

# Partitioning of energy intake to heat, protein, and fat in growing pigs

J. van Milgen<sup>1</sup> and J. Noblet

Unité Mixte de Recherches sur le Veau et le Porc, Institut National de la Recherche Agronomique,  
35590 Saint-Gilles, France

**ABSTRACT:** Modeling aspects of energy metabolism in growing pigs involves establishing “rules” on the partitioning of dietary energy between protein deposition (PD), lipid deposition (LD), and heat production (HP) at a given point in time, as well as the changes that occur during growth. Growing pigs rarely retain more than 50% of their ME intake; the remainder is lost as heat. Part of the heat loss is due to the heat increment, which includes the transformation of dietary nutrients to PD and LD, and to the associated energy (ATP) cost. Consequently, different nutrients are used with different efficiencies and, due to the ATP cost associated with protein synthesis and turnover, PD is energetically less efficient than LD. Different modeling approaches have been adopted to represent partitioning of energy between PD and LD (e.g., by assuming minimal ratios of LD:PD, marginal LD:PD, and lipid:protein mass or the existence of an upper limit to PD). Most of the HP is associated with biophysical processes (e.g., “maintenance,” physical activity) requiring ATP, which are not directly related to PD and LD. Since it is virtually impossible to obtain direct estimates of these ATP require-

ments, indirect methods must be used. For example, the cost of maintenance may be estimated by measuring the fasting HP. Estimates of the fasting HP typically range from 700 to 800 kJ/(kg of BW<sup>0.60</sup>·d), which corresponds to 50 to 60% of the total HP. Also, HP associated with physical activity is an important component of HP (15%), but can be variable between individual animals. Feed intake in nonproducing, mature mammals theoretically equals maintenance energy requirements. This implies that, while maturing, maintenance will become an increasingly important component of energy intake. In addition, while maturing, a decreasing fraction of the energy intake above maintenance is used for PD. The result is that PD typically reaches a maximum at 60 to 80 kg in growing pigs and decreases thereafter. In contrast, with aging, an increasing fraction of the available energy is used for LD, and maximal LD may not be reached before slaughter (110 to 130 kg). In modeling, this has been represented by assuming that the aforementioned energy partitioning rules (e.g., minimal LD:PD ratio, upper limit to PD) change with BW and/or age.

Key Words: Energy, Pigs, Heat Production, Lipids, Models, Pigs, Protein

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## Introduction

Growing pigs rarely retain more than 50% of the GE given. Although for most diets 80 to 90% of GE is digested, not all this energy is available for metabolism as energy will be lost in the urine and as methane. The ME content of a diet is the difference between DE and these ‘material’ energy losses.

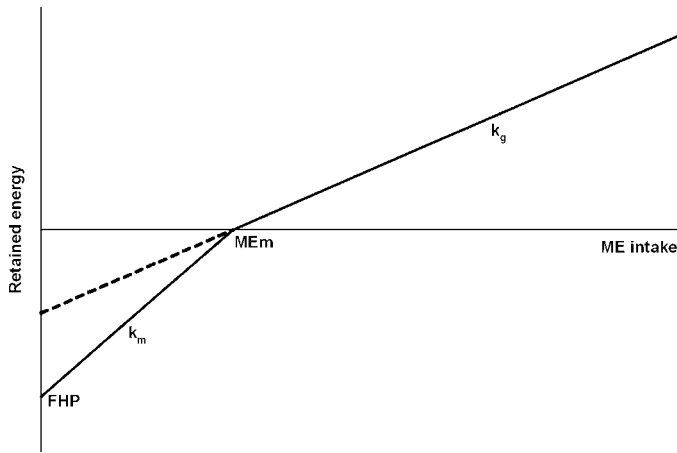
All ME not retained by the animal is lost as heat. The retained energy (primarily protein and lipid) can be measured directly by the comparative slaughter technique. Although it requires simple equipment, it requires considerable labor and gives an estimate of

the average energy retention over a longer period of time. Alternatively, partitioning of ME can be determined by measuring heat production. Most commonly, indirect calorimetry is used, which is based on the measurement of gas exchanges between the animal and its environment. When nutrients are oxidized, animals consume oxygen and produce carbon dioxide, whereas methane is produced by gut microbes during fermentation. These gas exchanges and the nitrogen excretion from protein catabolism combined with the stoichiometry of nutrient oxidation allow calculation of heat production (Brouwer, 1965). Calorimetry has the advantage over the serial slaughter technique in that it can be used to measure energy balance over successive short periods of time, even within days. We have further refined this technique to obtain estimates of different components of heat production (van Milgen et al., 1997; van Milgen and Noblet, 2000). Both techniques provide an estimate of the total energy balance of the animal,

<sup>1</sup>Correspondence: phone: +33 2 23 48 56 44; fax: +33 2 23 48 50 80; E-mail: jaap.vanmilgen@rennes.inra.fr.

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**Figure 1.** Relation between energy retention and ME intake. FHP = fasting heat production;  $ME_m$  = ME intake for maintenance;  $k_g$  = energy efficiency for growth; and  $k_m$  = relative efficiency of using dietary ME for maintenance compared to using ME from body reserves.

which, in combination with the nitrogen balance, allows calculation of lipid retention. The calorimetry technique typically gives higher estimates for energy and protein retention than does the comparative slaughter technique (Quiniou et al., 1995; Birkett and de Lange, 2001b). Although heat production may be affected by ambient temperature and health status, these aspects will not be considered here.

### Early Energy Models

Early models addressing the response of an animal to a changing energy supply date back almost a century ago (for reviews, see Blaxter, 1962, and Emmans, 1995). Energy retention was seen as a two-stage process (Figure 1), with a breakpoint at the ME supply resulting in zero energy retention ( $ME_m$ ). The slopes of the line segments represent the energy efficiencies below maintenance ( $k_m$ ) and for growth ( $k_g$ ). At zero energy intake, animals will mobilize body reserves in order to cover the energy requirements for maintenance. It is important to realize that with increasing ME intake, dietary energy will progressively replace energy from body reserves to cover maintenance up to the point where the dietary ME supply equals  $ME_m$ . The  $k_m$  is therefore the efficiency of using dietary energy relative to using energy from body reserves to cover the maintenance energy requirement. The fact that it is a relative efficiency is the main reason that  $k_m$  is greater than  $k_g$ . If body reserves are used less efficiently than dietary energy for maintenance purposes, then  $k_m$  will exceed unity (see also the section on “partitioning of heat production–maintenance”).

The assumption of constant energy efficiency above maintenance is difficult to justify. If the composition of the gain changes with ME intake, and if the efficiencies

of protein and lipid deposition are different,  $k_g$  cannot be constant. To account for this, Kielanowski (1965) proposed that the ME intake of animal could be seen as the sum of the maintenance energy requirement and the energy required for protein and lipid deposition:

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

where PD and LD are the protein and lipid deposition (kJ/d), respectively, and  $k_p$  and  $k_f$  are the corresponding energy efficiencies. Although it is acknowledged that there is considerable variation in reported energy efficiencies,  $k_p$  is typically much smaller than  $k_f$  (0.60 and 0.80, respectively; Noblet et al., 1999). Consequently, more energy is required to deposit 1 kJ of energy as protein than as lipid. Due to the greater energy density of lipid, approximately 50 kJ of ME (39.8/0.80) is needed to deposit 1 g of lipid, whereas approximately 40 kJ of ME (23.8/0.60) is needed to deposit 1 g of protein. The efficiency of protein deposition is not to be confused with efficiency of depositing lean tissue, which consists primarily of water and protein. The result of the association of water and protein is that less feed energy is required to deposit 1 g of lean tissue than 1 g of adipose tissue. Kielanowski’s approach has been criticized (Bernier et al., 1987; Emmans, 1995; Birkett and de Lange, 2001b) for various reasons including reversion of the controlled variable (ME intake) and the observed effect (changes in PD and LD) and multicollinearity or intercorrelation between the predictor variables resulting in inconsistent parameter estimates. In addition, the equation only considers “animal” aspects of energy metabolism, and differences in energy efficiencies between nutrients are not considered.

### Partitioning of Heat Production

#### Maintenance

The concept of a maintenance energy requirement has been widely adopted by animal nutritionists, even though it may be difficult to define and/or measure it unambiguously (Knap, 2000; van Milgen et al., 2000). The idea behind this concept is to separate production costs from the maintenance cost by assuming additivity of the two processes. The ARC (1981) defined maintenance as “the requirement of nutrients for the continuity of vital processes within the body so that the net gain or loss of nutrients by the animal as a whole is zero.” Feeding pigs at maintenance energy level does not imply that a constant body weight is maintained. During short periods of time, pigs can deposit protein at the expense of body lipid while maintaining zero energy retention and while gaining body weight (Le Dividich et al., 1980). It is unlikely that body lipids are used for protein deposition when growing pigs are fed to maintain body weight for prolonged periods of time (Lister and McCance, 1967). However, such experi-

ments may have severe consequences on the normal physiology of the animal. Despite the criticism and problems of measurement, the concept of maintenance has been widely adopted in animal nutrition.

The metabolic rate (or heat production per unit of time) has in the past been expressed relative to the body surface area. The surface areas of two bodies of similar shape and density but of different size are in proportion to the two-third power of their weights (Kleiber, 1975). Consequently, metabolic rate would be proportional to  $BW^{0.67}$ . Differences in BW should not be seen as the ultimate cause of changes in maintenance energy expenditure or metabolic rate, but rather as a convenient way to scale these (see Kleiber, 1975, for a critique on surface law theory). In many textbooks on energy metabolism,  $ME_m$  is assumed to be proportional to the three-quarter power of BW. This value originates from the comparison of fasting heat production (FHP) between different species of mature animals (Kleiber, 1975). When the maintenance energy expenditure is compared for animals of different BW within a species, the power is typically lower than 0.75 and, for growing pigs, a value close to 0.60 is often found (Brown and Mount, 1982; Noblet et al., 1999). The mode of expression has an important impact on estimated  $ME_m$  requirements at different body weights, and thus on predicted energy retention. For example, suppose that one has obtained a reliable estimate of  $ME_m$  at 60 kg of BW. If maintenance is constant per kg of  $BW^{0.60}$ , it would result in a 18% higher maintenance requirement at 20 kg of BW compared to assuming a constant maintenance requirement per kg of  $BW^{0.75}$ . However, at greater BW, the ranking is reversed so that at 120 kg of BW,  $ME_m$  is 10% lower when using the power 0.60 compared to using 0.75. Moreover, the choice of the power not only affects the maintenance energy requirement, but also the estimated energy efficiencies of protein and lipid deposition (Bernier et al., 1987; Noblet et al., 1999).

The maintenance energy requirement is essentially an ATP requirement. For a given ATP requirement, and with the knowledge that the efficiency of ATP synthesis differs between nutrients, the ME requirement for maintenance will be diet-dependent. This problem is partially circumvented in net energy systems, which use the FHP as an estimate of the maintenance energy requirement (Noblet et al., 1994). Although the FHP can be measured during reasonably standardized conditions, it varies with the length of fasting period and feeding level prior to fasting (Koong et al., 1982; de Lange et al., 2002). During fasting, energy from body reserves is mobilized in order to generate ATP for essential functions. However, normally fed growing animals will seldom mobilize body reserves (other than glycogen) in order to supply energy for essential functions. The direct utilization of measured FHP as an estimate of maintenance requirements is therefore, from a physiological point of view, incorrect. The extrapolated FHP obtained through regression (Figure 1) does not suffer

from this drawback since nutrients for maintenance are (statistically) supplied by the diet, and the efficiency of ATP synthesis from the diet is accounted for. Birkett and de Lange (2001b) argued that the extrapolated FHP is independent of the diet, but depends on the relative contribution of protein and lipid to energy gain or loss. In a recent study on the energetic efficiencies of different nutrients (van Milgen et al., 2001), we estimated that the extrapolated FHP was 62% of the measured FHP in growing pigs. It was hypothesized that when growing animals are fasted for a short period of time, visceral organs will diminish rapidly in size, and nutrients from these organs (primarily proteins) will be catabolized to provide energy for maintenance functions. The efficiency of using energy from body reserves for these functions was greater than when using dietary protein (52%), but smaller than when using starch or lipid (84 and 88%, respectively), even though the latter are accompanied by an additional energy cost for ingestion, digestion, and absorption. Corresponding  $k_m$  values would be 84 (i.e., 52/62), 135, and 142% for protein, starch, and lipid, respectively.

The genotype (or leanness) also appears to have an important impact on FHP, with lower estimates for obese Meishan barrows and higher estimates for lean Piétrain boars (van Milgen et al., 1998). Exploiting data on the body composition of these pigs, it was concluded that viscera had a greater contribution to total FHP that did total muscle mass. This hypothesis is consistent with the aforementioned observation that the previous plane of nutrients affects FHP (Koong et al., 1982; de Lange et al., 2002). Some nutritional models directly or indirectly account for this by assuming that maintenance is a function of protein mass, protein turnover, or growth rate (Whittemore and Fawcett, 1976; Moughan and Smith, 1984; Knap and Schrama, 1996). Measured values for activity-free FHP range from 700 to 800 kJ/(kg  $BW^{0.60} \cdot d$ ) in growing pigs offered feed close to ad libitum (Le Bellego et al., 2001; van Milgen et al., 2001; Le Goff et al., 2002). Taking into account  $k_m$  and the energy cost of physical activity (see next section), current estimates for  $ME_m$  typically range from 850 to 1,000 kJ/(kg  $BW^{0.60} \cdot d$ ) (Noblet et al., 1999).

### *Physical Activity*

Heat production due to physical activity is an important source of variation between different animals and may be affected by housing conditions. Energy expenditure per hour of standing appears at least fourfold greater in pigs than in other domestic species (Noblet et al., 1993). Different techniques exist to measure physical activity, including measurement of standing duration, motion detection, or force detection (e.g., Schrama et al., 1996; van Milgen et al., 1997). Heat production due to physical activity is estimated from statistical relations between the variation in heat production and variation in recorded physical activity. Consequently, the definition of "physical activity" has

an important impact on the heat production with which it will be associated. For example, in our laboratory, we measure activity as the standing duration (through interruption of infrared beams) and by continuous recording of vertical forces the pig exerts on its cage. It appears that approximately 60% of the total force is recorded when animals are lying (approximately 21 h/d) and the rest while standing (Le Goff et al., 2002). Changing our notion of activity (i.e., force detection rather than standing duration) has since doubled the heat production that we attribute to physical activity. Our current estimate is approximately 200 kJ/(kg BW<sup>0.60</sup>·d) (Quiniou et al., 2001; van Milgen et al., 2001), which corresponds to 3 h of standing per day. This estimate is of similar magnitude as values determined by motion detection for group-housed pigs kept in a respiration chamber (Schrama et al., 1996). Physical activity appears rather variable between individual animals and can be affected by feeding level, type of diet, and genotype (Susenbeth and Menke, 1991; Schrama et al., 1996; Le Goff et al., 2002). Because of its contribution to heat production and thus to energy retention, it is important to obtain reasonable indicators of physical activity.

#### *Thermic Effect of Feeding*

The previous two components are mainly (but not exclusively) determined by the animal. The thermic effect of feeding (**TEF** or heat increment) is defined as the difference between the total heat production minus FHP and heat production due to physical activity (van Milgen and Noblet, 2000). In our quantification of components of heat production, we further distinguish a component that has a distinguishable dynamic relation to patterns of feed intake (the short-term TEF) and one that does not (long-term TEF). The long-term TEF is calculated by difference between the basal heat production in the fed state and the FHP. Processes such as hindgut fermentation and intermediary metabolism are thought to contribute to the long-term TEF. Heat production due to feed intake, digestion, and absorption are assumed to be part of the short-term TEF. The distinction between these two phenomena is, of course, arbitrary, but is required to estimate the different components of heat production. In most situations, it will be more practical to study the effect of diet variation on total TEF.

Different biophysical and biochemical processes contribute to the TEF. For instance, although lipid is quantitatively the most important form of energy storage in the body, dietary energy is mainly supplied as starch. The biochemical efficiency of the conversion of starch to lipid is 84% (Baldwin, 1995), so that for this conversion, at least 16% of the dietary energy is lost as heat. Theoretical efficiencies of using nutrients for lipid deposition decrease in the following order: lipid, starch, and protein. Experimentally determined values were 0.88, 0.84, and 0.52 for lipid, starch, and protein, respectively

(van Milgen et al., 2001)—values that are similar to those used in the NE system (0.90, 0.82, 0.58; Noblet et al., 1994). In addition to the cost of nutrient transformation, the ATP utilization associated with metabolism has an important impact on TEF. Synthesis of a peptide bond from amino acids requires at least 5 ATP and, based on the efficiency of ATP synthesis, the maximal efficiency of protein deposition ranges from 85 to 90%. However, experimentally observed  $k_p$  values (approximately 60%; Noblet et al., 1999) suggest that considerably more ATP is required, and protein turnover (i.e., the repeated synthesis and breakdown of peptide bonds) may be one of the reasons for this difference (Reeds et al., 1981).

As indicated above, dietary protein is an inefficient energy source when used for purposes other than protein deposition. Apart from the material energy loss, four ATP are required to synthesize 1 mol of urea (2 ATP/mol N). This explains part, but far from all, of the energy loss associated with protein-rich diets. Le Bellego et al. (2001) observed that replacing 1 g of protein (given in excess of PD) with 1 g of starch lowered the heat production of pigs by 7 kJ. A considerable part of this heat production could be due to a diet-induced protein turnover (Reeds et al., 1981; Roth et al., 1999). The metabolic efficiencies of using dietary protein for protein deposition or for other energetic purposes (lipid deposition or ATP synthesis) were found to be of similar magnitude (van Milgen et al., 2001). The low energetic efficiency of using dietary protein implies that sufficient amino acids should be supplied in order to exploit the animals' potential to deposit lean tissue, but excess supply should be avoided (both from an energetic and environmental perspective). This favors diets with a balanced supply of amino acids. It has been shown that diets with CP levels as low as 12.3% can be used in growing pigs without affecting growth performance (Le Bellego et al., 2001; Noblet et al., 2001).

#### **Partitioning of Energy Retention Between Protein and Lipid Deposition**

Protein deposition in growing pigs not only depends on the supply of available amino acids, but also on the supply of energy. Although different mechanisms have been proposed to represent the relationship between PD and energy intake (e.g., ARC, 1981), the linear-plateau model has been most widely adopted. It assumes that PD increases linearly with energy intake up to a point where other factors start limiting protein deposition. The  $PD_{max}$  is the upper limit of PD, whereas the slope of the relation is determined by the partitioning of ME intake between PD and LD. Whittemore and Fawcett (1976) assumed that growing pigs maintain a minimal ratio between LD and PD, which thus determines the slope of the relation between PD and energy intake. Kyriazakis and Emmans (1992a,b) suggested that the efficiency of using ideal protein was a linear-plateau function of the dietary energy:protein

ratio. However, as this function intersects the origin, the approach is essentially similar to a linear-plateau function between PD and energy intake (by multiplication of both sides of the equation by the dietary protein supply). De Greef and Verstegen (1995) argued that if there are linear relations between PD and LD on the one hand and energy intake on the other hand, the LD:PD ratio will vary with energy intake due to the existence of intercepts at zero energy intake. They proposed existence of a minimal marginal LD:PD ratio (i.e., the ratio between the slopes of the linear line segments). De Lange (1995) assumed that the partitioning of energy retention was governed by the body lipid:protein mass ratio, rather than a constant LD:PD ratio or marginal LD:PD ratio. Koong (1977) and van Milgen and Noblet (1999) reversed Kielanowski's equation by specifying two related equations for PD and LD:

$$\begin{aligned} \text{PD} &= k_p X(\text{ME} - \text{ME}_m) \\ \text{LD} &= k_l(1 - X)(\text{ME} - \text{ME}_m) \end{aligned}$$

In these equations, the energy supply above maintenance ( $\text{ME} - \text{ME}_m$ ) is partitioned into a fraction designated toward protein deposition ( $X$ ), whereas the complement ( $1 - X$ ) is designated toward lipid deposition. These equations are functionally the same as Kielanowski's (resulting in similar values for  $k_p$  and  $k_l$  as in the original equation), but require a specific definition of energy partitioning (here specified as " $X$ "). The partitioning of energy above maintenance will be affected by factors such as feeding level and body weight. Both approaches presumed that reducing feed intake increases  $X$  and thus results in leaner animals. Koong (1977) assumed that  $X$  varied with energy intake according to a Michaelis-Menten equation, whereas van Milgen et al. (2000) assumed that  $X$  was a linearly declining function of energy intake, up to the point where  $\text{PD}_{\text{max}}$  starts limiting PD. The latter results in a curvilinear plateau model for the relation between PD and energy intake. The approach described above indicates that both PD and LD are equal to zero when ME intake equals  $\text{ME}_m$ . As indicated earlier, there is experimental evidence that at low energy intakes, growing animals can mobilize body lipid while depositing protein (Le Dividich et al., 1980). However, such a physiological scenario is difficult to reconcile with the concept of maintenance (van Milgen et al., 2000). Nevertheless, a positive PD and negative LD remain possible if  $X$  is allowed to be greater than one.

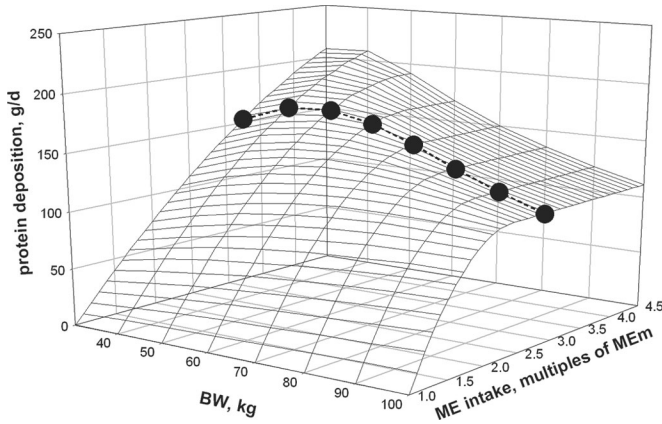
Apart from choosing a mechanism of energy partitioning (e.g.,  $\text{PD}_{\text{max}}$ , minimal LD to PD, minimal marginal LD to PD, minimal L to P,  $X$ ), the parameters that describe these mechanisms will most likely change during the course of growth. Moreover, they depend on genotype, sex, and environmental conditions. Using animals fed close to ad libitum, van Milgen and Noblet (1999) observed that extremely lean boars maintained a constant partitioning of energy within the observed

BW range (20 to 100 kg). For five other types of animals (including Large White females and barrows), the fraction of energy designated toward PD declined linearly with increasing BW. For the latter groups, this resulted in increased fatness as body weight increased. Black et al. (1976), using the linear-plateau model, assumed that the slope of the relationship between nitrogen retention and ME intake declined exponentially with increasing body weight. The NRC (1998) used a similar approach based on DE.

The choice of an appropriate function to describe variation in  $\text{PD}_{\text{max}}$  has been the subject of a rather intense debate. One of the problems is that ad libitum feed intake is not necessarily sufficient to attain  $\text{PD}_{\text{max}}$ ; PD at ad libitum feed intake is therefore not to be confused with  $\text{PD}_{\text{max}}$ . Using different levels of feed intake at each BW, Möhn and De Lange (1998) observed little difference in  $\text{PD}_{\text{max}}$  at 25, 40, and 70 kg of BW. Black et al. (1986) described PD at ad libitum feed intake by an equation containing components of the logistic function, whereas the NRC (1998) used a polynomial function. Whittemore et al. (2001) described PD at ad libitum feed intake as a Gompertz function of present weight and mature BW. With this approach, PD reached a maximum at 60 to 80 kg of BW and approached zero as animals reached maturity. Van Milgen et al. (2000) also used a Gompertz function (for  $\text{PD}_{\text{max}}$ ), but described it as a function of age rather than mature BW. Although the choice between these functions (or any functions) will only marginally affect the predicted growth in pigs allowing ad libitum access to feed, it does affect results under specific growth conditions, such as compensatory growth. The underlying difference between these approaches is the question of whether growing pigs have a notion of "state" (i.e., current and mature body weight, protein, and/or lipid mass) vs. a notion of "age." Biological reality probably involves both.

In addition to these rather empirical descriptions of  $\text{PD}_{\text{max}}$ , some models are based on the separation of protein deposition in processes of synthesis and degradation. Pomar et al. (1991) assumed that protein synthesis was driven by a protein precursor pool, the kinetics of which varied according to a variant of the logistic function. Also, Lovatto and Sauvant (2003) described protein synthesis and degradation separately, each as an exponentially declining function of age (i.e., protein mass is described by a variant of the Gompertz function). These approaches undoubtedly represent biological reality better than empirical models of protein deposition. However, the difficulties that one will encounter during parameterization of these models will, in our opinion, preclude widespread practical utilization. Moreover, the types of functions that are used to pilot these models are very similar to models that consider protein deposition at a more aggregate level.

The hypothesis that energy partitioning at and below  $\text{PD}_{\text{max}}$  changes during growth results in relatively complicated PD response curves (e.g., Figure 9 in Black et



**Figure 2.** The response surface of protein deposition as a function of ME intake and body weight. For a given body weight, protein deposition is described by a curvilinear-plateau function of ME intake. The connected points indicate the feed intake capacity of a Large White barrow and the corresponding protein deposition.  $ME_m$  = ME intake for maintenance.

al., 1986 or Figures 3 and 4 in NRC, 1998). Figure 2 illustrates the PD response surface to ME intake during the growing and finishing period of pigs using the curvilinear-plateau model (van Milgen et al., 2000). The ad libitum feed intake is indicated by the dotted line. Light animals have a very high  $PD_{max}$ , which appears beyond the feed intake capacity, resulting in a PD that is much lower than  $PD_{max}$ . For heavier animals,  $PD_{max}$  is “within reach of appetite,” but its value is considerably lower. The result is that total protein deposition does not necessarily change much during the growing phase (25 to 100 kg). However, the sensitivity to a changing energy supply is much greater in lighter vs. heavier animals. A reduction in feed intake will therefore result in a reduction of both PD and LD in light animals, whereas it will mainly affect LD in heavier animals.

### Future Development of Energy Models

In the past, there have been different efforts to model metabolism, growth, and lactation (e.g., Pettigrew et al., 1992) based on biochemical pathways. This trend is currently continuing (Boisen, 2000; Chudy, 2000; Birkett and de Lange, 2001a), which is to be applauded because nutritional biochemistry contributes significantly to the overall energetic efficiency of growth. The consequence of this approach is that energy requirements are no longer expressed as DE, ME, or NE requirements, but rather as the nutrient (e.g., ATP) requirement for a specific process. Although such an expression may bear a close resemblance to physiological reality, we have to be careful in extrapolating this to the whole-animal level. If an animal requires ATP for a maintenance process (e.g., a sodium pump), it will convert a nutrient to ATP and then use this ATP for

this process. Both the conversion of the nutrient to ATP and the actual ATP utilization will result in heat production. One may argue that the latter is diet-independent, whereas the former is not. However, there is currently considerable doubt concerning the stoichiometry of ATP synthesis from different nutrients. In older biochemistry textbooks, it is assumed that 1 mol of glucose yields 38 mol of ATP. Uncertainties concerning the coupling of ATP synthesis to mitochondrial oxygen consumption have resulted in estimates that are much lower: 31 ATP/glucose (e.g., van Milgen, 2002). This “new” finding would require that ATP-based energy systems would have to revise the efficiencies of ATP synthesis from nutrients as well as the whole-animal ATP requirements, even though the heat production of the overall process has not been changed. A more mechanistic approach to whole-animal energy metabolism should definitely not be discouraged. It is an intellectual effort that will prove its usefulness in the future as these approaches allow for a better quantification of the (relative) contribution of different processes involved in energy metabolism. Nevertheless, it is essential that these approaches are able to predict traditional indicators of energy metabolism with which end-users are accustomed.

The separation of nutrient requirements into a component for maintenance and one for growth has been (and continues to be) the basis for many energy systems. The maintenance energy requirement for growing animals remains a fuzzy concept, for which there is currently no suitable alternative. Although there are many uncertainties concerning the factors that affect maintenance, there is at least one certainty: the ad libitum ME intake in a mature, nonproducing animal equals the maintenance energy requirement, and both PD and LD equal zero (within very narrow margins). The argument that Whittemore et al. (2001) make in favor of the Gompertz function to describe  $PD_{max}$  (i.e., it equals zero for mature animals) can also be made for the ad libitum feed intake capacity above maintenance. Consequently, total feed intake consumption above maintenance during the course of life should be in close relationship with mature BW and body composition. This is a phenomenon that is little exploited in most models since feed intake is seen as some function of BW without a specific relation to maturity. Alternatively, a reverse approach has been proposed (e.g., Kyriazakis and Emmans, 1999) where feed intake is predicted relative to the growth potential. These approaches differ fundamentally in the way growth and feed intake are interpreted in terms of cause and effect. In the first approach, feed intake (while ignoring the force that drives it) results in growth, whereas in the latter approach, the animal has the desire to attain maturity and feed intake is a consequence of this. The very short life span of growing pigs (relative to maturity) probably makes the first approach easier to implement in pig growth models. However, if recovery mechanisms, such as compensatory feed intake and gain (e.g., after a period of heat

stress or after disease), are to be included in growth models, a more mechanistic description of feed intake regulation will be required.

It would not be realistic to suggest that current models (or those developed in the near future) are able to predict growth. Most models use both feed intake and the upper limit of protein deposition as user inputs. Rather than predicting growth, these models analyze growth by indicating the (nutritional) factors that are potentially limiting performance. Through its relation with body water, calibration of protein deposition is essential in order to “predict” growth. On the other hand, lipid deposition is calculated as the energy retention after protein deposition and its associated cost, and maintenance is accounted for. Although lipid deposition has less influence on performance than has protein deposition, it has an important impact on carcass quality. Errors in establishing the maintenance energy requirement will therefore have the greatest impact on lipid deposition. An alternative approach would be to use lipid deposition capacity or lipid mass as a user input (e.g., based on backfat thickness measurements) and consider maintenance, rather than lipid deposition as the residual phenomenon. Such an approach does not necessarily change the PD and LD response curves to energy, but it will shift our focus of attention from trying to predict the response at the maintenance feeding level to predicting the response at the ad libitum feeding level. From both a biological and experimental point of view, such an approach may prove to be more fruitful.

### Implications

Feed intake capacity and the partitioning of metabolizable energy between protein deposition, lipid deposition, and heat production in pigs change considerably during the growing and finishing periods. Although this review only addresses the energy aspects during the course of life, these changes also affect other aspects of nutrition. For example, the partitioning of energy between protein deposition and lipid deposition determines amino acid requirements. As this partitioning changes during growth, so will the optimal ratio between amino acids and energy. Traditionally, nutrient requirements originated from feed recommendation tables, and feeds were formulated to meet or exceed these requirements. As systems of energy and amino acid utilization become more refined, the classical notion of “requirement” and “feed value” becomes less clear. The use of mathematical models then becomes essential to quantify the growth response of an animal to changes in nutrient supply.

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