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MODELING THE RESPONSE OF GROWING PIGS TO NUTRITION

JAAP VAN MILGEN, JEAN NOBLET, JEAN-YVES DOURMAD AND LUDOVIC BROSSARD

INRA, UMR1079 SENAH, F-35590 Saint-Gilles, France
Agrocampus Ouest, UMR1079 SENAH, F-35000 Rennes, France

Introduction

Animal production is constantly facing new challenges. After World War 2, increasing productivity and efficiency were key issues to ensure food supply. Since then, other dimensions have become issues in animal production including animal health, food quality and security, environment, animal welfare and consumer and citizen expectations. Feed is the most costly component to pig production and feeding is a means to greatly influence many of the dimensions cited previously. Because of the complexity of livestock production systems, modeling has become an increasingly important method to understand and to integrate knowledge on how the animal responds to different challenges, including feeding. The basis of modeling is the development of response curves (e.g., based on experimental research or analysis of literature data) and integrating these response curves in a model. The purpose of this paper is to indicate how different models have been developed and what the main internal driving forces of these models are, focusing on the similarities and differences taken by different model developers. We do not intend to make any judgment on these models as all have been developed with a specific objective in mind and they should be evaluated according this objective. We will also indicate how models can be used as decision support systems, including decisions related to feed formulation.

Empirical growth models

Modeling growth is not something new. For example, the logistic growth function was developed more than 150 years ago to describe (population) growth. The logistic function is an S-shaped curve and is commonly written as:

$$W = \frac{W_0 \cdot W_f}{W_0 + (W_f - W_0) \cdot \exp(-k \cdot t)}$$

where W is the weight of the animal at a given age, W_0 is the initial weight, W_f is the mature body weight, k is a shape parameter and t is the age of the animal. Written in the integrated form, the logistic function assumes that age (or time) is the driving force for growth. Animals grow because they get older. The logistic function is also frequently written (and used) as a differential equation that describes the change in growth ($\partial W/\partial t$) and not the change in weight (W) of the animals:

$$\frac{\partial W}{\partial t} = k \cdot W \cdot (W_f - W)$$

The logistic function written in differential form does not include time as a driving force for growth as it depends on 2 constants (k and W_f) and the current weight (W) of the animal. It is thus the current state of the animal (W) and not the age that is the driving force for growth. According to France and Thornley (1984), this is the rate-state formalism where "the rate of a process is a function of the state of the system". We will come back to this point later on but it illustrates an important concept in the biology of growth.

The Gompertz function is somewhat similar to the logistic function and can also be described in the integrated form (as a function of time) or in differential form. In differential form, it can be written as:

$$\frac{\partial W}{\partial t} = W \cdot (a \cdot \exp(-k \cdot t))$$

or as:

$$\frac{\partial W}{\partial t} = k \cdot W \cdot \ln\left(\frac{W_f}{W}\right)$$

Depending on how the differential equation is written, either the state (the current body weight *W*) or the state and age of the animal are considered as driving forces for growth.

Considering growth only as a function of state or time is, at least for nutritionists, a somewhat limited point of view. Parks (1982) considered this type of model as an "output-only" model and he developed an extensive theory on the relationship between cumulative feed intake and body weight gain in animals. Stated simply, he considered growth as the result of changes in feed intake and feed efficiency:

$$\frac{\partial W}{\partial t} = \left(\frac{\partial W}{\partial F}\right) \cdot \left(\frac{\partial F}{\partial t}\right)$$

where $\partial W / \partial F$ is the feed efficiency and $\partial F / \partial t$ the feed intake. A specific equation for feed efficiency will be required so that it becomes zero as animals approach maturity. There are two schools of thought of addressing growth in relation to feed intake. The equation above indicates that animals grow because they eat, which is the so-called "push" approach. Why an animal eats is then a different question. The equation can also be reversed so that feed intake is considered the result of a desire to grow and this is referred to as the "pull" approach. The pull or push approach may be consider a chicken-or-egg issue but, as we will indicate later on, the relationship between feed intake and growth is extremely important and tightly regulated.

The first nutritional growth models for pigs

One of the first nutritional models describing growth in pigs was proposed by Whittemore and Fawcett (1974). They stated that "a simple model is described which enables the prediction of the magnitude and direction of the responses of growing pigs to different energy and protein intakes". We will describe the model here in some detail mainly to illustrate that the models published since then are based on more or less similar principles. The model of Whittemore and Fawcett (1974) calculates protein and lipid deposition from which body weight gain is determined. Protein deposition is determined by two different scenarios, depending if the dietary protein is limiting or not. When protein supply is limiting, protein deposition is simply the product of feed intake and the gross efficiency of protein utilization. Similar to the feed efficiency concept of Parks (1982), the gross efficiency of protein utilization declined with increasing body weight. When protein supply is in excess of requirement, Whittemore and Fawcett (1974) assumed that the protein deposition is constant (110 g/d) between 20 and 100 kg body weight. Lipid deposition can be then calculated from the energy balance by considering the ME intake, the maintenance energy requirement (a function of metabolic body weight), and the energy costs of protein and lipid deposition (respectively 60 and 53.5 kJ/g). All ingested energy not used for maintenance or for protein deposition will be retained as lipid. Lipid deposition is thus considered an energy sink. Protein and lipid deposition were then used to calculate respectively lean and fat gain. This tissue gain, combined with body ash gain and contents of the gastrointestinal tract, determine total body weight gain. In their model, Whittemore and Fawcett (1974) also accounted for the fact that the energy efficiency to deposit lipids from (excess) dietary protein is lower than from carbohydrates.

Whittemore and Fawcett (1976) further refined their initial model because, as they stated, it was inflexible with respect to maintenance and protein deposition, protein quality was not taken into account, and the model did not function correctly at low nutrient intakes. They acknowledged that the

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observed energy cost of protein deposition was considerably greater than the theoretical value of protein (peptide) synthesis. Because of protein turnover (i.e., the repeated synthesis and breakdown of peptide bonds), Whittemore and Fawcett (1976) suggested to specially represent protein synthesis in the model. This approach allowed them to specifically account for the energy cost of protein synthesis and protein turnover. They also proposed to represent the maintenance energy requirement not only as some function of metabolic body weight, but to include protein mass as contributor to the maintenance energy expenditure. The energy cost of protein turnover therefore contributes to both the maintenance energy expenditure and to the cost of protein deposition.

To account for the fact that protein deposition may be limited by the protein quality of the diet (i.e., the amino acid content), Whittemore and Fawcett (1976) included the biological value of protein as a potentially limiting factor for protein deposition. Actual protein deposition was assumed to depend on three criteria: the supply of available protein, the maximum protein deposition, and the energy supply. The hypothesis that protein deposition also depends on energy supply changes, to some extent, the idea that lipid is only an energy sink. When energy intake is reduced, both protein and lipid deposition may be affected. Whittemore and Fawcett (1976) developed a relationship between protein retention and energy intake which has become known as the linear-plateau relationship (Figure 1). The linear part of this relationship is determined by a minimum lipid-to-protein deposition and they proposed a value of 1 for this ratio. Thus, irrespective of the genetic potential of the animal and the supply of amino acids, the pig would always deposit a minimum of one gram of lipid for each gram of deposited protein. The plateau-phase marks another important concept now widely used in the nutritional modeling of growth of pigs. It indicates that there is an upper limit to protein deposition (usually referred to as *PDmax*), which may differ depending on the breed or sex. Increasing the energy supply above what is required to attain *PDmax* would not result in additional protein deposition. This additional energy supply would thus only favor lipid deposition.

Whittemore (1983) further refined the model mainly in two aspects. In the previous
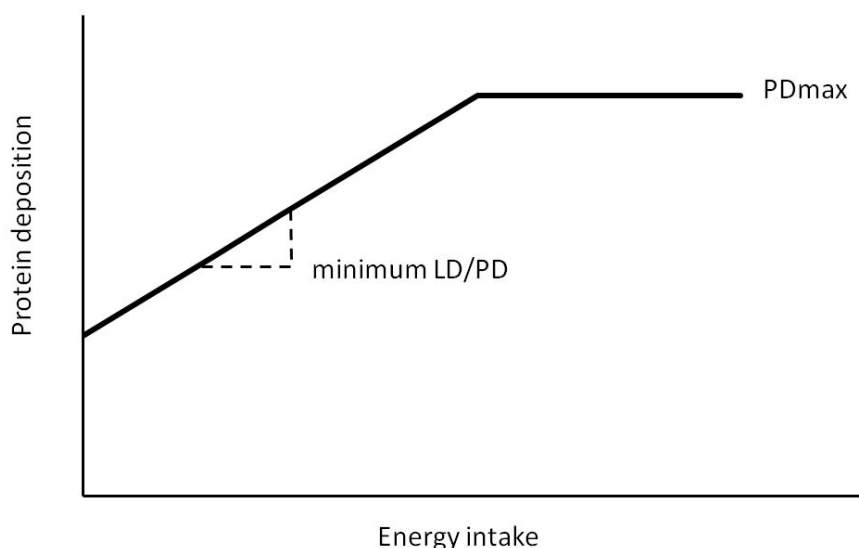

Figure 1. The linear-plateau relationship between protein deposition and energy intake in growing pigs as proposed by Whittemore and Fawcett (1976). The upper limit to protein deposition is indicated by PDmax. The slope of the line is affected by a minimum lipid to protein deposition ratio.

version, he assumed that there was no inefficiency of protein utilization when the profile of amino acids corresponded to that of ideal protein (with 7% Lys in ideal protein). He acknowledged that this may not be the case, and proposed that the efficiency of ideal protein utilization could range between 0.85 and 1.00. He also suggested that the minimum lipid-to-protein deposition ratio may depend on the

phenotype of the animal. The basic concept of the model proposed by Whittemore and Fawcett can therefore be summarized as:

- growth in pigs can be determined by modeling protein and lipid deposition; body weight (and body water and ash deposition) can be determined from body protein and lipid mass
- there is an upper limit to protein deposition in growing pigs
- there is a minimum lipid to protein deposition ratio
- actual protein deposition is determined by the two factors given above plus protein quality (i.e., supply of essential amino acids)

PDmax: an upper limit to protein deposition

Like Whittemore and Fawcett (1976), Moughan *et al.* (1987) assumed that *PDmax* may vary between sexes and genotypes, but remains constant during the growing period. This approach has received some criticism (Emmans and Kyriazakis, 1997) as they argued that as the animals mature, growth should stop and so should protein deposition. In the Auspig model, Black *et al.* (1986) assumed that the *PDmax* varied with body weight and degree of maturity:

$$PDmax = k \cdot W^b \cdot \frac{(P_{maturity} - P)}{P_{maturity}}$$

The last term in this equation, which bears some resemblance to the logistic and Gompertz functions indicated earlier, represents the degree of maturity and it becomes close to zero when the current protein mass (P) approaches the mature protein mass ($P_{maturity}$). Because the exponent b is positive, the term W^b increases with increasing body weight. The *PDmax* is then result of two mechanisms that act in opposite directions. This approach has been criticized by Emmans and Kyriazakis (1997) for two reasons. First, the proposed equation depends directly on body weight and an increase in, for example, fat mass would thus increase *PDmax*. A second criticism is that the equation proposed by Black *et al.* (1986) requires three constants (k, b, and $P_{maturity}$), all of which have to be known to characterize a phenotype. Emmans and Kyriazakis (1997) proposed to use the Gompertz function to describe the change in *PDmax* as a function of current protein mass, using two constants (k and $P_{maturity}$).

The question whether *PDmax* should be considered constant or not during the growing period depends largely on the model objectives. It is evident that when growth is considered over the full growth trajectory (i.e., up to maturity), some mechanism in the model should be included to ensure that growth (and thus protein deposition) declines towards zero when the animal approaches maturity. However, in reality pigs are slaughtered well before their mature body weight. Considering a change in protein deposition between 20 and 110 kg body weight implies that the model user should be able to provide the information how this protein deposition changes. It is a tradeoff between biological reality and the principle of Occam's razor (or the law of parsimony), which states that "entities should not be multiplied unnecessarily".

What is the relation between lipid and protein deposition?

Black *et al.* (1986) indicated that not only *PDmax* but also the minimum lipid-to-protein deposition ratio may change during growth. Based on experimental data, they proposed that the slope of the relationship in Figure 1 declines with increasing body weight. In other words, a 20 kg pig will use an additional 1 MJ of extra energy more for protein deposition (and less for lipid deposition) than a 100 kg pig. De Greef and Verstegen (1995) pointed out that there is not necessarily a constant lipid-to-protein deposition ratio, which is due to the very concept of the linear-plateau relationship. They argued that the presence of an intercept in the linear-plateau relationship (Figure 1) implies that the lipid-to-protein deposition ratio cannot be constant. Alternatively, one may assume the existence of a minimum marginal lipid-to-protein deposition ratio; each additional unit of energy supply results in a constant partitioning between extra lipid and extra protein deposition. De Lange (1995) proposed another variant in which the lipid-to-protein mass ratio (and not the deposition ratio) was assumed to be constant.

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In the InraPorc[1] model (van Milgen *et al.*, 2008), we slightly changed the concept of the linear-plateau model proposed by Whittemore and Fawcett (1976). We used a curvilinear-plateau relationship and applied this to the energy intake above maintenance energy expenditure. We also forced the relationship through the origin so that, at maintenance energy intake, both protein and lipid deposition equal zero. This concept is illustrated in Figure 2. It is based on the hypothesis that the maintenance energy expenditure is somehow "inevitable" and that the animal has to partition the energy supply above maintenance between protein and lipid deposition (van Milgen *et al.*, 2000). An increase in energy intake can increase both protein deposition and lipid deposition, but lipid deposition will typically increase faster than protein deposition. The fact that we forced the response curves through the origin has been subject to some criticism. The main critique is that pigs can deposit protein at the expense of
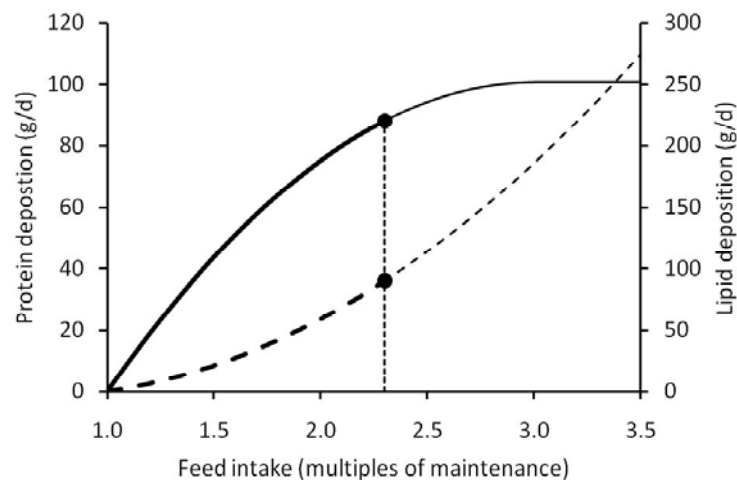

Figure 2. Curvilinear-plateau relationship between protein deposition (solid line) and lipid deposition (dashed line) and the energy intake in growing pigs as used in the InraPorc model. The solid dots indicate the actual protein and lipid deposition for an animal consuming feed ad libitum. The positioning of these points on the curves will change during growth.

lipid, a situation that can occur for example immediately after weaning. The main reason why we chose this approach was to keep the model as simple as possible (Occam's razor). Inclusion of an intercept would imply an additional constant that would have to be provided by the model user. The experimental evidence of a positive PD and negative LD is in conflict with the very concept of maintenance, which is of course more a problem for the concept than for the animal itself. By definition, at maintenance energy intake no energy is retained so that PD + LD = 0. Although this does not exclude that PD could be positive while LD would then be negative, it imposes the constraint that all energy mobilized from LD should be deposited as PD. In other words, the energy efficiency with which this occurs should equal 100%.

Maintenance energy expenditure

The concept of maintenance is widely used in animal nutrition even though there has been quite some debate on how it should be interpreted and estimated in growing animals. Virtually all nutritionists have a gut feeling what maintenance is. They know that it is possible to offer feed at 2-times or 3-times the maintenance energy expenditure and that it impossible to feed a growing animal at 10-times maintenance. Although the maintenance energy expenditure represents a large part of the energy utilization of the animal, it is very difficult to feed a growing animal to maintenance energy requirement. One of the few studies that we are aware of is that of Lister and McCance (1967) who offered feed to a piglet so that it maintained its body weight at 5 kg for one year. One of the surprising

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[1] InraPorc is a model and software tool that allows evaluating the consequences of using different nutritional strategies on performance of growing pigs and sows. It can be obtained from www.rennes.inra.fr/inraporc/.

outcomes of that study was that the animal maintained its growth potential when it was offered feed *ad libitum* (after one year of feed restriction), but that it did not attain the same mature body compared with piglets that had not been not restricted. This also illustrates that both "state" and "age" affect the growth of animals. Maintenance can also be estimated by offering feed at different levels to growing animals and then estimate the maintenance energy expenditure by extrapolation to zero energy retention. Because the lowest levels of feed intake typically are in the range of 70% of *ad libitum* intake, the estimate of the maintenance requirement results from a rather important extrapolation.

The maintenance energy expenditure has traditionally been expressed relative to the metabolic body weight ($BW^{0.75}$). This mode of expression originates from comparing the maintenance energy expenditure between mature, non-producing animals of different species. In growing pigs, we found that the maintenance expenditure could be better described relative to body weight raised to the power 0.60 (van Milgen *et al.*, 1998). Nevertheless, we observed differences in the fasting heat production (i.e., an indicator for maintenance) between different types of pigs, part of which seemed due to difference in the contribution of visceral organs. Other indirect indications suggesting that the visceral organs play a role in the maintenance energy expenditure include the observation that feed intake level before fasting affects the fasting heat production (de Lange *et al.*, 2006). It is for this reason that in the InraPorc model, maintenance energy expenditure is represented as a power function of BW and of feed intake. A somewhat similar approach was taken by Black *et al*. (1986), who assumed that the maintenance energy expenditure was a power function of protein mass and daily gain.

Feed intake in relation to energy balance

Ad libitum feed intake is probably one of the factors that received the least attention in nutritional models of growth, especially in models that use a "push approach". In these models, an asymptotic model of energy intake versus body weight is frequently used:

$$Feed\ Intake = a \cdot (1 - \exp(-b \cdot W))$$

Simply stated, the more the animal weighs, the more he will eat. One of the problems with this approach in the "push" models is that there is virtually no limit to feed intake (other than *a* at infinite *W*). As lipid deposition is considered as an energy sink, this also means that there is virtually no limit to lipid deposition. In most models, there is some built-in mechanism to limit protein deposition. In the logistic and Gompertz function, protein deposition approaches zero as the animals approach their mature protein mass. However, also feed intake should approach the maintenance energy expenditure as animals approach mature body weight. This also illustrates that maintenance is an important concept in biology and should be (or could be) one of the driving forces for the regulation of feed intake. It is for this reason that we included a feed intake function in InraPorc where feed intake is expressed as multiples of the maintenance energy requirement. With this function, as the animal matures, feed intake will gradually approach the maintenance energy requirement and thus the animal will stop growing.

Just a numerical example to illustrate how well food intake (and energy expenditure) is regulated. Imagine that you take every day 1 cube of sugar in your coffee or tea (i.e., 1 cube of sugar per day). This single daily cube will provide you with 100 kJ/d and will allow you to gain 770 g of lipid in a single year. Over 50 years, this represents close to 40 kg of lipid and this is what is called in human nutrition the "energy gap". It is of course difficult to imagine that this severe obesity is just a matter of a single sugar cube per day and it is likely that, in reality, there is a tight regulation between energy intake and energy expenditure. If the energy gap is not accounted for, running simulation models for longer periods of time will have an impact on the predicted lipid deposition. In a recent modeling workshop held in Paris, the remark was made that "Molly" (a nutritional model for dairy cows) became fat when run over long periods of time. This is also the reason why in the sow module of InraPorc (Dourmad *et al.*, 2008), the maintenance energy expenditure can (or should) be adjusted to avoid severe over- or under-predictions of backfat thickness if the model is run over several parities.

The problem of the energy gap is probably better accounted for in "pull" models. These models not only use a potential protein deposition curve (e.g., a Gompertz cruve) but they use a similar approach for potential lipid deposition. As animals mature, both protein and lipid deposition

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approach zero and feed intake (i.e., the result of the "pull" approach) will approach maintenance energy expenditure. For example, in the Auspig model (Black *et al.*, 1986), feed intake is driven by protein and energy retention.

Towards a more mechanistic approach of modeling growth

A growing animal consumes carbohydrates, protein, lipid, and fiber as substrates and deposits these nutrients mainly as protein and lipid. Typically not more than half of the energy an animal consumes can be deposited by the animal, and the remainder is mostly lost as heat. This heat loss should not be considered as a biological inefficiency of the animal as there are many essential physiological processes that require energy, mostly in the form of ATP. Animals use nutrients for ATP synthesis and when the ATP is used for a physiological function (e.g., for muscle contraction) the energy will be released as heat. The concept that the efficiency of energy transformation differs between nutrients is incorporated in most nutritional models, even though different approaches have been taken.

The complexity of nutrient transformations has lead to development of more mechanistic nutritional growth models. Halas *et al*. (2004) proposed a model where the intake of protein (lysine and the other amino acids), cell walls, starch, sugar and fat were used as model inputs. Intermediary metabolism was represented by a pool of acetylCo, which can be used to synthesize ATP or fatty acids. In doing so, they could directly account for the fact that the efficiency of lipid deposition differs between nutrients such as carbohydrates and lipid. A similar approach was developed by Birkett and de Lange (2001). Biochemistry undoubtedly plays a role in the efficiency of nutrient transformation and it was for this reason that we developed a "biochemical calculator" (van Milgen, 2002), which allows quantifying the energy efficiency of different biochemical pathways. Despite this knowledge, we decided not include this biochemical knowledge in the InraPorc model (van Milgen *et al.*, 2008) and we decided to use empirical, experimental efficiency values to transform inputs (dietary nutrients) into outputs (body protein and lipid). The main reason for this was that biochemistry explains part, but far from all of the efficiency of nutrient transformations. For example, in the net energy system the efficiency to deposit lipid from dietary lipid is much lower than the theoretical value (90 vs 97%). At the same time, the theoretical and experimental efficiencies of lipid deposition from starch are almost identical (around 84%). Also, the efficiencies to synthesize ATP are very similar for starch and lipid. Part of the explanation of the "low" experimental efficiency may be the fact that some dietary lipids will be oxidized (e.g., used for ATP production). Oxidative muscles can and will use lipid as an energy source, even if there is a net *de novo* lipogenesis. This means that, at the level of the whole animal, part of the lipid supply will be used for ATP synthesis, while at the same time the animal uses other nutrients to synthesize lipids. This will result in a lower efficiency compared with the situation where all lipids are deposited and glucose is used for ATP synthesis. This "inefficiency" may be due to the spatial organization of the animals (i.e., different processes in different tissues) or to temporal events (i.e., post-prandial storage of energy as lipid followed by reutilization). Although we acknowledge that biochemistry contributes to the efficiency of nutrient utilization, we estimated that the current knowledge of these nutrient cycles is insufficient to use this information in a practical model. Of course, this does not exclude to include these concepts in research models that are used to improve our understanding of biology.

Halas *et al*. (2004) also argued that it might be useful to specifically represent different body protein pools, rather than considering all body protein as the same. The main reason for this was that protein turnover rates differ largely between tissues. Compared with other protein pools, the protein turnover rate is very high in visceral organs. Because protein turnover is energetically costly and nutrition can alter the relative contribution of the different pools to total body protein, the specific representation of these pools can be justified.

The concept of different pools was also used by Lovatto and Sauvant (2003), who considered different anatomical pools (carcass, viscera and plasma) and nutrient pools (e.g., individual amino acids, glucose and non-esterified fatty acids). Their main contribution was by considering that growth was regulated by homeostatic and homeorhetic controls. The homeorhetic control determines the long-term trajectory of growth, which was represented by anabolism and catabolism of tissues. Lovatto and

Sauvant (2003) chose to describe the fractional rates of anabolism and catabolism as exponentially declining functions of time. For a growing animal, the fractional rate of anabolism will typically be greater than that of catabolism, resulting in growth of the animal. As time progresses, these fractional rates converge towards a common value and deposition (the difference between anabolism and catabolism) comes to a halt. Time was therefore considered an important driving force for the homeorhetic control. Lovatto and Sauvant (2003) considered that the rates of anabolism and catabolism could be modified by the nutrient supply, accounted for by the homeostatic regulation of growth. Compared with a standard situation, the relative contributions of anabolism and catabolism will be changed. This may result in faster growth when nutrient supply is large or slower growth (or even nutrient mobilization) when nutrient supply is limited.

The development of more mechanistic models of growth provides researchers with a challenging task. For example, the control mechanisms developed by Lovatto and Sauvant (2003) deal with very different time scales, ranging from minutes for the homeostatic controls to months (or years) for the homeorhetic controls. Nevertheless, the animal also deals with this reality and rapid changes in nutrient supply (e.g., immediately after a meal) have to be dealt with keeping a larger objective (attaining maturity) in mind. The concept of these control mechanisms is an important step forward and is a good basis on which future research models can be built.

Creating simplicity in complexity

Although numerous nutritional models of growth have been proposed, most of these have only been proposed in scientific papers. To our knowledge only the models of TMV (1991), NRC (2003), and InraPorc (Dourmad *et al.*, 2008, van Milgen *et al.*, 2008) have been made available as software tools to be used by larger audience. Some other models have served to develop proprietary tools.

One of the main challenges in tool development is to simplify the model. The problem is not so much the simplification of the model structure itself, but more in developing a tool that can work with a limited set of user inputs (i.e., models that have a low information requirement). Because pigs in different environments behave differently, the model user should be able to provide quantitative information indicating how the environment and the pigs differ from one situation to another. Mechanistic growth models typically rely on tens (if not hundreds) of model parameters that may potentially change from one situation to another and most of this information will be not accessible to the model user. In developing a tool, it is therefore important to fix a maximum number of parameters, while capturing most of the observed variation in a limited set of relevant model parameters. In InraPorc, this is done by characterizing an animal by its (*ad libitum*) feed intake curve and the corresponding growth curve (Figure 3). The choice of these two traits has some important implications. The first implication is that we consider the animal as a phenotype and not as a genotype. Pigs of the same genotype and kept under different conditions will eat and grow differently. Secondly, we consider both feed intake and growth to some extent as model inputs. The question if an animal grows because he eats, or that he eats because he wants to grow is therefore not (or less) relevant. Lastly and perhaps most important, our goal is to construct a dynamic pattern of feed intake and growth and to compare different feeding strategies. Our view is that the essence of nutrition comes down to knowledge of performance (i.e., growth) and feed intake, and that a dietary nutrient requirement is essentially determined by the ratio of these two traits. Because these traits change during growth, knowledge of only the average feed intake and growth rate is insufficient.

The feed intake curve is modeled directly and different modes of expression for *ad libitum* feed intake are available (including a function where feed intake is proportional to maintenance). As indicated earlier, the growth curve is not modeled directly, but is modeled through the protein deposition curve. Because of the association of protein and water in lean mass, the shape of the protein deposition curve essentially determines the shape of the growth curve. Two additional parameters can be modified by the user of InraPorc, provided that sufficient information is available to do so. The first parameter concerns a correction factor for maintenance. By default, maintenance is set to "100%" and

calculated from body weight, feed intake, and a standard level of activity. When the user increases the default maintenance values, more energy will be used for maintenance and less for lipid

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deposition. The last parameter that can be changed is what we called *BW PDmax*. Similar to the approach of Black *et al*. (1986), we assumed that young animals cannot always eat sufficiently to attain the upper limit to protein deposition (see Figure 2). The *BW PDmax* indicates at which body weight the pig can just eat sufficiently to attain *PDmax* and the default value to this parameter is 70 kg. Before this body weight, a small reduction in feed intake will affect both protein and lipid deposition, while for body weights greater than *BW PDmax*, only lipid deposition will be affected. The parameter *BW PDmax* is useful mainly in situations where feed is not offered *ad libitum*. This can for example occur if wet feeding systems are used or when animals are fed
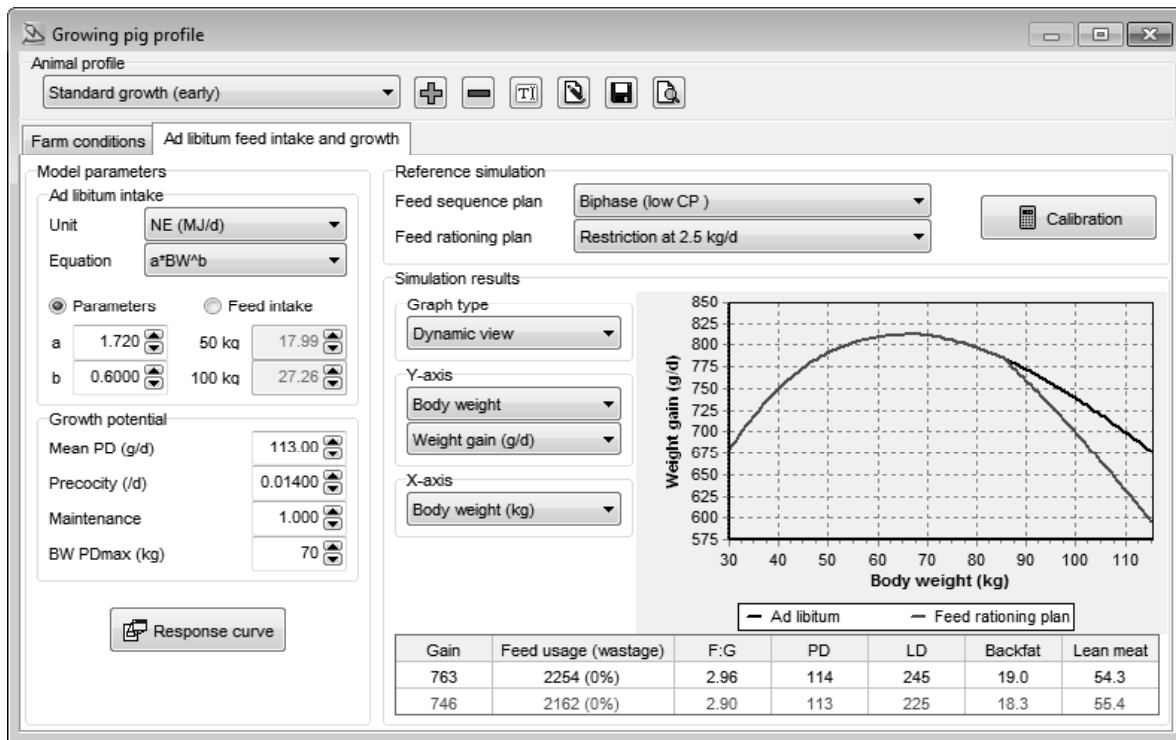

Figure 3. Screen capture of the InraPorc program. In the left-hand panel, the parameters of the animal profile are defined. The right-hand panel shows the result of a simulation when this pig is offered feed ad libitum or when a specific feed rationing plan is applied (in this case, feed intake is restricted to a maximum of 2.5 kg/d).

restrictively at the end of the finisher phase to avoid excessive fattening. If animals are offered feed *ad libitum* all the time, there will be no use in changing this value (as it will not come into play).

Apart from these values of the animal profile that the user can change, there are numerous parameters that are hard-coded in the software and which the user cannot change. For example, the relation how body weight and feed intake affect the maintenance energy requirement cannot be changed by the user. Also, the efficiencies with which the animal uses essential amino acids cannot be changed. We determined these efficiencies on the concept of ideal protein, although we acknowledge that there may be some debate on how this ideal amino acid pattern should look like. It clearly illustrates the difficulties in the developing a tool, as choices have to be made which boxes should be opened up (with the risk that the user gets lost) compared to those that should be fixed (with the risk that advanced users become frustrated because they do not agree with our point of view).

Feed formulation

Least-cost feed formulation is based on the principle of formulating a complete diet at the lowest cost while ensuring that the nutritive value of the diet matches or exceeds the nutrient requirement of the animal. In least-cost feed formulation, the assumption is made that nutrient values of feed ingredients are additive and the nutrient value of a complete diet is simply the sum of the nutritive values of the feed ingredients. Interactions between feed ingredients or between the diet and the animal are not accounted for.

Least-cost feed formulation is usually carried out by linear programming and a simple example of this is given in Figure 4, using digestible lysine and NE as nutritional constraints and corn and soybean meal as the only feedstuffs. The solid lines in the figure indicate the
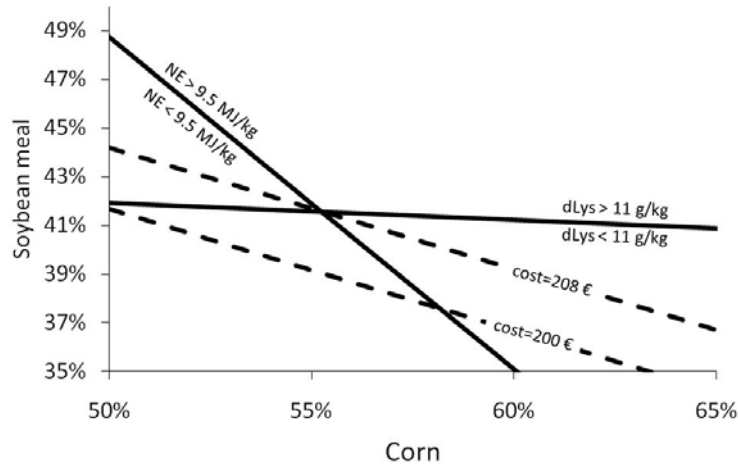

Figure 4: Graphical illustration of the concept of least-cost feed formulation using two feed ingredients (corn and soybean meal), and two nutritional constraint (net energy and digestible lysine).

lysine and NE requirements. If a complete diet is to be formulated that meets or exceed the nutrient requirements, the solution is to be found the upper right-hand of the graph. The dashed lines indicate lines of equal cost using the two ingredients. The minimum cost of a diet that meets both nutritional constraints is 208€ and this diet contains 55.2% corn and 41.6% soybean meal (i.e., the sum is less than 100%). Adding the latter as an additional constraint would increase the feed cost to 212€ (58.7% corn and 41.3% soybean meal). A change in the relative prices of corn and soybean meal will change the slope of the lines of equal cost and can potentially change the least-cost solution.

One of the problems with least-cost feed formulation is that the nutrient value of a feed and the nutrient requirement of the animal are seen as fixed values. However, the concept of nutrient values and nutrient requirements used in least-cost feed formulation does not provide information on how the animal responds when the nutrient supply is below the requirement. For 200€ we could formulate various other diets in which lysine, NE or both would be limiting. It is possible that this reduction in feed cost would outweigh the reduction in performance due to the fact that animals were fed below the requirement. This aspect can be dealt with only if we replace the concept of "requirement" by a concept of "response", and it goes without saying that this is where models come into play. However, from a mathematical point of view, the problem will become more complicated. Rather than solving the problem of least-cost formulation by linear programming, most nutritional growth models are nonlinear and include discontinuous events. The maximization of some objective function (e.g., profit) is then more complicated to solve (Sirisatien *et al.*, 2009, Niemi *et al.*, 2010). Nevertheless, such an approach would be a major step forward and will probably help in making models more accessible and useful to a larger audience.

Dealing with variation and populations of animals

By far most nutritional models of growth are deterministic by nature. This means that for a given set of model inputs, the model will always predict the same outcome because deterministic models do not account for variation or uncertainty. This is also one of the reasons why we warn users of the (deterministic) InraPorc model, that model predictions of nutrient requirements may be too low when applied to a population of animals. A simple example will illustrate this. The InraPorc model can be used to predict the nutrient requirement (e.g., lysine) of the average animal. If a population of animals is offered feed according to this requirement, approximately half of the population would perform as intended because they received at least what was required, whereas the other half of the population would perform below their potential because they received less than required. Because

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variation exists between animals, it is very difficult to speak about *the* nutrient requirement of animals. But how should animals be fed then? It goes without saying that you probably would not formulate a diet that would meet or exceed the nutrient requirements of all individuals in a population. All technically possible, it would have an enormous impact on the cost of feed and you would likely be soon out of business. Accounting for variation between animals in models is a rather complicated task. The simplest approach would be just to include some random variation in the model output, but this would not help much answering this question. An alternative would be to include random variation is several model parameters, but this typically results in an overestimation of the observed variation in the population. The reason for this is that not all variation is random. For example, there are random elements in both daily gain and feed intake, but there is also a strong correlation between these. It is likely that animals that will eat less than average will also have a lower than average growth rate. We are currently trying to quantify this covariance for a number of key parameters in InraPorc, based on observed variation in feed intake and growth in different populations of pigs. With this knowledge, it is easy to run the model with brute force numerous times (e.g., 1000 times) to evaluate how a population of animals responds to nutritional strategies. This approach has been used by Brossard *et al.* (2009) who estimated that the nutrient requirement (in this case lysine) of 90% of the population can be met if the supply level is 10% above the requirement of the average animal. However, the relationship between the requirements of the average animal and that of the population is not fixed and depends on the price of feed ingredients (Quiniou *et al.*, 2007).

Another potential for modeling is the development of precision feeding. Rather than accepting variation within a group by trying to make the best of it, precision feeding deals with gathering information from the animal so that each individual can receive a feed (in terms of quality and quantity) that fits a given production objective. Based on frequent information obtained from the animal such as measurements of body weight and feed intake, this information is used in a model that is running in real-time, and a decision is then made how the animal should be fed. For example, Parsons *et al.* (2007) used visual image analysis to rapidly and frequently evaluate growth of individual animals. Pomar *et al.* (2009) estimated that using a precision feeding system, feeding costs may be reduced by almost 5%, while nitrogen and phosphorus excretion can be reduced by almost 40%. Although we are still in the very beginning of developing these systems, it may mark the beginning of a new era of model utilization.

Conclusions

Considerable progress has been made in the area of model development. As models are developed with different objectives in mind, different types of models have been developed. Models have contributed to improve our understanding how living organisms work, but there is still a (very) long way to go. These models differ largely from "operational" models that can be used in decision support systems. The information that can be obtained in a pig production setting is probably one of the main factors that limit a more widespread use of models. With little or no information as input, there will be little or no information as output. As always: "information is the key to success".

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