated wood (birch, muka)	–	80	228	42	82	568	7.8	2.5
Office paper	–	7	838	55	19	81	1	–
Newsprint	–	7	689	9	37	358	1	–
Cellulose from sawdust	940	4	864	25	7	100	–	–

NFE, nitrogen-free extract.

changes in photoperiod and in part to quantitative and qualitative changes in the nutrition available to the grazing animal in the course of the year, as well as to changes in physiological state (e.g. pregnancy and lactation) which tend to be associated with season.

Energy intake can affect wool production, particularly at high levels of protein intake. The major nutrient determining wool production is protein, or more specifically the sulphur-containing amino acids methionine and cysteine, since 13% of the wool protein, keratin, is cystine, which is derived from them. Ruminants can synthesize methionine in the rumen, by a pathway that is dependent on adequate sulphate in the diet. Methionine undergoes conversion to cysteine, most probably in the liver, and it is the rate at which cystine is synthesized from cysteine in the wool follicle that determines the rate of fibre growth.

The length of the wool fibre and the fibre diameter (D), which are the main determinants of fleece weight (W), are both affected by nutrition. The ratio $W:D^3$ is relatively insensitive to nutritional influence and can be regarded for most purposes as remaining constant for individual animals. This affords a means of assessing the wool production potential of sheep subjected to different nutritional regimes. (AJFR)

Working animals Draught animals are normally fed only on low quality roughage, such as maize stover and standing hay, because that is the only feed available. Better quality feeds are used for other farm animals such as dairy cows, pigs or poultry. When fed on such low-protein feeds, cattle are not able to consume more energy than 1.4 times their daily maintenance requirement. Cattle undertaking a day's medium to heavy work could easily use up energy at a rate of 1.8 times their maintenance requirement. Under such conditions these animals will lose weight. In some parts of the tropics, especially where the rains fall for only 3 months in the year, the quality of the available grass is so low during the dry season that the animals may lose weight even when they are not working. They may then reach the ploughing and planting season in an underfed condition. When they are worked they will lose more condition and may eventually be unable to complete a full day's work.

Because females breed their own replacements, the total herd size needed to maintain a working animal population can be reduced by two-thirds if female animals are the main source of power. This reduction in herd size is desirable when the land available for animal feeding is limited. However, if the cows are required both to work and to produce milk, their energy

Working animals play a substantial role in many developing countries.

requirements are considerably increased. A cow working for 6 h day^{-1}, and producing 5 l milk at the same time, has to consume 2.0–2.2 times its maintenance requirement if body weight and milk production are to be maintained. Such levels of intake require the feeding of grain in addition to fibrous feeds such as dry savannah grass. An alternative strategy could be to organize the breeding programme so that the cows produce milk at times when they are not required to work.

Work does not significantly increase the protein requirement and any extra that is needed can easily be supplied by the food given to provide the extra energy for work. This is true even when the quality of the feed is low. Therefore, when calculating the feed requirements for work, the energy requirement is much the most important consideration.

To maintain energy balance, working animals must consume energy equivalent to the sum of their maintenance energy needs and the energy expended doing work. Much of the energy used by a draught animal is used simply in walking. This can vary from 1.5 to 8.0 J m^{-1} kg^{-1} liveweight, according to ground surface. The former figure would relate to an animal walking on a smooth road, the latter to an animal walking through a muddy paddy field. The net energy (NE) required from the food for work is 3.3 times the work accomplished, to allow for the mechanical inefficiency of work. Thus, an animal achieving 3 MJ of work a day in pulling a plough would need to use 9.9 MJ NE. Assuming that the efficiency of converting metabolizable energy (ME) into NE for work is 66%, this means that the animal would need an extra 9.9/0.66 MJ (15 MJ) ME each day to accomplish this amount of work without losing weight.

Work does not seem to increase the food intake of working cattle, though it may for horses. Large working horses have a greater capacity for work than cattle and may have an energy requirement up to 2.5 times maintenance. The amount of food that working cattle will consume depends on their size and the quality of the food offered. It can range from 4.0 kg dry matter day^{-1} for an ox of 250 kg on a low quality diet to > 13 kg day^{-1} for one of 700 kg on a high quality diet. (AJS)

Further reading

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X

Xanthine oxidase A molybdenum-containing enzyme widely distributed in milk, small intestine, liver and kidney. Xanthine is produced in the breakdown of the purine bases adenosine and guanosine. Xanthine oxidase utilizes molecular oxygen (O_2) in the conversion of xanthine to uric acid and hydrogen peroxide (H_2O_2). (NJB)

Xanthophyll A yellow carotenoid, also called lutein, $C_{40}H_{56}O_2$, molecular weight 569. Produced by polymerization of isoprenoid units, it is one of the accessory pigments in plants that absorb light. It has no vitamin A activity. (JAM)

Xerophthalmia A condition in which the cornea dries and thickens. It is caused by severe vitamin A deficiency in calves deprived for a long period of green forages or other sources of vitamin A. Other species deprived of vitamin A show corneal keratinization. (WRW)

See also: Eye diseases; Night blindness; Vitamin deficiencies

Xylan A homopolysaccharide of xylose, having (1→4)-linked β-D-xylopyranosyl residues. It is classified as a hemicellulose. The homoglycan is uncommon and the term xylans refers to branched polymers in which the backbone consists of xylose residues and the branches of other sugars. D-Xylans are the most common of the hemicelluloses, occurring in all parts of land plants, primarily as structural components. They may account for up to 30% of the dry weight of woody tissue in angiosperms. The most common side chains are arabinose, the disaccharide of arabinose or a methylated glucuronic acid (*O*-acetyl-L-arabino)-(4-*O*-methyl-D-glucurono)-D-xylan; a substantial portion of xylans are acidic due to this side chain. Arabinose side chains are common in the endosperm of barley, wheat and rye. D-Xylans are also major structural components of maize cobs, cereal hulls, brans and straws and fruit skins. Cottonseed bran and groundnut shells are industrial sources of xylose. Xylans are major substrates for ruminant fermentation. Some angiosperms secrete gum exudates and the side chains of the polysaccharides contain galactose and xylose, as well as arabinose and uronic acids. Xylans are also skeletal glycans in some algae, e.g. *Chlorophyta* or green algae. (JAM)

See also: Arabinoxylans; Carbohydrates; Dietary fibre; Hemicelluloses; Structural polysaccharides; Xylanases; Xyloglucans; Xylose

Xylanases Enzymes that hydrolyse chains of xylose residues. For example, 1,4-β-D-xylanase acts on the (1→4)-β-D chains of xylans, arabinoxylans, glucuronosylans and related polymers. These microbial enzymes work in concert with glycosidases and, in the case of D-xylans, β-D-xylosidases attack the non-reducing terminal sugar. They are usually isolated from bacteria, e.g. *Aureobasidium pullulans*, *Aspergillus niger* and *Trichoderma viride*. (JAM)

See also: Arabinoxylans; Carbohydrates; Dietary fibre; Xylan; Xyloglucans; Xylose

Xylitol Sugar alcohol, $C_5H_{12}O_5$, molecular weight 152, produced by reduction of the aldehyde group of xylose. (JAM)

See also: Carbohydrates

Xyloglucans Heteropolysaccharides consisting of a (1→4)-linked β-D-glucan core to which single (1→6)-α-D-xylose units are attached. The term is actually a misnomer, as L-fucose and D-galactose may also be linked to the xylose residues. Xyloglucans are the major hemicellulosic component of the cell wall of dicotyledonous plants. Their ability to hydrogen-bond with cellulose and thus connect cellulose fibres to pectic substances is due to the structural similarity between xyloglucans and cellulose. Despite the presence of side chains, the primary enzyme that attacks cellulose, endo-1,4-β-D-glucanase, also hydrolyses xyloglucans. Several xyloglucans can be extracted from seeds and are important industrially because they form gels. These seed components stain blue with iodine and are collectively known by the archaic term amyloid. (JAM)

See also: Carbohydrates; Dietary fibre; Hemicelluloses; Structural polysaccharides

Xylose A pentose monosaccharide, $C_5H_{10}O_5$, molecular weight 150, widely distributed in plants, almost exclusively as a component of polysaccharides. Xylose is the major constituent of the hemicelluloses in wood, straw, maize cobs, groundnut shells, grain brans and hulls. Small intestinal absorption is by passive diffusion. (JAM)
See also: Arabinoxylans; Carbohydrates; Dietary fibre; Hemicelluloses; Monosaccharides; Xylan; Xyloglucans

Y

Yam Yams include taro or cocoyam (*Colocasia esculenta* (L.) Schott), winged yam or water yam (*Dioscorea alata* L.), yellow yam (*Dioscorea cayenensis* Lam.), Chinese yam (*Dioscorea esculenta* (Lour.) Burk.) and white yam (*Dioscorea rotundata* Poir). They are starchy tubers, grown primarily as human food. The aerial parts can be used for ruminant feed, and the peel from tubers for pig feed. Tubers are more palatable cooked than raw, as cooking destroys the alkaloid diocorene. Considerable variation is found in the growth habit amongst the varieties listed. Climbing varieties are found with small leaves, while non-climbing varieties have large leaves.

Cocoyam is a tuberous plant with large leaves, similar in shape to elephant ears. Cattle and sheep find the leaves very palatable. In feeding trials with poultry, cocoyam meal has been shown to be a poor substitute for maize meal, depressing growth and food conversion efficiency. Cocoyam contains up to 0.4% of oxalates but their effects can be reduced by cooking or the addition of calcium carbonate to the ration. Cooked cocoyam is often fed to pigs.

Winged yam is the main cultivated variety, with very large tubers and a climbing growth habit. Leaves are smaller than those found on cocoyam. Tubers are grown for human food but the peel is a valuable feed for livestock.

Yellow yam tubers do not store well. Peelings are used for pig feed.

Chinese yam is a climbing variety that produces small oval tubers that are sweet in taste and have thin peel. The peel can be used for pig feed.

White yams are grown widely in West Africa and have tubers that store well. As with other varieties, the peel can be fed to pigs.

(LR)

Further reading

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Yeast *Saccharomyces* yeast is most frequently used in ruminants, to increase beneficial bacterial populations in the rumen, leading to increased feed intake, weight gain, milk yield and feed conversion efficiency. The yeasts commonly used are *Candida pin-*

Typical composition of yam products (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Cocoyam leaf, fresh	8.2	25.0	12.1	12.4	10.7	39.8	1.74	0.58
Cocoyam leaf meal	–	23.2	13.2	9.9	5.9	57.4		
Cocoyam tubers, fresh	26.2	8.7	1.7	4.0	0.4	85.2		
Cocoyam meal	95.2	2.9	0.7	4.9	3.4	87.9		
Winged yam leaf, fresh	24.1	12.0	25.3	7.9	2.3	52.5	0.95	0.16
Winged yam tuber peel, fresh	25.9	11.7	6.6	9.5	1.0	71.2		
Yellow yam tuber peel, fresh	21.7	7.4	7.6	7.5	0.7	76.8		
Yellow yam meal	98.9	5.34	5.39	3.93	0.80	84.5		
Chinese yam tuber peel, fresh	7.0	10.0	7.6	6.3	0.9	75.2		
White yam tuber peel, fresh	17.7	11.2	9.5	9.8	1.2	68.3		

tolopesii, *C. saitoana*, *Torula utilis* and *Saccharomyces cerevisiae*. Yeast is also used in diets, particularly for non-ruminants, as a source of protein and B vitamins. Fodder yeast can be grown on various by-products, including citrus press liquor, potato pulp, apple pomace, molasses, sulphite waste liquor from the paper industry, wood and fruit wastes. Cattle can be fed 1–2 kg day^{-1}, and lambs at 1.25% and steers at 1.85% of the total diet. Calves can be fed 3–5% or 2 g kg^{-1} of starter diet. Pigs can be fed 5% (sows 100–400 g day^{-1}) and poultry at 9% for male chicks and 2–3% of total diet for female chicks. The dry matter (DM) content of yeast is usually about 891 g kg^{-1} and the typical nutrient composition (g kg^{-1} DM) is crude protein 499, crude fibre 15, ash 85, ether extract 13, NFE 388, calcium 1.3 and phosphorus 15.6. (JKM)

Yeasts as probiotics: *see* Probiotics

Yeasts in gastrointestinal tract: *see* Gastrointestinal microflora

Yellowtail (*Seriola quinqueradiata*) A member of the tuna family, farmed in sea cages in Japan and some Far East countries at a water temperature range of 12–30°C. Those with a market size of 5 kg or less and those over 5 kg are called hamachi and buri, respectively. Larvae are fed live food organisms (e.g. rotifers and artemia), enriched with n-3 fatty acids. Grower diets consist of either trash fish supplemented with vitamin supplements or soft extruded feeds. Wild juveniles are also used for farming and they are gradually weaned on prepared feeds. (SPL)
See also: Marine fish

Yolk pigments Poultry cannot synthesize carotenoids *de novo* and so yolk colour is determined by the pigments consumed in the feed. Pigments that occur naturally in the feed may be present in the non-ester form, limiting their bio-availability, and may fluctuate according to harvesting, drying and storage conditions. To enable egg producers to control yolk colour, ingredients such as astaxanthin, β-apo-8′-carotenoic acid-ethylester, canthaxanthin, citranaxanthin, lutein, xanthophyll and zeaxanthin may be added to the feed. However, as for other additives, the amounts that may be added may be limited by legislation. (NS)

Yolk sac The yolk sac is one of the first extra-embryonic membranes to form during embryogenesis. This membrane enables the embryo to access the nutrients, primarily lipids, contained within the yolk. It is a bilayered structure: the inner membrane (endoderm) takes up nutrients by non-specific phagocytosis and transports them to the vascularized outer membrane (mesoderm), from which they are transported to the developing embryo. Prior to exporting the lipids, hydrolysis, re-esterification and the synthesis of lipoproteins takes place within the membrane. In the domestic chicken the membrane begins to form on day 1 of incubation and by day 5 the membrane encapsulates the yolk. The membrane is attached to the embryo at the midgut by the so-called yolk stalk but there is little evidence for nutrients being taken up directly during embryogenesis via the stalk. The rapid uptake of lipids by the yolk sac membrane in the last week of incubation is mirrored by the accumulation of the fat-soluble antioxidant vitamin E (the concentration in the embryo's liver increases by up to fivefold during the last week of incubation). While its prime function is to provide a surface for the uptake of nutrients, the yolk sac membrane also, in the first week of incubation, provides a surface for the exchange of respiratory gases, a function performed in the latter stages of incubation by the chorio-allantoic membrane. (NS)

Ytterbium Ytterbium (Yb) is a rare-earth metal with an atomic mass of 173.04. There is no known nutritional value of Yb for animals. Because of its low rate of absorption in the gut, it is often used as a marker to measure digesta flow. (PGR)

Yuca: *see* Cassava

Z

Zein The major storage protein in the endosperm of maize. It contains very little lysine or tryptophan and in consequence has a very low biological value. (MFF)

Zeolites Microporous crystalline solids with well-defined structures. They generally contain the elements silicon, aluminium and oxygen in their framework and cations, water or other molecules within their pores. Many occur naturally as minerals, being widely distributed in oceanic sediments and volcanic regions. Others are manufactured commercially for specific uses.

Zeolites are often referred to as molecular sieves because they are porous. They are used in a variety of applications with a global market of several million tonnes per annum. Major uses include petrochemical cracking, water purification and softening and in the separation and removal of gases and solvents.

The unique microporous nature of zeolites makes them excellent catalysts and they are often referred to as shape-selective catalysts. These shape-selective properties are also the basis for their use in molecular adsorption. (MG)

Zinc Zinc is a mineral element with a molecular mass of 65.39. It is an essential dietary component for all farm animals. Zinc is one of the most biologically active mineral elements; it is an indispensable part of over 200 enzymes in mammalian systems. All known classes of enzymes have at least one representative that contains Zn. In addition, Zn helps to regulate gene expression by virtue of its ability to associate with histidyl and sulphydryl groups in proteins to maintain structural integrity and facilitate receptor binding to specific DNA sequences. These protein structures are called Zn fingers; two examples in mammalian systems are the androgen and glucocorticoid receptors. Although Zn has no redox potential, it can influence oxidative processes, especially those involving iron and possibly copper, by protecting sulphydryl groups from oxidation.

Ingested Zn is absorbed primarily from the upper small intestine. The specific mechanisms of absorption have not been completely defined but probably involve specific divalent cation transport proteins that are located in the plasma membranes of the enterocytes. These include DCT1 for Zn influx and ZnT-1 and -2 for Zn efflux.

After Zn is absorbed into the blood, it is transported to the liver and other organs bound mostly to serum albumin. Transport proteins similar to those found in the intestine probably influence uptake into the liver and other tissues. Zinc concentration in the serum or plasma is approximately 1.0 mg l^{-1}. During low dietary intakes of Zn, plasma Zn concentration can decrease to one-third of the normal value within a very short time. Plasma Zn is often used to assess the Zn status of an animal, but other factors such as stress and infection can affect plasma Zn as well and lead to false indications of Zn status. Excess Zn in the diet will increase plasma Zn concentrations above normal; however, most animals are able to adapt to reasonably high intakes by reducing the rate of absorption, which may return plasma Zn to near normal. Zinc itself is not highly toxic but if relatively high amounts are ingested over a long period, copper and iron absorption can be depressed and lead to deficiencies of these minerals.

Zinc deficiency in mammals manifests itself in numerous and varied physiological abnormalities. For example, the initial response, after a few days of consuming a low Zn diet, can be low plasma Zn. This is soon followed by a reduction in food intake and a slowing of body weight gain in young animals, or weight loss in mature animals. Extended intakes of low Zn diets can result in skin lesions usually referred to as parakeratosis. Pigs are especially sensitive to Zn deficiency and readily develop these lesions. Even a marginal Zn deficiency can cause reproductive failure, especially in males. Sperm maturation is dependent on Zn, and if the deficiency becomes severe the defects are not reversible. Supplementing the diet with adequate Zn can reverse most other signs of the deficiency.

Zinc is present in many forages and plant seeds at concentrations ranging from 20 to 50 mg kg^{-1} and these will often supply the required amount of Zn. However, because of the amount of fibre in forages and phytic acid in seeds, the bioavailability of Zn can be limited by impaired absorption. The US National Research Council sets the requirement of Zn for most farm species, including dairy and beef cattle, horses, goats and poultry, at 30–40 mg kg^{-1} diet; and for sheep, between 20 and 33 mg kg^{-1} diet. The requirement for pigs is set somewhat higher, at 100 mg Zn kg^{-1} diet for young animals of 3–5 kg body weight, but then it drops to 50 mg kg^{-1} diet for those weighing 50–120 kg. The Zn requirement of commercially reared fingerling channel catfish was found to be 20 mg kg^{-1} dry diet. (PGR)

See also: Absorption; Availability; Copper; Iron; Metallothionein

Further reading

Hambidge, K.M., Casey, C.E. and Krebs, N.F. (1986) Zinc. In: Mertz, W. (ed.) *Trace Elements in Human and Animal Nutrition.* Academic Press, New York, pp. 1–137.

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Zooplankton Tiny aquatic animals that drift freely in the water. They are the main consumers of the primary producers, phytoplankton. Several groups of these microscopic animals make up zooplankton, from the larvae of large fish and invertebrates, to fully grown worms and crustaceans. Zooplankton are often classified by their size and categories include macrozooplankton (visible range), mesozooplankton, microzooplankton (20–200 μm) and nanozooplankton (2–20 μm). Their guts produce countless faecal pellets contributing greatly to the marine 'snow' and thereby accelerating the flow of nutrients and minerals from surface waters to the bottom of the seas. Most marine fish hatcheries culture zooplankton such as rotifers, artemia and copepods to feed small larvae before they are ready for formulated diets. (SPL)

See also: Aquatic organisms; Fish larvae; Live fish food; Phytoplankton; Rotifer

Zymogens Enzymatically inactive precursors of proteolytic enzymes. Zymogens are typically synthesized by cells in an inactive precursor form and are then later activated in response to a physiological event. For example, pancreatic zymogens (trypsinogen, chymotrypsinogen, procarboxypeptidase and proelastase) are digestive enzymes, released from the pancreas in an inactive proenzyme form, that are converted to activated forms in the small intestine through a series of reactions initiated by the enzyme enteropeptidase (also known as enterokinase). This group of zymogens is also called pancreozymin. The zymogens are delivered to the small intestine by the pancreatic duct, where they are activated by specific proteolysis. (GG)