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CHAPTER 9

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Introduction

Feed is the most costly component of monogastric livestock production and energy represents the largest cost factor in the feed. Energy is not a nutrient but it is a property of nutrients and objects. Because energy exists in different forms, it is difficult to give a unique definition of energy but it is frequently referred to as the 'ability to perform work'. Although chemical and thermal energy are the most frequently used and relevant forms of energy in animal biology, there are several other forms of energy. The first law of thermodynamics states, that in a closed system, energy can be transformed from one form to another, but cannot be created or destroyed. For example, the chemical energy of a nutrient can be only partly retained in the body of a growing animal and the remainder will be lost as chemical energy in the faeces, urine, and fermentation gases, and as thermal energy (i.e., heat) to the animal's environment.

The objectives of this chapter are to describe the way the growing monogastric animal uses energy from the diet for different purposes and the way this energy use is represented in different energy systems. We will also describe some of the physiological and biochemical factors contributing to the bioavailability of nutrients with respect to energy use.

Measuring energy and energy balances

The energy content of a nutrient or nutrients in a feed can be measured in a bomb calorimeter as the heat of combustion (ΔH) of the nutrient or feed under standard conditions. For example, the complete combustion of glucose is:

$$1\ C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ H_2O + 6\ CO_2;\ \Delta H = 2802\ kJ\ (or\ 15.6\ kJ/g\ glucose)$$

In biochemistry, the change in Gibbs free energy (ΔG) is commonly reported, which is useful to identify (amongst others) the direction of a biochemical reaction. Because ΔH is much easier to measure than ΔG, nutritionists commonly use ΔH as a mode of expressing energy. For a discussion on the preference of using ΔH over ΔG in animal nutrition, the reader is referred to chapter five of Baldwin (1995). Note that the ΔH is expressed in (kilo-)joules (J), which is the derived standard unit of the International System of Units, and 1 J is equivalent to the work of 1 N·m or 1 $kg \cdot m^2/s^2$. The "calorie" is still widely used by nutritionists and 1 "calorie" equals 4.184 J.

Energy systems tend to express the bioavailability or value of dietary energy in relation to the animal's energy requirement. Most energy systems in use nowadays are based on the different energy losses that occur during the digestive and metabolic processes. The gross energy (GE) of a diet corresponds to the heat of combustion and is, as such, a property of the diet. Due to incomplete digestion of the diet, energy is lost in faeces and subtracting these losses of the GE content results in the digestible energy (DE) content of the diet. Material energy losses also occur during fermentation (through fermentation gasses such as CH_4 and H_2) and in the urine (mainly as urea in pigs and as uric acid in poultry). The metabolizable energy (ME) content of the diet corresponds to the difference between DE and the material energy losses in fermentation gases and in the urine. The ME is only partially retained (and/or excreted) by the animal as products such as meat, milk, and eggs, and the remaining energy is dissipated as heat.

Quantifying the different steps from GE to DE, and from DE to ME relies on collecting samples of the feed, faeces and urine and measuring the heat of combustion of these samples with a bomb calorimeter. The DE content of a diet can be obtained in a balance trial in which total feed intake and faeces production are measured over several days. A representative

sample of both the diet and the faeces are taken and the energy content measured in a bomb calorimeter. The energy digestibility (dE) content of the diet can then be calculated as:

$$dE = (\text{feed intake} \times GE_{diet} - \text{faeces production} \times GE_{faeces}) / (\text{feed intake} \times GE_{diet})$$

Alternatively, dE can be obtained by inclusion of an indigestible marker in the diet (e.g., TiO_2, Cr_2O_3, or rare earth metals; see chapter 8).

Determining the ME content of a diet is similar to the procedure for DE but includes urine collection. Measurement of the fermentation gases is technically more difficult and requires specialized equipment.

Although the energy in excreted products such as milk and eggs can be measured relatively easily, this is less so for energy that is retained in the body (RE), which can be measured directly or indirectly. Measuring RE directly can be done using the comparative slaughter technique where at least two groups of animals are used. One group of animals is slaughtered at the beginning of the experiment and a similar group of animals is fed the experimental diet and slaughtered later on. By comparing whole body energy content of both groups of animals, RE can be calculated. Measuring whole body RE is a very laborious operation, especially for larger animals and it does not need much imagination to see the difficulty of obtaining a representative body sample of a 100 kg pig. Consequently, relatively few studies and data are available in which the whole body composition was measured in larger animals. Moreover, a relatively long measurement period is required to ensure sufficient energy retention. To its advantage, it does measure RE directly and the composition of the gain in terms of nutrients or among tissues can be measured as well.

Retained energy can also be obtained indirectly by measuring the heat production (HP) and subtracting this from the ME content. However, measuring HP requires specialized equipment such as respiration chambers. In a respiration chamber, gas exchanges (essentially O_2, CO_2 and CH_4) between the animal and its environment are measured allowing the determination of the O_2 consumption and production of CO_2 and CH_4. During metabolism, the animal consumes O_2 and produces CO_2 and CH_4 and these measurements, combined with the nitrogen (N) balance, are indicative for HP of the animal. The technique is referred to as indirect calorimetry because heat (‘calor’ in Latin) is measured indirectly from gas exchanges and N excretion in the urine. The HP is calculated according to the Brouwer equation (Brouwer, 1965), which is derived from the stoichiometry of energy transactions (Gerrits *et al.*, 2015b):

$$HP\ (kJ/d) = (16.175 \times O_2 + 5.021 \times CO_2 - 2.167 \times CH_4 - 5.992 \times N)$$

where O_2, CO_2, and CH_4 are the volumes of these gases produced or consumed (l/d), and N is the urinary N excretion (g/d). Animals (or a single animal) are usually kept in the respiration chamber for a week in which an energy balance and a N balance are carried out. The energy balance allows the determination of the retained energy, while the N balance allows the determination of the protein deposition. As energy is retained in the body almost exclusively as protein and lipid, the results of the energy and N balance studies can be used to calculate the lipid deposition. The gas exchanges can also be used to quantify the oxidation of protein, carbohydrate, and fat (Chwalibog *et al.*, 1992). Although the comparative slaughter technique and the indirect and direct calorimetry approaches are based on different principles, the difference in results between both techniques appears to be acceptable (Gerrits *et al.*, 2015b).

Indirect calorimetry also offers the possibility to analyse the dynamics of HP within a day (e.g., HP due to eating or physical activity of the animal). In a system in which the gas

production and different types of activity are measured continuously, it is possible to partition the HP into different components. In our laboratory, we have been measuring feed intake behaviour and physical activity continuously in animals in the fed and fasted state, which allows, through statistical modelling, a partitioning of the total HP to the fasting HP (FHP), the heat increment (or thermic effect of feeding), and the HP due to physical activity (Figure 1). The heat increment was further partitioned into a short-term component with a distinguishable relation to the intake of a meal (e.g., HP related to mastication, swallowing, and digestion) and a long-term component without a distinguishable relation to the intake of a meal (e.g., HP related to protein and lipid deposition). Figure 1 illustrates that the FHP represents a major proportion of total HP and also that HP increases considerably when pigs are active. The partitioning of HP depends on the way explicative traits such as physical activity are measured. In our first studies, we measured standing activity of pigs through the interruption of an infrared beam. In later studies, physical activity was measured through force sensors on which the cage was mounted, allowing the measurement of physical activity both in standing and laying positions. Different methodologies exist to measure physical activity and to relate these measurements to HP (Gerrits *et al.*, 2015a). Indirect calorimetry can also be used to measure the dynamics of nutrient oxidation. For example, Alferink *et al.* (2003) developed a technique in which $^{13}CO_2$ is measured continuously following the administration of a ^{13}C-labelled nutrient bolus.

Gross energy values of feed and nutrients

The GE content of a substance can be measured as its heat of combustion in a bomb calorimeter. As indicated in Figure 2, feed ingredients differ widely in their GE contents, ranging from approximately 15 kJ/g for ingredients rich in sugars and starch to approximately 39 kJ/g for fats.

The GE value of feed ingredients (kJ/g DM) and complete feeds can also be estimated from regression equations based on nutrient composition (g/g DM; Sauvant *et al.*, 2004):

$$GE = 17.3 + 6.17 \times \text{crude protein} + 21.93 \times \text{crude fat} + 3.87 \times \text{crude fibre} - 18.6 \times \text{ash} + \Delta$$

Where CP is the crude protein content in the ingredient and Δ is a correction factor depending on the type of feed, which ranges from -0.97 for soyabean hulls to 1.29 for corn gluten meal. Alternatively, the GE content can be estimated from an equation without intercept so that each coefficient corresponds, approximately, to the GE value of the different nutrients (from data of Noblet *et al.*, 1994):

$$GE = 22.6 \times CP + 38.8 \times \text{fat} + 17.5 \times \text{starch} + 16.7 \times \text{sugars} + 18.6 \times \text{residue}$$

where residue = OM – (CP + fat + starch + sugars). The difference in the coefficients for starch and sugars is essentially due to the degree of polymerization. The heat of combustion of glucose is 2802 kJ/mol. With a molecular weight of 180 g, maltose (the disaccharide of glucose) has a molecular weight of 2 × (180 - 18) = 342 g, resulting in a theoretical GE value of 16.4 kJ/g. If starch is seen as a glucose polymer of infinite chain length, its GE value would be 2802 / (180-18) = 17.3 kJ/g.

The GE content of crude fat is approximately 38.8 kJ/g, and results from the oxidation of three fatty acids (in the case of a triglyceride) and glycerol. The actual GE content of (crude) fat may vary somewhat with the fatty acid composition, as the GE content of fatty acids increases with chain length and decreases with degree of unsaturation.

Even more so than for crude fat and fatty acids, the GE content of crude protein varies with the amino acid composition of the protein and with the content of non-protein-nitrogen in the crude protein fraction. Relatively small amino acids such as aspartate, glycine and serine have low GE values (14 to 17 kJ/g) while larger amino acids such as the branched chain and aromatic amino acids have GE values closer to those of fatty acids (more than 30 kJ/g).

Digestible energy

Digestion refers to the process where ingested feed is broken down to smaller components in the gastrointestinal tract so that they can be absorbed by the animal. The process involves both mechanical and physico-chemical mechanisms (i.e., acidification and enzymatic hydrolysis). Due to the presence of microbes in the gastrointestinal tract, both microbial and host-animal enzymes contribute to the digestive process, resulting in different digestion end-products that can be absorbed by the host animal.

The DE content of a feed corresponds to the GE content minus the energy lost in the faeces. Energy in the faeces originates from undegraded dietary components, but the faeces also contain microbial mass resulting from hindgut fermentation. Part of the dietary energy is therefore digested, metabolized and stored as microbial energy, but is nevertheless considered as 'undigested energy' for the host animal.

Dietary fibre can only be digested through microbial digestion and, in monogastric animals, this occurs mainly in the lower tract. However, the capacity to digest fibre is limited and increasing the fibre content in the diet typically results in a reduction in total tract nutrient digestibility. In growing pigs, Le Goff and Noblet (2001) estimated that a 1% increase in the neutral detergent fibre (NDF) content in the diet resulted in a reduction of the energy digestibility of 0.9% (Figure 3). In these animals, the digestion of NDF was very limited and NDF was more or less an energy diluent. However, gestating sows are much more capable of digesting the same diet and a 1% increase in NDF content resulted in only a 0.64% reduction of energy digestibility. Factors such as feed intake level and retention time of digesta in the gastrointestinal tract contribute to the difference in digestibility between growing pigs and gestating sows (Le Goff *et al.*, 2002b). This illustrates that the energy digestibility is not a property of the diet alone, but it results from an interaction between the diet and the animal. Consequently, in the French tables of feed values (Sauvant *et al.*, 2004), two DE values are reported, one for growing pigs and one for sows.

Metabolizable energy

Energy losses in the urine and as fermentation gases are accounted for in the ME content of the diet. The ME:DE ratio is shown as a function of the NDF content of the diet in Figure 4, and as a function of the CP content of the diet in Figure 5 using data from the French tables of nutritional values of feed ingredients (Sauvant *et al.*, 2004).

Figure 4 shows that the ME:DE ratio declines with an increase in the NDF content of the diet and the associated energy losses are mostly due to energy losses as CH_4. As indicated earlier, sows digest dietary fibre better than growing pigs (Le Goff and Noblet, 2001) and, based on these data, Noblet *et al*. (2004) quantified the energy losses as CH_4 from the so-called 'digestible residue', which corresponds approximately to the digestible cell wall fraction. These energy losses were estimated at 0.67 and 1.34 kJ/g digestible residue for growing pigs and sows, respectively.

The ME:DE ratio also decreases with an increase in the CP content of the diet (Figure 5). These energy losses are mainly due to urea excretion in the urine, resulting from the deamination of amino acids from dietary protein that cannot be deposited as body protein.

After transamination, the amino-groups of the amino acids are carried by glutamate and aspartate, feeding the ammonia into the urea cycle:

$$2\ NH_3 + CO_2 + 4\ ATP \rightarrow \text{urea}$$

Urea has a GE content of 10.5 kJ/g and contains 47% N. The energy loss of urea, therefore, corresponds to 22.5 kJ/g N. Birds excrete N mainly as uric acid, which is synthesized from (amongst others) aspartic acid, glutamine, and glycine and the energy loss as uric acid corresponds to 34.4 kJ/g N.

The theoretical ME value of protein depends on the way the constituent amino acids are used. If all amino acids were to be deposited as body protein, there would be no production of urea and the ME value would then correspond to the DE value. On the other hand, if all amino acids were given 'in excess' without a net protein deposition (e.g., in mature non-producing animals), all digestible amino acids would be deaminated and the resulting N would be used for urea synthesis. However, the carbon chain of the deaminated amino acids can be used for other purposes, such as lipid deposition or for maintenance energy (i.e., ATP production). The theoretical ME value of an amino acid, therefore, ranges between two values: one when the amino acid is fully deaminated and where all N is used for urea synthesis and one where the amino acid is deposited as-is. Figure 6 illustrates these possible ME values for the amino acids. Amino acids such as glycine and serine only have one N atom and the carbon chains of these amino acids are relatively short. Consequently, there is a relatively large loss of energy in the urine when these amino acids are catabolized. A relatively large loss of energy in the urine also occurs when histidine and arginine are catabolized because these amino acids contain respectively three and four N atoms. The difference between the two ME values is small for the branched-chain amino acids (isoleucine, leucine, and valine) because these amino acids have a long carbon chain and only one N atom.

As for DE, these considerations illustrate that once a nutrient is ingested, its ME value is the result of the interaction between the diet and the animal. In growing pigs during the finishing phase, protein deposition is relatively constant or starts to decline while the feed intake capacity continues to increase. Over the course of the finisher phase, an increasing fraction of the amino acids in the diet will be deaminated, and the ME value of the protein (and of the diet) will, therefore, decline. It is needless to say that this is difficult to apply in practical animal nutrition without a modelling approach. In feed formulation, a value needs to be attributed to a feed ingredient independent of how the nutrients are used by the animal. In the French tables of nutritional values for pigs, it is assumed that 50% of the digestible protein is deposited and 50% is deaminated (Sauvant *et al.*, 2004). In poultry nutrition, it is common to correct ME values for zero N retention by subtracting the energy (as uric acid) of the actual or estimated N retention from the ME value. The resulting value is called the apparent ME value at zero N balance (AMEn). This value is lower than the actual ME because 30 to 50% of digestible N is typically excreted by the broiler.

Net energy

The NE content of a diet corresponds to the difference between ME content and the so-called heat increment and the energy expenditure for 'normal' physical activity. The heat increment is due to the fact that a producing animal loses heat due to the ingestion, digestion, and metabolism of the diet and of nutrients. The heat increment differs from the HP in that animals are producing heat even if they are not eating; the latter corresponds to the FHP. Consequently, the total HP corresponds to the sum of the heat increment, the HP for normal physical activity, and the FHP (Figure 7).

As indicated above, the retained energy corresponds to the difference between the ME intake and the total HP. The retained energy is positive in growing animals but it can be negative during specific periods such as in early lactation when the feed intake capacity is insufficient for milk production, or when animals are fasting. Quantitatively, energy is retained in the body mainly as protein and lipid. Circulating nutrients and body glycogen contribute quantitatively little to the body energy stores.

Figure 8 illustrates a classical representation of the relationship between retained energy and ME (the relation between HP and ME is similar, but flipped over a horizontal axis). The k_g corresponds to the energy efficiency of using ME for growth. In growing pigs, the k_g for a complete diet averages 74% (Noblet *et al.*, 1994). The k_g depends on the nature of the nutrient supply (e.g., the k_g will differ for diets rich in fibre or rich in lipid; see later) and, in theory, also on the way the animal uses the additional ME for additional protein or lipid deposition. The MEm is the ME for maintenance and corresponds to the ME intake at which the energy retention is zero. It is virtually impossible to obtain biologically meaningful data for growing animals fed at the maintenance energy level for longer periods of time. Under normal conditions, when animals are fed (close to) *ad libitum*, the ME intake corresponds to 2.5 to 3 times MEm. Actually feeding animals for longer periods of time at the energy maintenance level may correspond to a non-physiological situation. An example of this is the study of Lister and McCance (1967), who fed young piglets at a feeding level so that they would stop growing to maintain their body weight at 5.5 kg for one year. After one year of severe feed restriction, feed was offered at an *ad libitum* level to these piglets. Although they started growing at a level similar to that of their littermates who were not restricted, they stopped growing at the same chronological age, but at a much lower body weight than their littermates.

Figure 8 indicates two situations at which the ME intake equals zero and the resulting HP corresponds to the FHP. As indicated above for MEm, it is not possible to maintain animals for a long time in a fasting state without affecting their physiology. The FHPr corresponds to an extrapolation of the HP from data in which animals are fed at different levels of feed intake. This technique was used by Noblet *et al*. (1994) for the establishment of NE equations and they measured HP for 4 days at an ME intake level of 2.3 MJ/(kg $BW)^{0.60}$/d, followed by two days at 60% of this feeding level. The FHP can also be measured directly in a respiration chamber by withdrawing food for a short period of time (e.g., for 24 h). As indicated in Figure 8, the measured FHP (FHPm) can be greater than FHPr and there are two reasons that contribute to this difference. First, consider the range of ME intakes between 0 and MEm. Although we may assume that the energy requirement for basal physiological functions is the same at these two feed intake levels, the source of nutrients providing this energy differs. At FHPm, the required energy originates from mobilized body reserves such as glycogen, lipid, and protein, while at MEm all required energy is supplied by the diet. In between, the required energy will be provided by the two sources. Consequently, the slope between FHPm and MEm (i.e., k_m) is not an efficiency *per se*, but an efficiency ratio because it corresponds to the energy efficiency of using a dietary energy source for maintenance relative to the efficiency of using body reserves for maintenance. Being an efficiency ratio, k_m can be greater than 1 if nutrients from the diet are used more efficiently for maintenance than nutrients originating from body reserves. However, nutrients from the diet have to be ingested, digested, and absorbed and the energy costs associated with these processes contribute to MEm. The second reason for the difference between FHPm and FHPr is due to the assumption that the relationship between retained energy and ME intake is linear. There are several factors that challenge this assumption, including the partitioning of retained energy (between protein and lipid) and the effect of feeding level on the ME expenditure. For example, if a feed restriction

is applied, retained energy will be reduced but the reduction in protein and lipid deposition may differ. Because the energy efficiencies for protein and lipid retention differ (see later), so will the k_g and k_m. Also, it is known that the ME expenditure (or at least the FHP) is affected by the feeding level given to the animal before fasting (de Lange *et al.*, 2006; Koong *et al.*, 1982; Labussière *et al.*, 2011; Zhang *et al.*, 2014). From a biological point of view, the effect of feeding level on FHP appears logical. The FHP is typically measured during a 24 h period and the energy expenditure of organs active during normal feeding such as the intestines and the liver will still be high (awaiting the arrival of feed and nutrients). These organs adapt very rapidly to nutritional conditions such as the feed intake level and it is, therefore, not surprising to observe a relationship between FHP and feeding level. However, it raises the question as to which value for FHP should be used (Emmans, 1994; Noblet and van Milgen, 2013) in the determination of NE. It also casts doubts concerning the validity of the partitioning of energy expenditure between maintenance and the heat increment. Ideally, the (additional) energy expenditure related to the (additional) work of visceral organs should be attributed to the heat increment so that maintenance only includes the energy expenditure of visceral organs at a maintenance feeding level. However, the composition of the 'maintenance diet' will affect the energy expenditure of the visceral organs (e.g., the protein content will affect the energy expenditure of the liver to synthesize urea; Emmans, 1999). All in all, this shows that maintenance is a concept difficult to grasp physiologically in the case of producing animals.

Energy systems and energy values

The purpose of an energy system is to attribute an energy value to a feed ingredient or a complete feed so that these can be compared with the energy requirement of the animal. Although it may seem obvious that both 'value' and 'requirement' should be expressed at the same level (i.e., a DE value cannot be used to fulfil a ME requirement), care must be taken to cross-use information from different sources using the same mode of expression for energy, because methodological differences may lead to different values (Boisen and Verstegen, 1998a).

The nutrient and energy values for feed ingredients can be obtained from feeding tables proposed by different (national) organisations (Centraal Veevoederbureau, CVB, 2000; NRC, 2012; Sauvant *et al.*, 2004). Although they provide an indication of the 'typical' nutritional value of a feed ingredient, they are less suitable if the chemical composition of the ingredient to be used differs from that indicated in the table. Moreover, these tables do not (and cannot) provide nutritional values for all available ingredients, or for new ingredients coming to the market (e.g., different co-products). For these reasons, regression equations have been proposed that allow a prediction of the nutritional value of a feed ingredient from its composition. EvaPig® (www.evapig.com) is a free software tool to estimate energy values of feed ingredients and complete feeds. It is based on the French feed tables (Sauvant *et al.*, 2004), and allows calculation of the nutritional value of new ingredients or of ingredients that differ in composition from those given in the tables, based on information that the user can provide.

Digestible energy values are usually expressed on a faecal digestible basis, which contrasts with values for amino acids that are expressed on an ileal digestible basis. Although this choice does not have a direct implication for the DE values (e.g., both glucose and volatile fatty acids can be used by the host animal) it may, in theory, have an effect of the metabolic utilization of the digestion end-products. An increase in the proportion of feed that is digested (fermented) in the hindgut has been shown to result in a decrease in the NE:ME ratio (Just *et al.*, 1983). On the other hand, feeding fibrous diets may also reduce the physical activity of the animals, thereby, attenuating somewhat the low efficiency of fibre utilization (Rijnen *et*

al., 2003). The low energy efficiency value for fibre should not be interpreted as the end-products of fibre digestion being used with a low efficiency, because there are also energy losses as heat occurring during the fermentation process itself. Estimated NE:ME values of volatile fatty acids range from 60% (Imoto and Namioka, 1983; Jentsch *et al.*, 1968) to more than 80% (Jørgensen *et al.*, 1997).

Noblet and Perez (1993) and Le Goff and Noblet (2001) proposed different equations to predict the DE content of complete diets based on the information the user can provide (e.g., contents of GE, ash, protein, ether extract, and fibre fractions). In these equations, the different fibre fractions and ash have a negative impact on the DE value while protein, crude fat, and GE have a positive impact. Different equations have also been proposed to predict the ME content of complete diets (Le Goff and Noblet, 2001; Noblet and Perez, 1993) and for NE (Noblet *et al.*, 1994). Table 1 shows the contribution of nutrients to the different energy scales (data from Noblet *et al.*, 1994). Because the contribution of the different nutrients is expressed on a faecal digestible basis, the coefficients for DE correspond approximately to the GE values of the nutrients. The coefficients in the table illustrate that some energy is lost when DE is converted to ME for protein (due to urinary energy) and also for the residue (due to energy in CH_4 and H_2 resulting from the fermentation of fibre in the hind gut). Virtually no energy is lost in the conversion of DE to ME for lipids, starch, and sugars. The NE:ME ratio varies widely among the nutrients and is the highest for lipid, intermediate for starch and sugars, and the lowest for protein and the digestible residue (i.e., fibre). This means that dietary protein and fibre are used less efficiently in providing energy to the animal.

The fact that nutrients have different ME:DE and NE:ME values has an impact on the ranking of feed ingredients in the different energy systems. Table 2 lists the energy value of different feed ingredients relative to corn. Soyabean meal has an energy value similar to that of cereals in a DE system, but a much lower value in a NE system. Similarly, the energy value of ingredients rich in lipids is much greater in a NE system than in the ME or DE systems. The change in ranking in the energy values has consequences for feed formulation and, consequently, on feed cost. Also, because the energy value of protein sources is lower in a NE system, diets formulated on a NE basis will have a lower protein content (i.e., the value of protein will mainly be for providing amino acids and less for providing energy).

Energy requirements

In growing animals, energy is required for different functions such as maintenance, physical activity, growth, and thermoregulation. It is probably safe to assume that animals eat to meet their energy requirement when they can fully express their potential in terms of feed intake and growth. If the feed intake is lower than the desired feed intake (e.g., due to an imposed feed restriction, or to animal, dietary, or other environmental factors), it is assumed that growth will be given least priority among the aforementioned functions, and thus will be reduced. Also, it is likely that animals will try to eat to meet a NE target. In a mature, non-producing animal (or human) maintaining a constant weight, protein and lipid deposition are zero and all of the energy consumed must be released as heat, otherwise energy retention would be negative or positive resulting in weight loss or gain, respectively. Actually, it is surprising how well energy intake and/or energy expenditure are regulated, even in obese subjects, and this can be demonstrated easily in the following example. Consider a young adult of 20 years of age weighing 70 kg with an energy requirement of 12.5 MJ/d. This individual consumes just 0.5% more than his/her requirement, which corresponds to 62.5 kJ/d (i.e., the equivalent of approximately 3.6 g/d of starch). If we assume that this starch is used for lipid deposition (with an efficiency of 84%), the subject would gain about $62.5 \times 0.84 / 39.8 = 1.3$ g lipid/d. Although this may seem to be small, it represents 481 g/yr and the subject

would have gained more than 19 kg of lipid once he/she attained 60 years of age. In animal experiments, it would be virtually impossible to pick up a difference of 0.5% in food intake and we would consider energy intake and expenditure in such a situation to be equal. However, the consequences are considerable in the long term. This example is not given to minimize the problems of obesity in society, but to illustrate how well both energy intake and expenditure are regulated. Moreover, intake and expenditure are regulated unconsciously because who is able to manage his food consumption within a margin of a few grams of sugar per day? It shows that a mature subject essentially eats to meet the maintenance requirement (or that the subject adapts themaintenance requirement to the energy intake), making NE intake a strong candidate as a driving force regulating food intake.

The following two equations are typically used to partition the requirements for ME and NE between maintenance and growth (in a thermoneutral environment):

$$ME = MEm + PD/k_p + LD/k_f$$

$$NE = FHP + PD + LD$$

where PD and LD are the retained energy as protein and lipid, respectively, and k_p and k_f the corresponding energy efficiencies. Average values for k_p and k_f are close to 60 and 80%, respectively (Noblet *et al.*, 1999). It is clear from these equations that the notion of 'efficiency' is dealt with differently between both systems. In a ME system, the efficiency is seen as part of the energy requirement while in a NE system, the efficiencies are part of the feed value. In the equation for ME, the fact that nutrients are used with different efficiencies is ignored. It may, therefore, be more appropriate to consider k_p and k_f as the (average) costs of retaining energy as protein and lipid.

An important aspect in the determination of energy requirements and energy utilization is to identify the factor (or factors) determining MEm and FHP. The MEm and FHP are frequently expressed as a function of metabolic BW (BW^b). This approach has been criticized because, for a given BW, the body composition may differ between animals and the body protein mass is thought to have a greater contribution to MEm and FHP than the body lipid mass. Indeed, it appears that muscle has a much greater contribution to the FHP than fat, which has no or even a negative contribution to the FHP (van Milgen *et al.*, 1998). Moreover, the contribution of viscera (per gram of tissue) was four times more important than the contribution of muscle. Although it is acknowledged that different tissues contribute differently to MEm and FHP, BW is an accessible trait (i.e., it can be measured easily). In a large experiment, it was observed that MEm ranged from 936 kJ/(kg $BW^{0.60}$)/d in castrated Meishan pigs to 1122 kJ/(kg $BW^{0.60}$)/d in entire males of a synthetic line (Noblet *et al.*, 1999), and this difference may be caused by differences in body composition. At the same time, we did not observe a difference in MEm between Large White entire males, castrated males and females even though the body composition of these animals is likely to differ. Kolstad and Vangen (1996) also observed differences in MEm requirements between Landrace and Duroc pigs, even when corrected for the difference in body composition.

Body composition may not only be different between lines of pigs, but it will also change during the growth of the animal. The measurements of FHP that we carried out in our laboratory indicated that the FHP in pigs is best expressed relative to $BW^{0.60}$. This contrasts with the conventional scalar of 0.75 (i.e., the 'classical' metabolic BW), which is used to express the maintenance energy expenditure in mature non-producing animals of different species (Kleiber, 1975). Using the generic scalar of 0.75 to express metabolic BW for growing animals may, therefore, be inappropriate. The scalar of 0.60 appears appropriate only for growing pigs and different scalars should be used for growing animals of other species:

0.85 for veal calves, and 0.70 for turkeys and for broilers (Labussière *et al.*, 2015). The difference in the scalars for these species reflects differences in the allometric growth of visceral organs relative to the whole body (Labussière *et al.*, 2015).

Physical activity is an important contributor to the HP. The expenditure per hour of standing appears to be much greater in pigs compared with other livestock species (Noblet *et al.*, 1993). Even though pigs are standing only a few hours per day, physical activity represents more than 12% of the HP and more than 8% of the ME intake in growing pigs, and these figures are approximately double in restrictively-fed gestating sows (Noblet and van Milgen, 2013). In broilers, growing turkeys and veal calves, the energy expenditure for physical activity ranges between 8 and 13% of the ME intake (Labussière *et al.*, 2015). In addition, physical activity can be variable between individual animals and between groups of animals (e.g., depending on housing conditions).

There is no specific energy requirement for thermoregulation when pigs are kept under thermoneutral conditions because the heat generated for maintenance and the heat increment will be sufficient to maintain a constant body temperature. One may argue that at the lower critical temperature, energy is used with a 'biological' efficiency of 100% because all the ME intake is retained or used to maintain the animal's body temperature. The situation changes of course at temperatures below the critical temperature because the animal then specifically requires energy to maintain its body temperature, which is usually realised by an increase in feed intake.

Despite different factors affecting FHP and MEm, for growing pigs it is recommended to use values of 750 and 1000 kJ/(kg $BW^{0.60}$)/d for FHP and MEm, respectively. These values are similar to those observed by Zhang *et al*. (2014) in an experiment where HP and FHP were measured in pigs that were fed at levels ranging from 20% to 100% of *ad libitum* feed intake (for a limited number of days). The FHP in non-pregnant sows averaged 260 kJ/(kg $BW^{0.75}$)/d, which corresponded to an MEm of 387 kJ/(kg $BW^{0.75}$)/d (Le Goff *et al.*, 2002a). The latter value is lower than what is recommended for gestating and lactating sows (i.e., 440 and 460 kJ ME/(kg $BW^{0.75}$)/d, respectively (Noblet *et al.*, 1990)). In broilers, values of FHP measured in different experiments averaged 440 kJ/(kg $BW^{0.70}$)/d, which corresponds to approximately 570 kJ ME/(kg $BW^{0.70}$)/d (Noblet *et al.*, 2015). In veal calves, FHP varied from 270 to 310 kJ/(kg $BW^{0.85}$)/d depending on feeding level, and the associated MEm varied from 320 to 370 kJ ME/(kg $BW^{0.85}$)/d (Labussière *et al.*, 2011).

Other energy systems

Although ME and NE are the most dominant energy systems in use for livestock production, other systems have been proposed. In the effective energy system of Emmans (1994), part of the heat increment for urinary and faecal excretion is deducted from the ME supply (corrected for zero energy retention), while the heat increments for protein and lipid retention are included in the effective energy requirement. Because the components of HP are partitioned differently in the effective energy system compared to the ME system, the energy efficiencies for protein and lipid deposition are also different (48 and 71%, respectively in the effective energy system and 60 and 80% in the ME system).

The potential physiological energy (PPE) system was proposed by Boisen (2007) and is built on the premise that nutrients will be used for ATP synthesis, in addition to protein and lipid deposition. AcetylCoA plays a key role in the intermediary metabolism because it is a crossroad where nutrients are directed towards the TCA cycle for ATP production or towards *de novo* fatty acid synthesis. In the PPE system, a value is attributed to nutrients, representing their potential to produce ATP, using glucose as a reference (Boisen and Verstegen, 2000).

The PPE:GE ratio was the highest for carbohydrates and fatty acids (67%), followed by volatile fatty acids (59-65%) and, lastly, amino acids (32-60%).

For a comparison of different (and historical) energy systems for pigs, the reader is referred to publications by Noblet and Henry (1993), Kil *et al*. (2013) and Velayudhan *et al*. (2015).

Biochemical aspects of energy availability and utilization

Citing Stryer (1981), Boisen and Verstegen (1998b) indicated that 'in general, the intermediary metabolism of digested nutrients follows the most energy-economical metabolic routes'. Although this may be true at the cellular level, it does not necessarily hold true at the whole animal level (Emmans and Kyriazakis, 1995). For example, storage of energy (as body glycogen, lipid, or protein) inevitably involves energy losses. It would, therefore, be more efficient to avoid storage of energy at all and consume feed continuously and use the dietary energy directly for ATP production and/or growth. Of course, this does not occur because, among other things, the continuous consumption of feed incurs an energy cost of seeking and consuming feed. From a whole animal perspective, having distinct meal patterns and storing energy (temporarily) may, therefore, be a more efficient strategy than continuous feed consumption.

The PPE system of Boisen (2007) states that it concerns the 'potential' use of energy. Actual energy use is very complex and results from the interaction between the animal, its diet, and the environment. It is, therefore, unlikely that current systems based on 'value' and 'requirement' can be refined further without the use of modelling (Birkett and de Lange, 2001; Emmans, 1999). However, this does not necessarily mean that mechanistic modelling of energy utilization can be applied easily in practical animal nutrition. As will be shown in the following examples, there are different biochemical pathways that can and will be used by the animal. These pathways are not necessarily the most energy efficient, but they allow the animal to separate energy supply from energy requirements in time or in space (among tissues). Although modelling can be used to represent these pathways, the actual extent of usage of these pathways requires reliable information to be obtained under practical conditions. It is for this reason that the InraPorc model (Dourmad *et al.*, 2008; van Milgen *et al.*, 2008) and tool (http://inraporc.inra.fr/inraporc/index_en.html) that we developed uses empirical equations of energy utilization and is not based on biochemical pathways.

To evaluate the contribution of biochemistry to the efficiency of energy utilization, we developed a model (which can be programmed easily in a spreadsheet) with which the user can construct different biochemical pathways (van Milgen, 2002). The model consists of a list of partial pathways in which the catabolism and anabolism of nutrients are expressed as a function of intermediary metabolites and co-factors. The partial pathways are used to construct and balance complete pathways in such a way that no intermediary metabolites or co-factors other than ATP remain. In the original paper, an example was given for the synthesis of tripalmitin from glucose:

$$14 \text{ glucose} + 11.5\ O_2 \rightarrow 1 \text{ tripalmitin} + 33\ CO_2 + 15.5 \text{ ATP}$$

The GE contents of tripalmitin and glucose are 31,741 and 2,820 kJ/mol, respectively so that the energy efficiency of the lipid synthesis from glucose can be calculated as $31{,}741 / (14 \times 2{,}820) = 80\%$. The 15.5 ATP produced may save 15.5 / 38 moles of glucose (assuming that 38 ATP can be produced from 1 mole of glucose, using integer P / O ratios) so that the efficiency can also be calculated as $(31{,}741 + 15.5 / 38 \times 2{,}820) / (14 \times 2{,}820) = 83\%$. Note that this efficiency is similar to the NE:ME for starch (Table 1).

Table 3 expands on the preceding example by using the tripalmitin for ATP synthesis. This occurs for example in sows where energy is stored as lipid during gestation and mobilised later during lactation to be used by the sow or the piglets to produce ATP. It, therefore, represents the temporary storage of energy as tripalmitin before being used for ATP synthesis, resulting in the overall equation:

$$14 \text{ glucose} + 84\ O_2 \rightarrow 84\ CO_2 + 424.5 \text{ ATP}$$

which corresponds to 30.3 ATP/glucose. The indirect use of glucose therefore has an efficiency of 79% compared with the direct use of glucose for ATP synthesis (38 ATP/glucose).

Another example affecting energy efficiency is the use of the Cori-cyle. In this cycle, glucose is used to produce ATP anaerobically, resulting in the production of lactate. This allows for rapid muscle contractions without using O_2. The longissimus muscle is such a fast-twitch glycolytic muscle, white in colour because it contains less myoglobin (to carry O_2) and with fewer mitochondria compared with red muscles. To avoid lactate accumulation (and cramp) in the muscle, the lactate has to be reconverted back to glucose in the liver. The anaerobic ATP production in the muscle yields 2 ATP but the regeneration of glucose from lactate in the liver requires 6 ATP. The Cori-cycle is thus associated with a net loss of 4 ATP. The energy efficiency of the Cori cycle is therefore not greater than (38 – 4) / 38 = 89% of the efficiency of using glucose to synthesize ATP.

A final example concerns protein synthesis and degradation. Protein synthesis (i.e., the synthesis of a peptide bond) requires ATP but the quantity of ATP required is not exactly known and seems to range between 4 and 5 ATP per peptide bond, including the cost of amino acid transport and RNA synthesis (Waterlow, 2006). Also the hydrolysis of a peptide bond may be associated with an ATP cost. For the sake of simplicity, let us assume that 5 ATP are required for the synthesis of a peptide bond and that no ATP is required for its hydrolysis. If glucose would be the source for ATP synthesis (i.e., the most efficient way of synthesizing ATP), 371 kJ/peptide bond would be required. Because the GE values of amino acids differ (Figure 6), so will the efficiency of the peptide synthesis. For example, glycine has a GE content of 970 kJ/mol. Synthesis of a Gly-containing peptide, therefore, occurs with an energy efficiency of 970 / (970 + 371) = 72%. On the other hand, the efficiency of peptide synthesis involving large amino acids is much greater (e.g., the efficiency of a Trp-containing peptide would be 5,630 / (5,630 + 371) = 94%). The ATP cost, therefore, depends on the amino acid composition of the protein and, for a protein like casein, the efficiency would be around 87%. However, these calculations assume that peptides are synthesized and deposited without considering protein turnover (i.e., the repeated synthesis and hydrolysis of a peptide bond). The turnover rates of protein differ among tissues and the fractional synthesis rates range from around 4%/d in muscle to more than 100%/d in splanchnic tissues (Waterlow, 2006). Each cycle of protein turnover would therefore add 371 kJ/peptide bond and with 3 complete turnover cycles (i.e., four times synthesis and three times degradation), the energy efficiency of exported casein in the milk would be 64%.

Table 4 summarizes different routes of ATP production from glucose, relative to the direct production of ATP. All of these routes are operational in (tissues of) animals, illustrating the complexity of metabolism and the difficulty we may have to represent this reliably in energy evaluation systems or models. Let us compare the NE:ME ratio for lipid deposition from dietary lipids used in empirical systems (i.e., estimated from experiments, where NE:ME is approximately 89%) with the theoretical biochemical efficiency. The synthesis of body lipid from dietary lipid involves at least the hydrolysis of the triglyceride into a monoglyceride and

two fatty acids, followed by the re-esterification of the triglyeride. The cost of this esterification is equivalent to 4 ATP which, if provided by glucose, is equivalent to 4 × 74.2 = 297 kJ. Compared with the GE value of tripalmitin (31,740 kJ/mol), the biochemical energy efficiency of lipid synthesis from dietary lipid is, therefore, very high (99%). What then could explain the difference between the empirical and theoretical efficiencies? First, the associated costs of lipid metabolism (e.g., the cost of transport as chylomicrons) are not accounted for in the biochemical efficiency. Also, dietary lipids are not necessarily used only for lipid deposition. It is possible and likely that some dietary lipids are used for ATP synthesis (with an efficiency similar to that of glucose) while dietary glucose is used for lipid deposition. In an empirical energy system, this would be quantified as the (apparent) NE:ME value for dietary lipid. Because the biochemical efficiency of lipid deposition from glucose is lower than that from lipid, the apparent NE:ME value for dietary lipid may be lower than the biochemical efficiency.

Conclusion

Energy metabolism is a complex process and involves all dietary nutrients. Although energy is a property of nutrients and thus a unifying concept in itself, energy is lost by the animal in different ways and the resulting energy systems, therefore, come in different flavours. There is undoubtedly an interest and need to understand the physiological and biochemical processes behind energy utilization in livestock. However, the complexity of these processes and the difficulty of obtaining reliable information to quantify these processes is such that it is unlikely that a physiological and biochemical representation through modelling can replace the existing empirical energy systems in the foreseeable future. It is good to acknowledge that the notions of energy ‘value’ and ‘requirement’ have their limitations, but current energy systems have been proven to be very robust, which is a major asset in practical animal nutrition.

Table 1 Coefficients used to estimate the DE, ME, and NE contents of diets from the composition of digestible nutrients (g/g; van Milgen *et al.*, 2008; adapted from Noblet *et al.*, 1994).

Parameter	dProtein	dLipid	Starch[a]	Sugars[a]	dResidue[b]
DE (kJ/g)	23.31	39.00	17.45	16.62	16.61
ME (kJ/g)	20.34	39.00	17.45	16.62	15.51
NE (kJ/g)	12.08	35.01	14.32	11.94	8.64
ME:DE (%)	87	100	100	98	93
NE:ME (%)	52	90	82	72	52

[a]Starch and sugars are assumed to be 100% digestible.
[b]The residue corresponds to the difference between organic matter and the CP, EE, starch and sugar contents; d = digestible.

Table 2 Energy values for selected feed ingredients relative to the energy value of corn (maize) in different energy systems (%; from Sauvant *et al.*, 2004).

Ingredient	Energy			
	Gross (GE)	Digestible (DE)	Metabolisable (ME)	Net (NE)
Corn[a]	100 (18.7)	100 (16.4)	100 (16.0)	100 (12.8)
Wheat	97	97	97	94
Sorghum	101	100	100	99
Soyabean meal	105	102	95	72
Wheat bran	101	65	63	56
Soya oil	210	203	207	232

[a]Values between parentheses indicate the energy value in kJ/g.

Table 3 Stoichiometry of lipid synthesis from glucose and subsequent oxidation of lipid to produce ATP.

Eq	multiply	reaction	ATP	NADHc	NADHm	FADH2	NADPH	CO_2	O_2	NH_3	OAA	αKG	PYR	ACA	GLC	SER
1	12	GLC → PYR	24	24	0	0	0	0	0	0	0	0	24	0	-12	0
2	24	PYR → ACA	0	0	24	0	0	24	0	0	0	0	-24	24	0	0
42	3	ACA → C(16:0)	-69	-24	0	0	-18	0	0	0	0	0	0	-24	0	0
43	18	NADPH synthesis	-1.5	0	0	0	18	9	0	0	0	0	0	0	-1.5	0
45	1	3(C16 :0) + GLC → lipid	-7	-1	0	0	0	0	0	0	0	0	0	0	-0.5	0
11	-1	NADHc ↔ NADHm	0	1	-1	0	0	0	0	0	0	0	0	0	0	0
10	23	NADHm oxydation	69	0	-23	0	0	0	-11.5	0	0	0	0	0	0	0
		Balance 1	15.5	0	0	0	0	33	-11.5	0	0	0	0	0	-14	0
		lipid → 3(C16 :0) + GLC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	3	C(16:0) → ACA	-6	0	21	21	0	0	0	0	0	0	0	24	0	0
19	1	glycerol → ACA	1	2	1	0	0	1	0	0	0	0	0	1	0	0
3	25	OAA + ACA → αKG	0	0	25	0	0	25	0	0	-25	25	0	-25	0	0
4	25	aKG → OAA	25	0	50	25	0	25	0	0	25	-25	0	0	0	0
11	2	NADHc ↔ NADHm	0	-2	2	0	0	0	0	0	0	0	0	0	0	0
10	99	NADHm oxydation	297	0	-99	0	0	0	-49.5	0	0	0	0	0	0	0
12	46	FADH2 oxydation	92	0	0	-46	0	0	-23	0	0	0	0	0	0	0
		Balance 2	409	0	0	0	0	51	-72.5	0	0	0	0	0	0	0
		Overall balance	424.5	0	0	0	0	84	-84	0	0	0	0	0	-14	0

Eq = equation number (van Milgen, 2002), GLC = glucose, PYR = pyruvate, ACA = acetylCoA, OAA = oxaloacetate, αKG = α-ketoglutarate, SER = serine, NADHc = cytosolic NADH, NADHm = mitochondrial NADH.

Table 4 Energy efficiency of using glucose directly or indirectly to synthesize ATP.

Direct	74.2 kJ/ATP = 100%
Via glycogen (in the muscle)	97%
Via glycogen (in the liver)	95%
Via glutamate (as free amino acid)	95%
Via lactate (Cori-clycle)	89%
Via glutamate (as amino acid in protein)	82%
Via lipid	79%

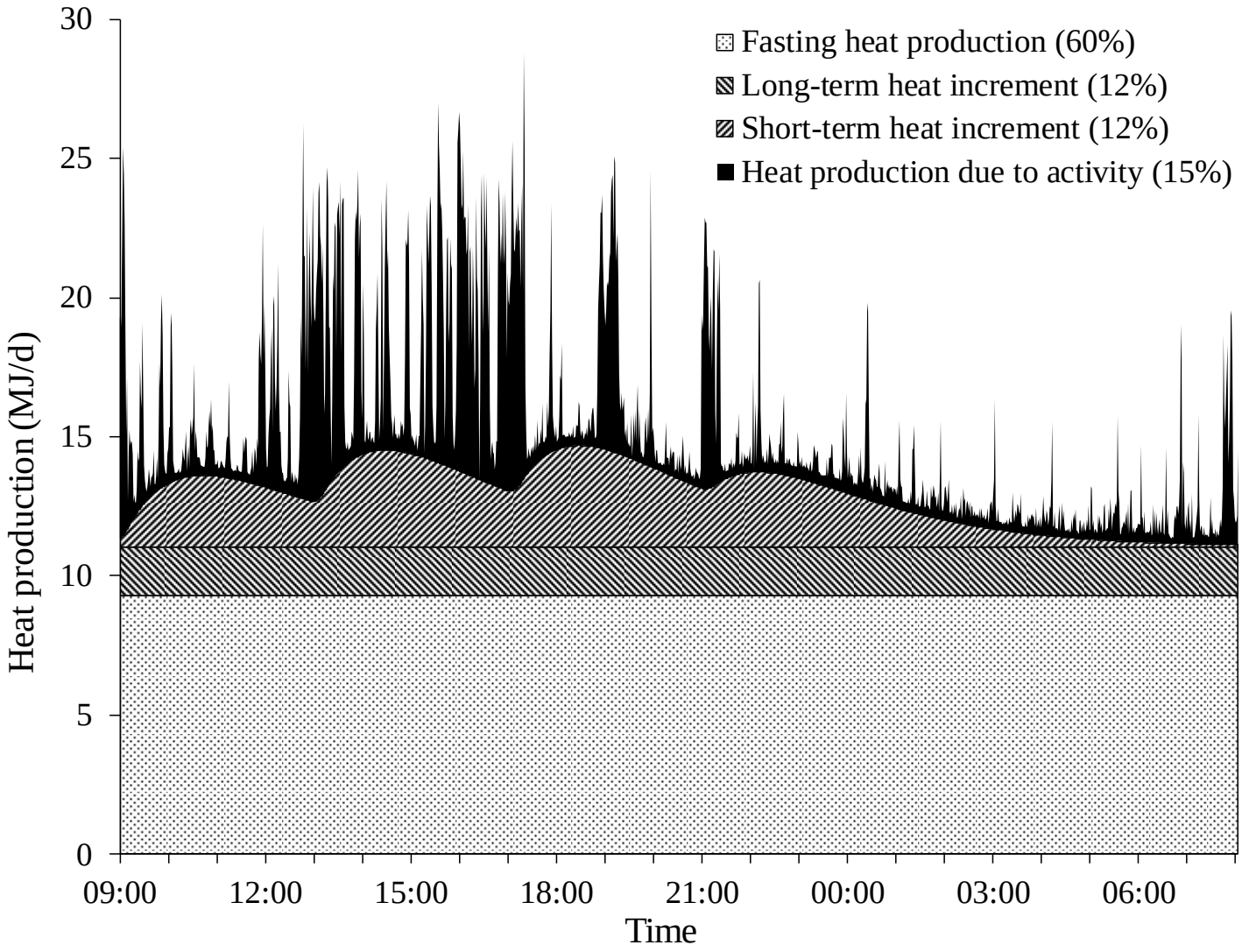

Figure 1: Partitioning of heat production in growing pigs between the fasting heat production, long- and short-term heat increment, and the heat production due to physical activity (after van Milgen *et al.*, 1997).

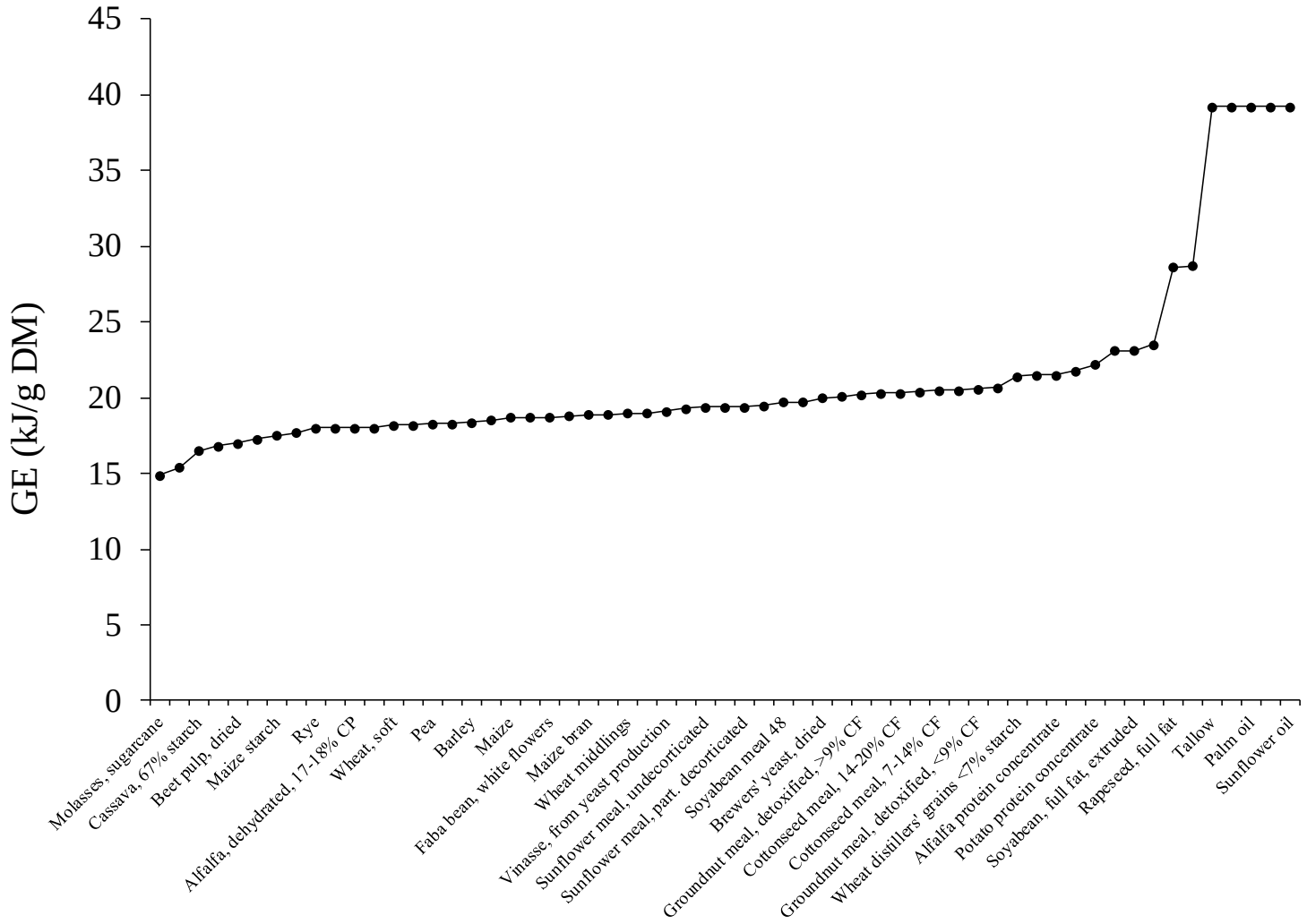

Figure 2: Gross energy values of feed ingredients (from Sauvant *et al.*, 2004).

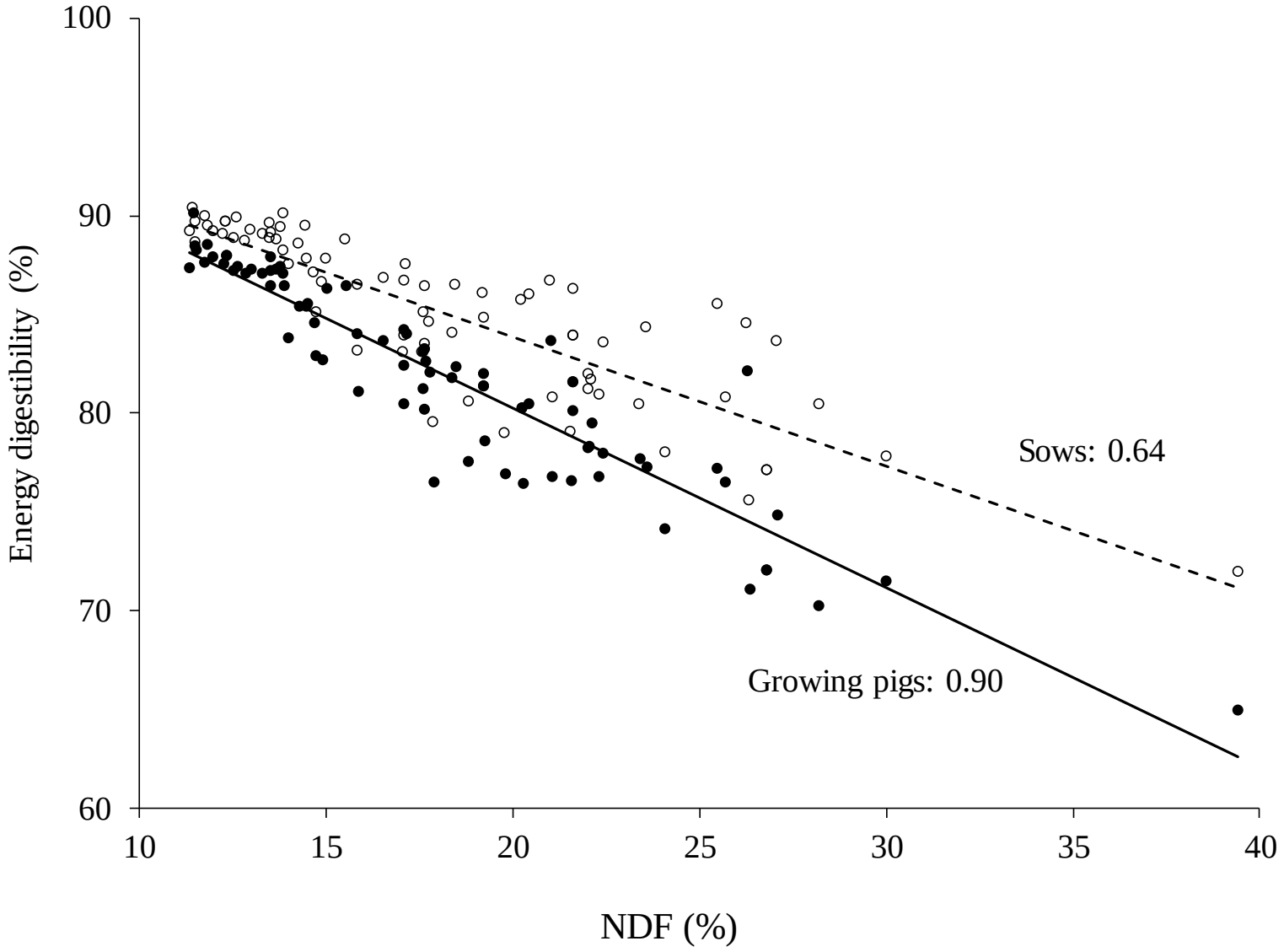
100
90
80
70
60
Energy digestibility (%)
10
15
20
25
30
35
40
NDF (%)
Sows: 0.64
Growing pigs: 0.90

Figure 3: Relation between the energy digestibility in growing pigs and sows and the NDF content of the diet. (● growing pigs, ○ sows, from Le Goff and Noblet, 2001).

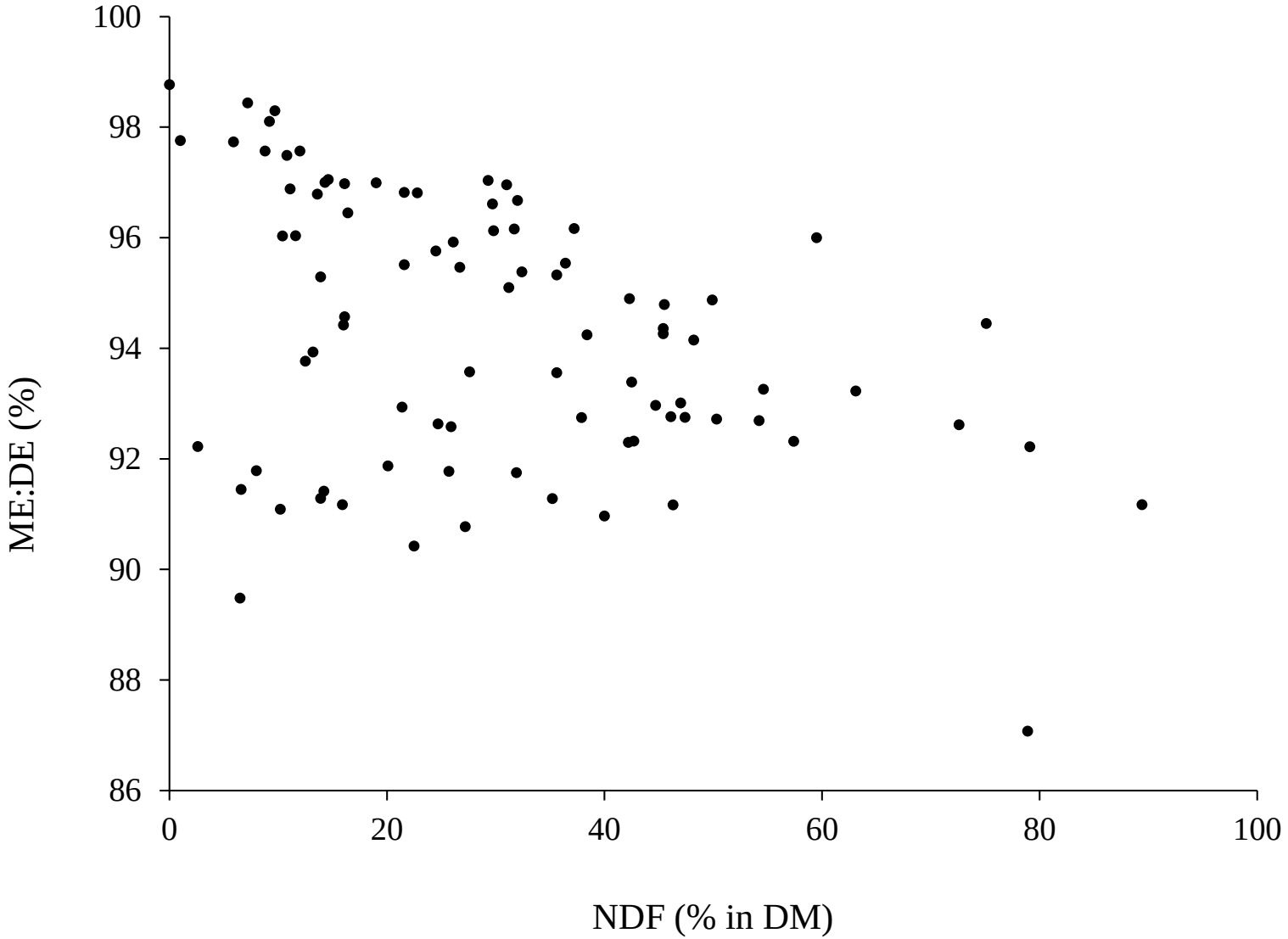

Figure 4: Relation between the ME-to-DE ratio and the NDF content of various feed ingredients (from Sauvant *et al.*, 2004).

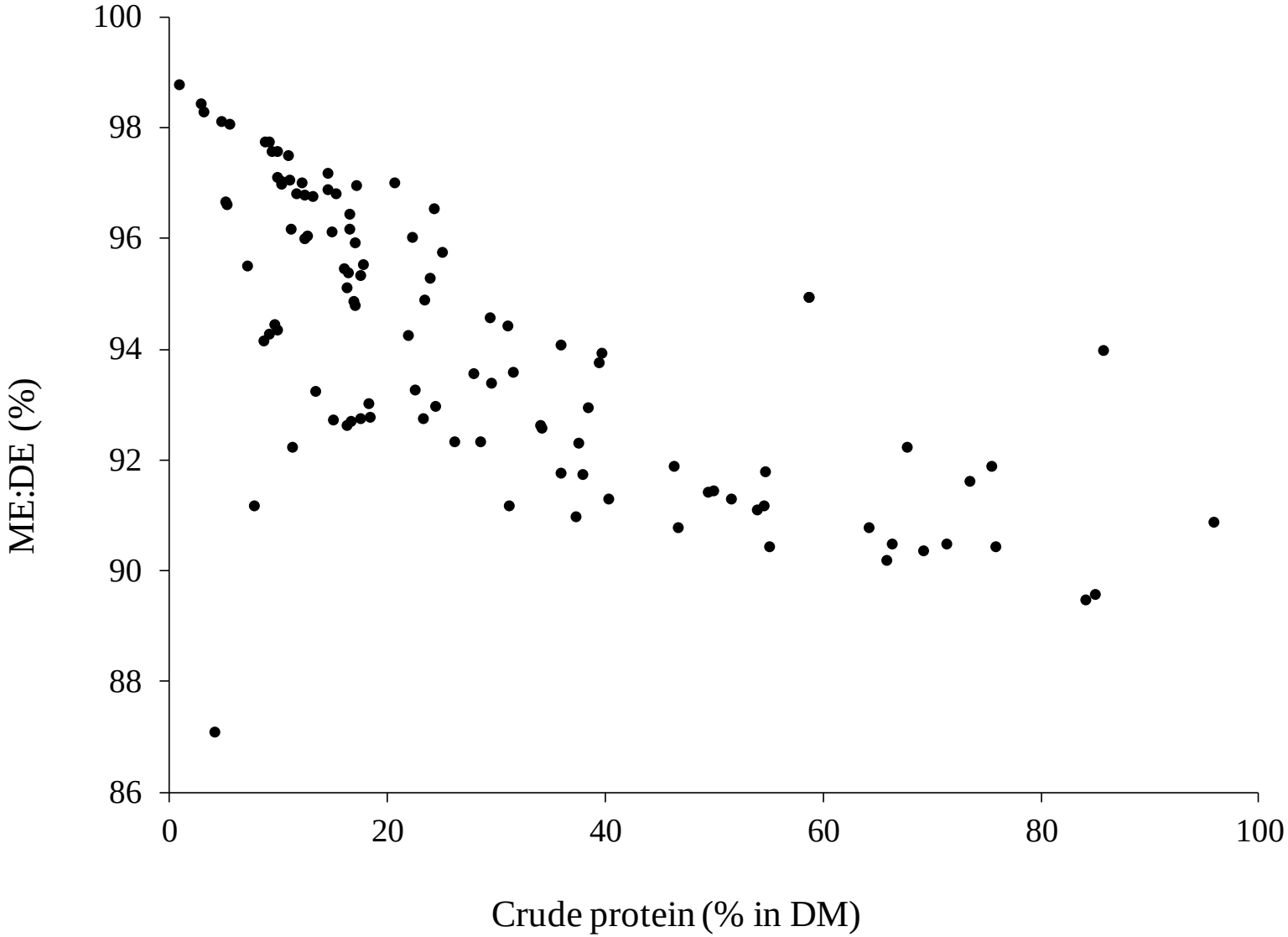

Figure 5: Relation between the ME-to-DE ratio and the crude protein content of various feed ingredients (from Sauvant *et al.*, 2004).

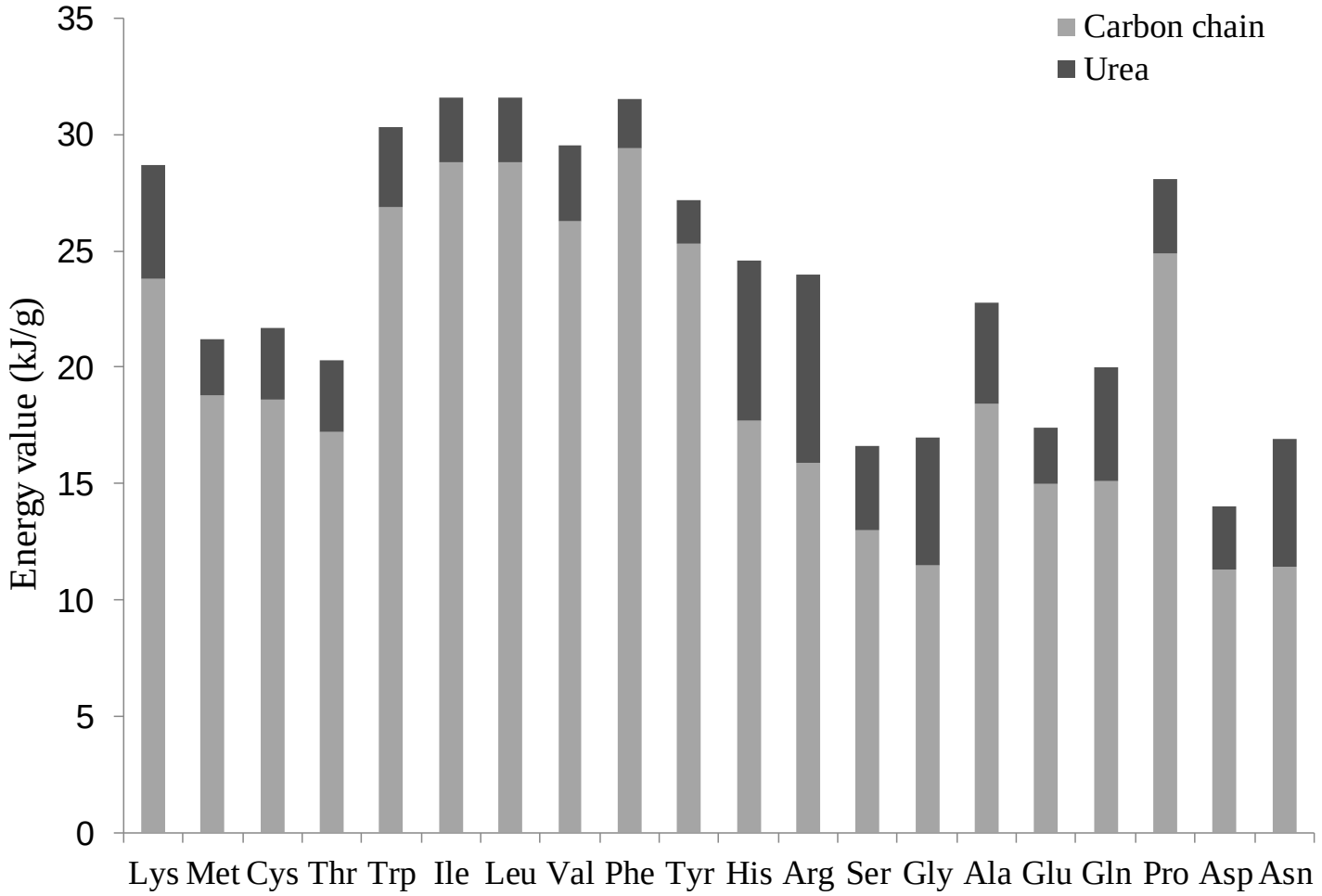

Figure 6: Metabolizable energy (ME) values of amino acids depending on their utilization. If the amino acid is deposited as protein, its ME value corresponds to height of the bar (carbon chain + urea). If the amino acid is deaminated, its ME value corresponds to the value of the carbon chain and the urea energy is lost in the urine (after van Milgen, 2002).

Footnote: Lys – Lysine; Met – Methionine; Cys – Cysteine; Thr – Threonine; Trp – Tryptophan; Ile – Isoleucine; Leu – Leucine; Val – Valine; Phe - Phenylalanine ; Tyr - Tyrosine ; His - Histidine ; Arg – Arginine; Ser – Serine; Gly – Glycine; Ala – Alanine; Glu – Glutamic acid; Gln – Glutamine; Pro – Proline; Asp – Aspartic acid; Asn – Asparagine.

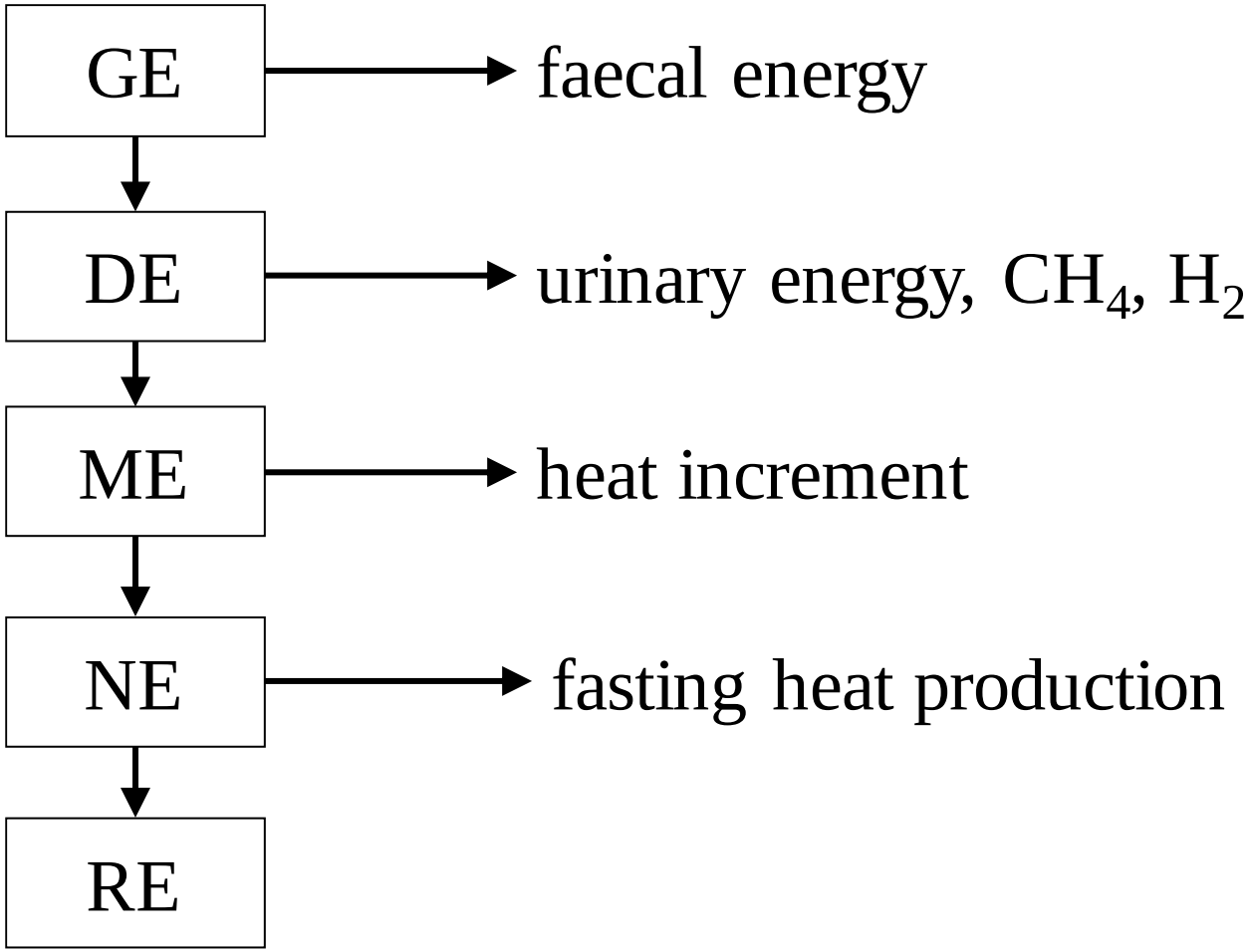

Figure 7: Relationship between energy systems.

Footnote: GE – Gross Energy; DE – Digestible Energy; ME – Metabolisable Energy; NE – Net Energy; RE – Retained Energy.

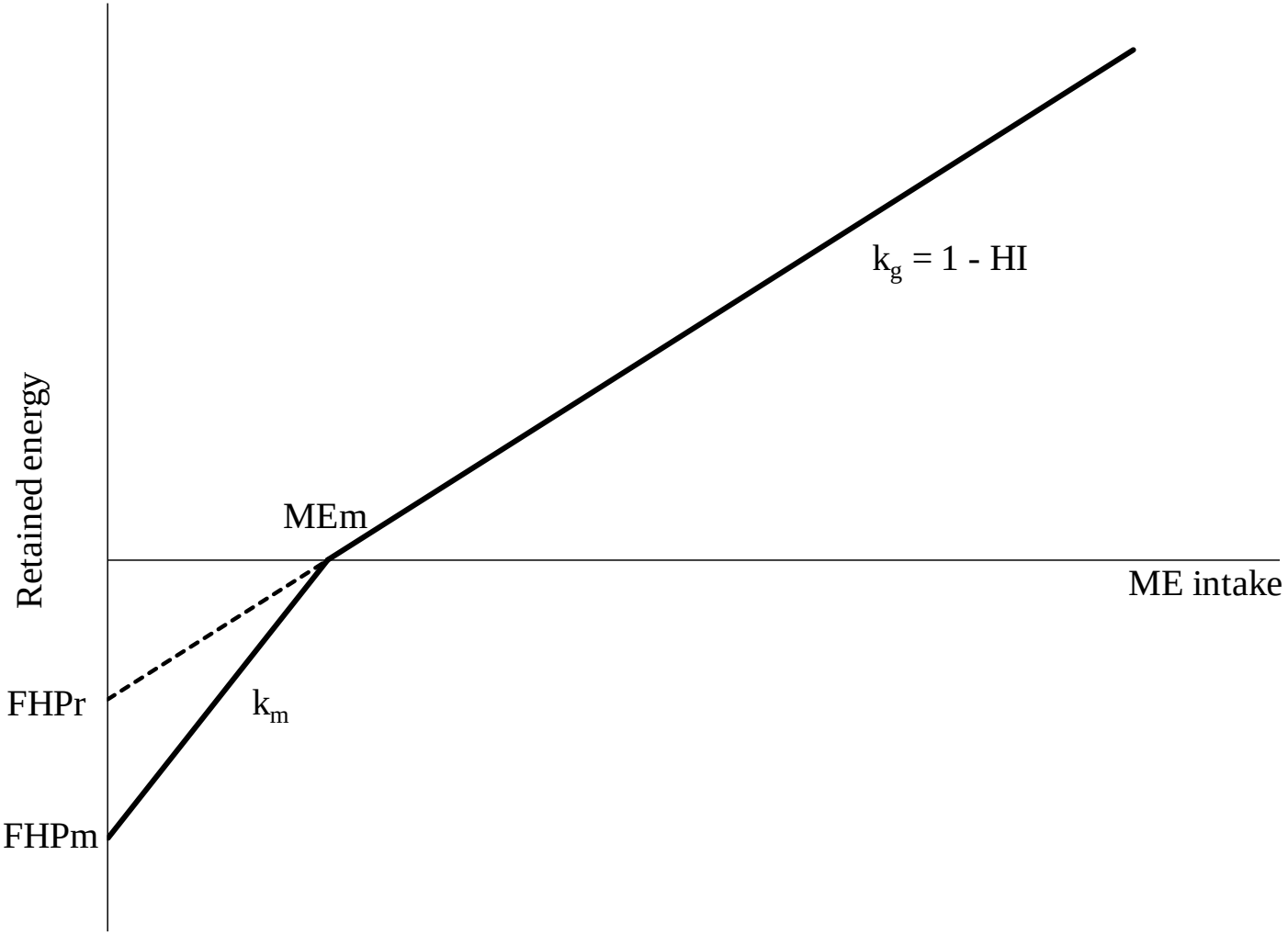

Figure 8: Relationship between retained energy and the metabolizable energy (ME) intake. FHPr = fasting heat production obtained by linear regression; FHPm = measured fasting heat production; HI = heat increment; k_g = energy efficiency for growth; k_m = relative energy efficiency for maintenance; MEm = maintenance energy requirement.

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