11 Evaluation of foods: energy content of foods and energy partition

The major organic compounds in foods are required by animals as building blocks for the synthesis of animal products such as milk and eggs. They are also required as sources of energy to support work done. A unifying feature of these diverse functions is that they all involve a transfer of energy. This applies when chemical energy is converted from one form to another (for example, when body fat is synthesised from dietary carbohydrate), and equally when nutrients are oxidised and converted to mechanical or heat energy. The ability of a food to supply energy is therefore of great importance in determining its nutritive value. This chapter and the next will discuss factors affecting the energy content of foods, the partition of food energy within the animal, the measurement of energy metabolism and the different methods used to express energy supply.

11.1 ENERGY DEMAND

Before discussing the factors that affect energy supply from foods, it might be useful to briefly explain the factors affecting energy demand, although these factors will be discussed in more detail in Chapters 14, 15 and 16. An animal requires energy for both maintenance and production. The energy requirement for maintenance represents the energy required for vital body processes that are essential for life – for example, the work associated with essential muscular activity (e.g. beating of the heart), the work associated with active transport (movement of dissolved substances against the concentration gradient) and the energy associated with the synthesis of essential body constituents such as enzymes and hormones. An animal deprived of food continues to require energy for these processes, otherwise it would die. In a starved animal, the energy required for vital body processes is derived from the catabolism of body reserves – initially glycogen, but then body fat and protein. In a fed animal, the primary demand for energy is to meet this maintenance requirement and to prevent the catabolism of body tissues.

When energy in food is used for maintenance, the animal does no work on its surroundings and all the energy used is converted to heat, which, although useful for maintaining body temperature, is expended from the animal's body. In a fasting animal, the amount of heat produced is equal to the energy derived from tissue catabolism, which, when measured under specific conditions, is known as the animal's basal metabolic rate or fasting metabolism. The way in which estimates of basal metabolism are used to assess the maintenance energy requirement of animals is explained in Chapter 14.

The energy supplied by food in excess of the maintenance requirement is used for production. In young growing animals, energy is stored in new tissues primarily as protein. However, as animals mature, an increasing proportion is stored as fat. In pregnant and lactating animals, energy is stored in the products of conception (foetus and placenta) and in milk constituents, respectively. Other forms of production include the energy required for activity or exercise and the energy required for the synthesis of wool or eggs. No process, not even maintenance, has an absolute priority for food energy. For example, a young animal receiving adequate protein but insufficient energy for maintenance may still continue to deposit body protein, while breaking down body fat. Similarly, wool growth continues in animals at submaintenance energy intakes, and even in fasted animals.

11.2 ENERGY SUPPLY AND PARTITION

Gross energy (GE)

Energy is stored in the chemical components of food as chemical energy. The amount of chemical energy in a food is measured by converting it to heat and determining the heat production on burning. The amount of heat produced from the complete oxidation of a unit weight of food is known as its gross energy (GE) value, or heat of combustion. Gross energy is measured in an apparatus called a bomb calorimeter, which in its simplest form is a strong steel vessel (bomb) resting in an insulated bucket of water. The food sample is pelleted and placed in the bomb, which is then pressurised to 25 atmospheres with oxygen. The initial temperature of the water in the bucket is recorded before the sample is electrically ignited. The food sample burns vigorously in an atmosphere of oxygen, and the heat produced during oxidation is dissipated through the wall of the bomb, causing the temperature of the water in the bucket to rise. When equilibrium is reached, the final temperature is recorded. The quantity of heat produced is then calculated from the weight of the food sample oxidised, the weight of water, the temperature rise in the water and the specific heat capacities of the water and bomb. Bomb calorimetry is used to measure the gross energy content of whole foods and their components and the energy content of animal tissues and excretory products.

Some typical GE values for various foods are presented in Fig. 11.1. The primary determinant of the GE content of organic compounds is their degree of oxidation, expressed as the ratio of carbon plus hydrogen to oxygen. All carbohydrates have similar ratios and therefore have approximately the same GE content (17.5 MJ/kg DM). However, triglyceride fats typically have a higher ratio (contain less oxygen) and therefore have a higher GE value (39.0 MJ/kg DM). Individual fatty acids vary in their GE content depending on the length of their carbon chain and degree of

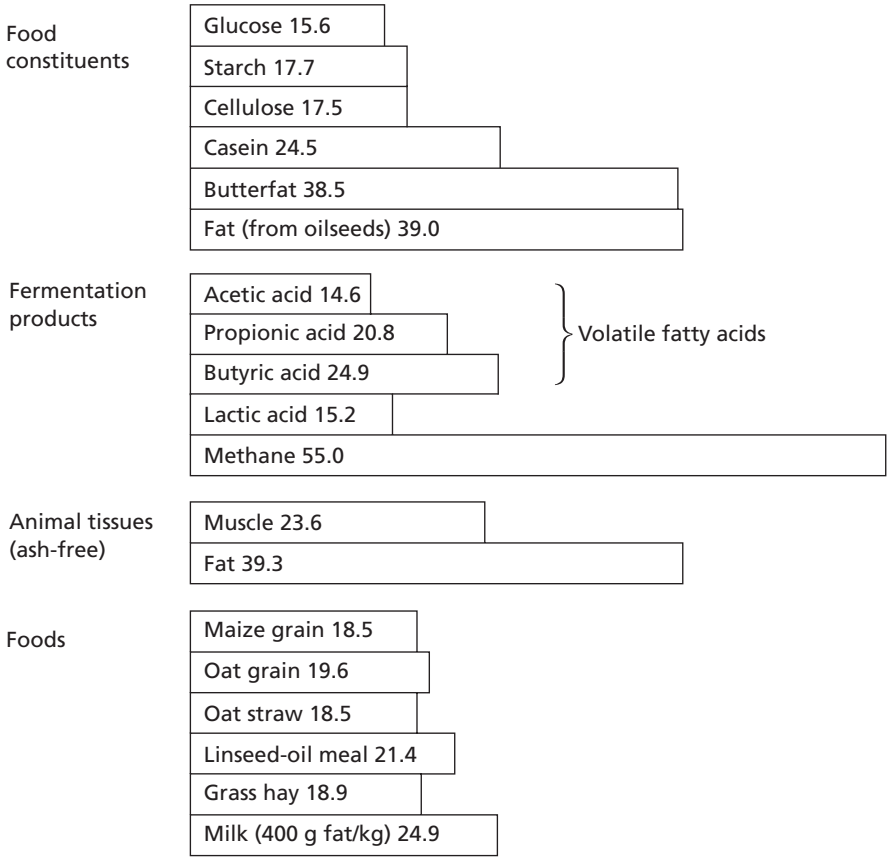

Fig. 11.1 Some typical gross energy values (MJ/kg DM).

saturation, with those with shorter chains (volatile fatty acids) and a greater number of double bonds having a lower energy content. Proteins have a higher GE content than carbohydrates because they contain the additional oxidisable elements nitrogen and sulphur. Methane has a very high GE content because it consists entirely of carbon and hydrogen.

In spite of the differences in GE content between different food components, the fact that carbohydrates are the predominate component in most foods means that GE values vary very little. Only foods rich in fat, such as full-fat soya bean meal with an ether extract of 222 g/kg DM, have significantly higher values. Similarly, those rich in ash, which has no nutritional value, have significantly lower values. Most common foods have a GE content of approximately 18.4 MJ/kg DM.

Not all the GE in foods is available for use by the animal. Some is lost from the animal as various solid, liquid or gaseous excretory products, and some is lost as heat. These energy losses are illustrated in Fig. 11.2. The subtraction of these losses from the food's GE content produces further measures of food energy supply. For example, subtracting the GE loss in faeces from the GE in food provides a measure of digestible energy. This and other measures of energy supply will now be discussed further.

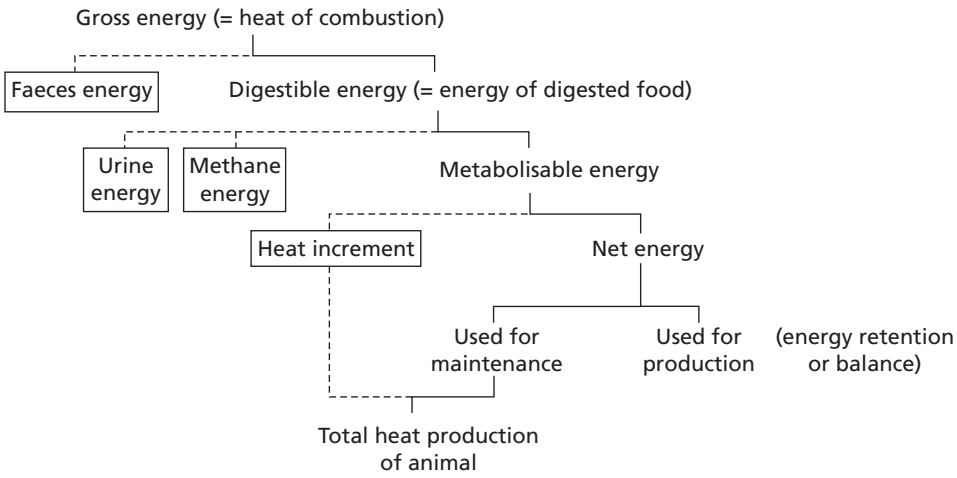

Fig. 11.2 The partition of food energy in animals. Losses of energy are shown as the boxed items on the left.

Digestible energy (DE)

Digestible energy represents energy absorbed by the animal. Apparent digestible energy is calculated as the GE provided by a unit of food minus the GE content of the faeces resulting from the consumption of that unit of food. An example of the calculation of digestible energy is provided in Box 11.1. As faecal energy loss represents by far the most important and variable loss of energy from animal foods, DE is a far better measure of the energy available to support animal production than GE. Digestible energy is often used as the measure of energy supply for pigs and horses, where additional energy losses in urine and methane are relatively small and consistent.

Metabolisable energy (ME)

In addition to energy losses in faeces, energy is also lost as energy-containing compounds in urine, and as combustible gases such as methane produced by microbial fermentation in either the rumen or hindgut. Metabolisable energy represents energy that is available for use by the animal and is calculated as DE minus energy lost in urine and combustible gases (see Box 11.1). Typically, 2–5 per cent of GE intake is lost in urine in the form of nitrogen-containing compounds such as urea, hippuric acid, creatinine and allantoin, and in non-nitrogen-containing compounds such as glucuronates and citric acid. The combustible gases produced in the rumen and hindgut consist almost entirely of methane (CH_4). Methane production is closely related to food intake, and at a maintenance level of nutrition approximately 7–9 per cent of the GE (11–13 per cent of DE) is lost as methane. At higher levels of feeding, the proportion falls to 6–7 per cent of GE, the reduction being most marked for highly digestible foods. With previously fermented foods, such as brewer's grain, methane production is low (3 per cent of GE). When methane production cannot be easily measured it can be estimated as 8 per cent of gross energy intake. Another approximation allows the ME value of ruminant foods to be calculated from their DE value

BOX 11.1 Calculation

Calculation of the digestible energy (DE) and metabolisable energy (ME) content of hay fed to sheep

In Box 10.1 in Chapter 10, data from a trial to determine the digestibility of a hay in sheep was presented. In addition to the data presented, samples of the feed and faeces were analysed in the laboratory for gross energy (GE) by bomb calorimetry.

	Feed	Faeces
Dry matter intake (kg/day)	1.63	---
Dry matter output (kg/day)	---	0.76
GE (MJ/kg DM)	18.0	18.7
GE (MJ/day)	29.3	14.2

Calculation of GE digestibility and digestible energy (DE)

$$\begin{aligned}\text{GE digestibility} &= (29.3 - 14.2)/29.3\\ &= 0.515\ (51.5\%)\\ \text{Digestible energy (DE)} &= 18.0 \times 0.515\\ &= 9.27\ \text{MJ/kg DM}\end{aligned}$$

Calculation of GE metabolisability (q) and metabolisable energy (ME)

In addition to faecal losses, assume a further 0.90 and 1.25 MJ/day are lost in urine and faeces:

$$\begin{aligned}\text{GE metabilisability (q)} &= (29.3 - 14.2 - 0.90 - 1.25)/29.3\\ &= 0.411\ (41.1\%)\\ \text{Metabolisable energy (ME)} &= 18.0 \times 0.411\\ &= 7.39\ \text{MJ/kg DM}\end{aligned}$$

ME can also be calculated from DE as:

$$\begin{aligned}\text{ME} &= 0.81 \times \text{DE}\\ &= 0.81 \times 9.27\\ &= 7.50\ \text{MJ/kg DM}\end{aligned}$$

by multiplying by 0.81. This implies that, on average, about 19 per cent of the energy apparently digested is excreted in the urine and as methane.

The ME value of a food is determined in a feeding trial similar to a digestibility trial, but in which urine and methane are collected as well as faeces. Metabolism cages for sheep and pigs usually incorporate a device for collecting urine. With cattle, urine is collected in rubber urinals attached below the abdomen for males and over the vulva for females, and is piped by gravity or suction to a collection vessel.

An alternative method of collecting urine from females, which is commonly used in pigs, is to insert a rubber catheter into the vagina.

When methane production is measured to estimate unproductive energy losses, the animal is usually kept in an airtight container known as a respiration chamber (see p. 279). More recently, the significance of methane production from ruminants in relation to global warming has stimulated the development of an alternative technique that allows methane to be measured from individual animals, whether confined or not. In this technique, a calibrated permeation tube containing sulphur hexafluoride (SF_6) is inserted into the rumen and releases SF_6 through a permeable membrane at a controlled rate. After a 5-day adaptation period, breath samples are collected from near the nose of each animal using capillary tubing over a 24-hour period into pre-evacuated canisters. The concentrations of SF_6 and CH_4 are measured by gas chromatography and the methane emission rate, corrected for background levels, is calculated as:

$$QCH_4 = QSF_6 \times [CH_4]/[SF_6]$$

where $[CH_4]$ and $[SF_6]$ are measured concentrations in excess of background, and QSF_6 is the rate of SF_6 release from the permeation tube.

For poultry, ME is measured more easily than DE because the faeces and urine are voided together through the cloaca. A rapid standardised method has been developed for determining the ME value of poultry foods. Cockerels are fasted (or fed a small quantity of glucose solution) for 48 hours until their digestive tract is empty, and then force-fed a single meal (30–40 g) of the food under investigation using a stainless-steel funnel and plunger inserted carefully down the oesophagus into the crop. Excreta are then collected until all the residues arising from the single meal have been voided. At the same time, the small quantities of excreta voided by fasted (or glucose-fed) birds are collected, as a measure of endogenous losses. The energy derived from these endogenous losses is then subtracted from the energy derived from the excreta of the fed birds, and so the estimate of ME obtained is a true rather than apparent value (see p. 255). This is known as true metabolisable energy (TME) and is not directly comparable with measures of ME obtained using other techniques.

Factors affecting the metabolisable energy value of foods

The ME values of a number of feeds are presented in Table 11.1. It is clear that, of the energy losses so far considered, faecal losses are by far the most important. Even for highly digestibility foods such as barley, twice as much energy is lost in the faeces as in the urine and methane. The main factors affecting the ME value of a food are therefore those that influence its digestibility. These have been discussed earlier (see Chapter 10). The emphasis here is on urine and methane losses.

The ME content of a food will vary depending on the species of animal to which it is fed or, more specifically, the type of digestion to which it is subjected. Fermentative digestion, in either the rumen or hindgut, incurs losses of energy as methane. A lesser effect of the intervention of microorganisms in digestion is an increase in energy losses in urine (as the breakdown products of microbial nucleic acids are excreted) or faeces (microbes synthesised in the hindgut and excreted). In general, energy losses in urine and methane are greater in ruminants than in non-ruminants. Consequently, foods such as concentrates, which are digested to the same extent in ruminants and non-ruminants, will have a higher ME for non-ruminants than

Table 11.1 Energy partition and metabolisable energy values for some typical foods (MJ/kg DM)

Animal	Food	Gross energy	Energy lost in			ME
			Faeces	Urine	Methane	
Fowl	Maize	18.4	2.2	–	–	16.2
	Wheat	18.1	2.8	–	–	15.3
	Barley	18.2	4.9	–	–	13.3
Pig	Maize	18.9	1.6	0.4	–	16.9
	Oats	19.4	5.5	0.6	–	13.3
	Barley	17.5	2.8	0.5	–	14.2
	Coconut cake meal	19.0	6.4	2.6	–	10.0
Sheep	Barley	18.5	3.0	0.6	2.0	12.9
	Dried ryegrass (young)	19.5	3.4	1.5	1.6	13.0
	Dried ryegrass (mature)	19.0	7.1	0.6	1.4	9.9
	Grass hay (young)	18.0	5.4	0.9	1.5	10.2
	Grass hay (mature)	17.9	7.6	0.5	1.4	8.4
	Grass silage	19.0	5.0	0.9	1.5	11.6
Cattle	Maize	18.9	2.8	0.8	1.3	14.0
	Barley	18.3	4.1	0.8	1.1	12.3
	Wheat bran	19.0	6.0	1.0	1.4	10.6
	Lucerne hay	18.3	8.2	1.0	1.3	7.8

ruminants (see ME values for barley in Table 11.1). However, fibrous foods fed to non-ruminants will also incur losses due to fermentative digestion in the hindgut. In ruminants, foods such as silages, which have already been fermented before consumption by the animal, will incur smaller energy losses during digestion, but will have already incurred energy losses in the silo. Thus, silages contain less fermentable metabolisable energy (FME) than comparable foods such as hays. However, this difference is of greater significance in the protein than energy nutrition of ruminants (see Chapters 8 and 13). A final comment on the effect of animal species is that differences between cattle and sheep in losses of energy as urine and methane are small and of no significance.

The ME value of a food will vary depending on whether the amino acids supplied are retained by the animal for protein synthesis or deaminated and their nitrogen excreted in the urine as urea. For this reason, ME values are sometimes corrected to zero nitrogen balance by deducting either 28 kJ (pigs), 31 kJ (ruminants) or 34 kJ (poultry) for each 1 g of nitrogen retained. The factor most appropriate to each species of animal depends on the extent to which nitrogen is excreted as urea (gross energy 23 kJ/g nitrogen) or other compounds (e.g. uric acid, 28 kJ/g nitrogen). If an animal is excreting more nitrogen in its urine than it is absorbing from its food (i.e. is in negative nitrogen balance, see Chapter 13), then some of the urine nitrogen is not derived from the food, and in this case the ME value must be subjected to a positive correction.

In ruminants, increasing the level of feeding and the manner in which food is processed may affect its ME value. As discussed earlier (see Chapter 10), increasing the level of feeding, or the grinding and pelleting of forages, may result in higher rates of passage and increased faecal energy loss (see Table 10.3 in Chapter 10). However, this may be partly offset by a reduction in rumen retention time, and a decrease in energy losses as methane. In general, level of feeding is thought to have only a minor effect on the ME value of high-quality diets, with ME values greater than 11.5 MJ/kg DM. In a recent study conducted as part of the Feed into Milk Project, where the ME values of 59 diets determined in sheep at maintenance (M), or beef and dairy cows at 4.8 × M were compared, no clear effect of feeding level was observed. It was recommended that only a small fixed factor is needed to correct ME values used at production levels for values determined in sheep at maintenance:

$$\text{ME production} = \text{ME maintenance} \times 0.98$$

In poultry, the grinding of cereals has no consistent effect on ME values.

In theory, it should be possible to prevent methane production in the rumen, and thereby avoid losing 8–12 per cent of gross energy intake in this form. Methane production can be supressed by adding anti-microbial agents to the diet (e.g. chloroform), but the consequences are not consistently favourable. Energy may be diverted to another gaseous by-product, hydrogen (see Fig. 8.8, Chapter 8). Furthermore, the rumen microorganism may adapt to the presence of the agent and revert to the synthesis of methane. The coccidiostat monensin, which has been widely used as a growth-promoting agent in beef diets, is considered to be a methane suppressant. However, there is some evidence that methanogenic microorganisms can adapt to this agent. Since the ban on the use of antimicrobial growth promotors introduced by the EU in January 2006 and the recognition that methane from ruminants is an important greenhouse gas, there has been renewed interest in alternative methods of reducing methane production using products such as yeast cultures and plant extracts (see Chapters 8 and 24).

Heat increment of foods

The energy losses arising with the ingestion of food are not only associated with the chemical energy lost in faeces, urine and methane, but also heat. Animals are continuously producing heat and losing it to their surroundings, either directly by radiation, conduction and convection, or indirectly by the evaporation of water. If a fasting animal is fed, its heat production will increase above the level represented by basal metabolism within a few hours. This increase is known as the heat increment of the food, which in human beings is quite marked after a large meal. The heat increment may be expressed in absolute terms (MJ/kg DM) or relatively as a proportion of either GE or ME. Unless the animal is in a particularly cold environment, this heat energy is of no value to the animal and must be considered an energy loss, similar to those lost in other excretory products.

The causes of the heat increment are to be found in the processes associated with digestion of foods and metabolism of the nutrients derived from them. The act of eating, which includes chewing, swallowing and the secretion of saliva, requires muscular activity, for which energy is supplied by the oxidation of nutrients. In ruminants chewing fibrous foods, the energy cost of eating is estimated to be 3–6 per cent of

ME intake. However, the energy cost of rumination is much lower and is estimated to be about 0.3 per cent of ME intake. Ruminants also generate heat through the metabolism of their gut microorganisms; this is estimated to amount to about 7–8 per cent of ME intake (or alternatively 0.6 kJ per kJ of methane produced).

More heat is produced when nutrients are metabolised. For example, it was shown in Chapter 9 that if glucose is oxidised for the formation of ATP, then the efficiency of free energy capture is only about 0.52, with 0.48 being lost as heat. Moreover, the efficiency will be even less if temporary storage of nutrients is required (e.g. glucose stored as glycogen) because more reactions are required. Similar inefficiency is apparent in the synthesis of the body's structural constituents. For example, the linking of one amino acid to another requires the expenditure of four pyrophosphate high-energy bonds, and if the ATP that provides these is obtained through glucose oxidation, then about 2.5 MJ of energy will be released as heat for each kilogram of protein formed. Protein synthesis, it should be noted, occurs not only in growing animals but also in those kept at a maintenance level, in which protein synthesis is a part of the process of protein turnover (see p. 227). Protein metabolism is estimated to account for about 10 per cent of the animal's heat production. The animal also expends high-energy phosphate bonds to do the work involved in the movement of substances (e.g. Na^+ and K^+ ions) against concentration gradients. This so-called 'ion pumping' may also contribute 10 per cent of the animal's heat production. Heat is produced within the body in those regions with the most active metabolism. Thus, it has been estimated that in ruminants, which have a large and metabolically active gut, as much as half of the total heat production originates from the gut and liver.

We shall see later that the heat increment of foods varies considerably, depending on the nature of the food, the type of animal consuming it and the various processes for which nutrients are used.

Net energy (NE) and energy retention

The net energy (NE) value of a food is calculated by subtracting the heat increment from the ME value. The NE value represents the energy that is available for useful purposes, such as body maintenance and production (see Fig. 11.2). Net energy used for maintenance is used primarily to perform work within the body and leaves the body as heat. That used for production is either stored in the animal body as fat and protein, or leaves the body as the chemical energy in milk, eggs or wool. This is often referred to as the animal's 'energy retention'. It is important to understand that the total heat production of an animal represents the energy used for maintenance plus the heat increment. Only the heat increment is a true energy loss. The heat arising from the use of ME for body maintenance has been used to perform work within the animal and been degraded to a useless form during the process of utilisation.

11.3 ANIMAL CALORIMETRY: METHODS OF MEASURING HEAT PRODUCTION AND ENERGY RETENTION

Calorimetry is defined as the measurement of heat transfer. The partition of food energy presented in Fig. 11.2 illustrates that if the ME intake of an animal is known and total heat production is also measured, energy retention can be calculated by difference. Likewise, if energy retention is measured, total heat production can also

be calculated. In practice, the NE values of foods are determined by measuring either total heat production or energy retention.

The methods used to measure heat production and energy retention in animals can be quite complex, both in principle and practice. In addition, the complexity and cost of the apparatus required for large animal calorimetry limits its use to a small number of nutritional research establishments. As a result, animal calorimetry remains a specialist topic with which few nutritionists get involved. Nevertheless, the study of animal calorimetry is valuable to all students of nutrition because it reinforces the principles of energy metabolism.

The heat production of animals can be measured physically using a technique known as direct calorimetry. Alternatively, heat production can be calculated from the respiratory exchange of an animal. For this, a respiration chamber is used and the technique is called indirect calorimetry. Respiration chambers can also be used to measure energy retention using the carbon and nitrogen balance technique.

Direct calorimetry

Animals do not store heat, except for a relatively short period of time, so when measurements are made over a period of 24 hours or longer it is generally safe to assume that the amount of heat lost from an animal is equal to the amount produced.

To determine the heat increment of a food, animals are fed at two levels of ME intake and their total heat production measured at each level. The heat increment is calculated as shown in Fig. 11.3. Two levels of feeding are required because part

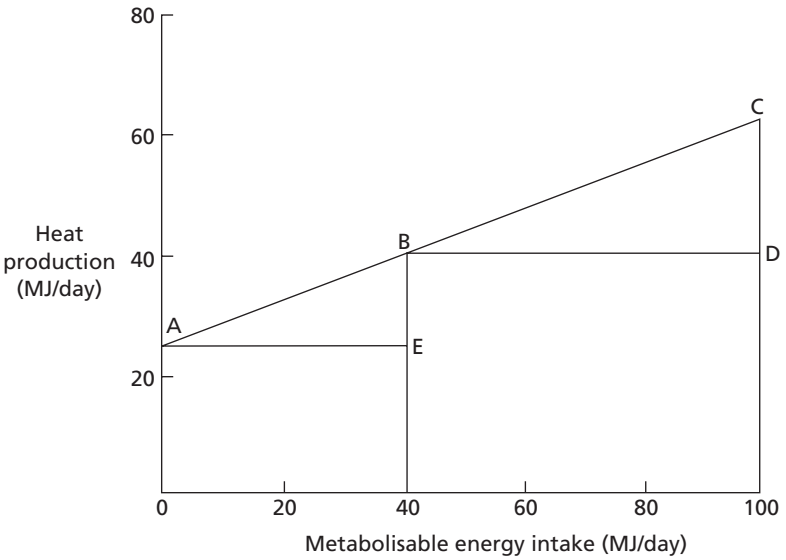

Fig. 11.3 The difference method for estimating the heat increment of foods: A is the basal metabolism and B and C represent heat production at metabolisable energy intakes of 40 MJ and 100 MJ respectively. For the sake of simplicity, the relationship between heat production and metabolisable energy intake is shown here as being linear, i.e. ABC is a straight line; however, as explained later in the chapter, this is not usually the case.

of the animal's total heat production is associated with its basal metabolism. An increase in food intake causes total heat production to rise, but the basal metabolism is assumed to remain constant. The increase in heat production is thus the heat increment of the additional food fed. The calculation of the heat increment of the food fed in Fig. 11.3 is presented in Box 11.2

Direct calorimetry is carried out using an animal calorimeter, which is essentially an airtight, insulated chamber. In most early calorimeters, sensible heat losses from the animal (i.e. those associated with radiation, conduction and convection) were taken up by water circulating through coils within the walls of the chamber. Heat production was calculated from the flow rate of the water and the difference between its entry and exit temperatures. Evaporative heat losses were calculated by recording the volume of air drawn through the chamber and its moisture content on entry and exit. More recently, gradient layer calorimeters have been developed. In these, heat production is measured electrically as it passes through the wall of the chamber. This type of calorimeter lends itself to automation, and both sensible and evaporative heat losses can be recorded automatically. Because animal calorimeters are expensive and difficult to operate, most calorimetry is carried out using the indirect technique described in the next section.

BOX 11.2 Calculation

Calculation of the heat increment of feeding for a food based on direct calorimetry

In the calorimetry experiments presented in Fig. 11.3, food was fed at two levels to provide an ME intake of either 40 or 100 MJ/day.

Difference in ME intake (BD)	= 100 − 40	= 60 MJ/day
Difference in heat production (CD)	= 64 − 40	= 24 MJ/day
Energy retention (BD – CD)	= 60 − 24	= 36 MJ/day
Heat increment	= 24/60	= 0.40 (40%)

It is also possible to make the lower level of ME intake zero, and to estimate the heat increment as the difference in heat production between basal (fasting) metabolism and that produced in the fed animal.

Difference in ME intake (AE)	= 40 − 0	= 40 MJ/day
Difference in heat production (BE)	= 40 − 24	= 16 MJ/day
Energy retention (AE – BE)	= 40 − 16	= 24 MJ/day
Heat increment	= 16/40	= 0.40 (40%)

If a single food is being investigated, then it may be fed at both levels of ME intake. However, if the food is one that would not normally be fed alone, then the lower level may be derived from a basal ration and the higher level from the basal ration plus the food being investigated. For example, the heat increment of barley fed to sheep could be derived by feeding sheep on a basal ration of hay and then on an equal amount of hay plus some of the barley.