

Partitioning of limiting protein and energy in the growing pig: description of the problem, possible rules and their qualitative evaluation

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A core part of any animal growth model is how it predicts the partitioning of dietary protein and energy to protein and lipid retention for different genotypes at different degrees of maturity. Rules of partitioning need to be combined with protein and energy systems to make predictions. The animal needs describing in relation to its genotype, live weight and, possibly, body composition. Some existing partitioning rules will apply over rather narrow ranges of food composition, animal and environment. Ideally, a rule would apply over the whole of the possible experimental space (scope). The live weight range over which it will apply should at least extend beyond the 'slaughter weight range', and ideally would include the period from the start of feeding through to maturity. Solutions proposed in the literature to the partitioning problem are described in detail and criticised in relation to their scope, generality and economy of parameters. They all raise the issue, at least implicitly, of the factors that affect the net marginal efficiency of using absorbed dietary protein for protein retention. This is identified as the crucial problem to solve. A problem identified as important is whether the effects of animal and food composition variables are independent of each other or not. Of the rules in the literature, several could be rejected on qualitative grounds. Those rules that survived were taken forward for further critical and quantitative analysis in the companion paper. (Sandberg *et al.* 2005)

Swine: Growth: Partitioning: Protein: Energy

It is useful to see nutrient partitioning as the distribution of absorbed protein and energy, the only resources considered here, from an ingested food between protein and lipid retention, once the requirements for maintenance have been met. This is so both for models where food intake is considered as an input and those where food intake is a predicted outcome (Black *et al.* 1986; Emmans & Kyriazakis, 1997; van Milgen & Noblet, 1999). Even an animal fed *ad libitum* may still be limited in resources. Environmental constraints such as high temperatures (Campbell & Taverner, 1988; Collin *et al.* 2001) or feed factors such as bulk (Kyriazakis & Emmans, 1995) may prevent the animal from attaining the food intake needed for achieving potential growth. Emmans & Fisher (1986) recognised that to understand the partitioning of scarce resources, the composition of the food partitioned and the animal within which partitioning occurs, both need sufficient descriptions. In agreement with this view, Black *et al.* (1986) stated that 'a full understanding of the animal's response to variations in dietary conditions is required' in order to solve the problem of predicting performance.

The actual intakes of protein and energy will affect the rate of protein retention, which may be below its upper limit, PR_{max} , set by the genotype and the state of

the animal (Black *et al.* 1995; Schinckel & de Lange, 1996; Whittemore & Green, 2002; Wellock *et al.* 2004). Inevitably, intakes will also affect the rate of lipid retention. Rules of partitioning allow the prediction of the *actual* rates of both protein and lipid retention given the supply of ingested protein and energy. Combining partitioning rules with protein and energy systems allows the prediction of *actual* rates of protein and lipid retention.

An optimistic assumption is that general rules exist that govern the partitioning of scarce resources (Ferguson *et al.* 1994; Emmans & Kyriazakis, 1997). A different view is that both the kind of pig, and the state that it is in, will affect the partitioning of scarce resources (Fuller & Crofts, 1977; de Greef & Verstegen, 1995; Fuller *et al.* 1995). This is equivalent to saying that there are no general rules. Black *et al.* (1986) and van Milgen & Noblet (1999) propose the intermediate view that there are differences between genotypes and a general systematic effect of live weight.

The problem of nutrient partitioning in growing pigs has been considered in the reviews of Black & de Lange (1995), Susenbeth (1995), de Greef & Verstegen (1995), Schinckel & de Lange (1996), Emmans & Kyriazakis (1997), Whittemore *et al.* (2001), Moughan (2003a) and van Milgen & Noblet (2003). In no case, were all of

Abbreviations: *L*, mass of lipid; *P*, mass of protein; *PR*, protein retention.

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the proposed solutions described, contrasted and criticised both conceptually and against experimental data in the literature. As well as these reviews, the recent partitioning models proposed by Green & Whittemore (2003), van Milgen & Noblet (1999) and van Milgen *et al.* (2000) are considered here. There is no general agreement on what the rules of partitioning are. We describe first the solutions in the literature and then their ability to solve the partitioning problem is qualitatively assessed. A solution to the problem of partitioning as conventionally posed is needed before more complex situations, such as disease (Lochmiller & Deerenberg, 2000; Coop & Kyriazakis, 2001; Houdijk *et al.* 2001; Powanda & Beisel, 2003), can be properly considered. In a second accompanying paper we assemble and use a comprehensive and suitable set of data from the literature to evaluate quantitatively the various proposed rules (Sandberg *et al.* 2005).

Partitioning rules

The scope of the proposed rules

Any rule of scarce resource partitioning will operate over some range of inputs that may include food, animal and environmental variables. Descriptions of these inputs will therefore be required. These three classes of variables are considered in turn.

Food variables. The level of feeding can be between zero and *ad libitum*. Any rule should cover as much of the range as is possible. While force-feeding is possible it is not considered further here. The assumption usually made, for simplicity, is that no components of the food other than its protein and energy contents are affecting growth (Black *et al.* 1986; Whittemore, 1995). The protein and energy dimensions need clear descriptions that are sufficient for the proposed rule to be implemented.

Possible components of the description of the protein content of a food include the crude protein content (*CPC*, kg/kg) and its digestibility that may be apparent (d_a) or ileal (d_i), (Moughan, 2003*b*). The proportion of protein that is 'ideal' (v), in relation to a chosen reference protein is relevant (Fuller *et al.* 1989; Wang & Fuller, 1989). If the efficiency of retaining the first limiting amino acid differs between amino acids then the first limiting amino acid in the protein also needs to be known.

An energy content of the food (MJ/kg) is needed to turn a food allowance (kg/d) into an energy allowance (MJ/d). There are different solutions to this problem. Whittemore (1983) proposed using digestible energy, *DE*, with correction for the protein content of the food. van Milgen & Noblet (1999) used metabolisable energy, *ME*. Noblet *et al.* (1994) proposed that net energy, *NE*, could be used. Emmans (1994) proposed a scale called effective energy, *EE*, while Birkett & de Lange (2001*a,b,c*) used the 'explicit material flow of ATP'.

Animal variables. Partitioning rules intended to operate across kinds and states of pig need to include adequate descriptions of the animal. The dimensions of the description will include genotype and current state. A sufficient description of current state could include the degree of maturity either as live weight (van Milgen & Noblet, 1999) or as

protein weight (Whittemore & Fawcett, 1976; Whittemore, 1983; Emmans & Fisher, 1986). The description may also include the fatness of the animal and its age. Where live weight is the only state variable used, differences in body protein and lipid proportions cannot be dealt with. Knap *et al.* (2002) proposed that a reasonable body weight range to use would be 10–175 kg; ideally, the range would be from birth to maturity to cover all free-feeding pigs. Pre-natal partitioning of nutrients is not normally considered (Wellock *et al.* 2004).

Environment variables. Any partitioning rule would optimistically have adequate conceptual descriptions of how environmental factors may affect rules of partitioning. Partitioning rules often assume that there are either no environmental effects or, in the case of thermoregulation or activity, that the additional energy requirements can be added to maintenance (Whittemore & Fawcett, 1976; Black *et al.* 1986; Wellock *et al.* 2003).

Proposed rules of nutrient partitioning

Rules of partitioning found in the literature are presented in roughly chronological order.

Rule 1. Whittemore & Fawcett (1974) made protein retention (*PR*) a function of the crude protein content of the food (*CPC*, kg/kg) and food intake (*FI*, kg/d). They made the gross efficiency with which crude protein intake was retained, *Z*, dependent on live weight (*W*, kg) through the general constants *p*, *k* and *f*:

$$PR = FI \times CPC \times Z \text{ (kg/d)} \quad (1)$$

$$Z = p + k \times \exp(-fW) \quad (2)$$

An upper limit to *PR*, here called PR_{\max} , was a characteristic of the kind of pig but was independent of *W*. The amount of energy available after meeting maintenance and that needed for *PR* went to *LR* (lipid retention). The model was assumed to apply for dietary crude protein contents between 120 and 280 g crude protein/kg and $20 < W < 100$ kg. No other limits were stated.

Rule 2a. Whittemore & Fawcett (1976) proposed an alternative expression for *PR* and set a minimum for the ratio of lipid to protein in the gain. Protein retention was predicted from the ideal protein supply (*IP*, g/d) as the product of *FI*, *CPC*, d_a and the biological value of the protein, *v*. equations (8) and (12) in their paper lead to:

$$PR = IP / [(1 - \phi) + (\phi / (s \times (1 - u)))] \text{ (g/d)} \quad (3)$$

The value of $u = P/P_m$ is the degree of maturity in protein, where *P* is the current protein weight and P_m is the mature protein weight. The parameters, $\phi = 0.06$ and $s = 0.23$ were assumed to be constant across genotypes and degrees of maturity. Equation (3) makes the gross efficiency of using *IP* decrease as *u* increases. The gross efficiency is independent of *IP* at a given value of *u*. There are no effects of genotype other than on PR_{\max} as in Rule 1. The value of *LR* is calculated on energy grounds as in Rule 1, but now any demand for cold thermogenesis is met first. A further condition is that a minimum is set for the ratio of lipid to protein in the gain ($LR:PR$)_{min}. This

condition means that the value of LR cannot fall below $(LR:PR)_{\min} \times PR$.

The rules used by Moughan *et al.* (1987) and de Lange (1995) are essentially the same as those proposed by Whittemore & Fawcett (1976). The scope is the same as that of Rule 1 other than allowing the environment to be cold and food protein to vary in quality.

Rule 2b. Whittemore (1995) recognised that setting a minimum ratio of lipid to protein in the gain was an unsatisfactory concept. He proposed two other ratios instead. The first was a 'preferred' value for the ratio of the mass of lipid (L) to that of protein (P) in the body called $(L:P)_{\text{pref}}$. The second was a minimum value for this ratio $(L:P)_{\text{min}}$. The variable $(L:P)_{\text{min}}$ was proposed to 'ensure some level of fatness in the body' and 'to prevent undue use of L for the support of PR '. A value of 0.5 was proposed for $(L:P)_{\text{min}}$. The value for $(L:P)_{\text{pref}}$ was believed to be genotype- and sex-specific. It was not clear whether it varied as the pig grew. When $(L:P) > (L:P)_{\text{min}}$ then the model allows for lipid loss.

Rule 3. Fuller & Crofts (1977) presented an equation that related the scaled nitrogen retention to the protein and starch contents of the food. Differentiation of their equation (9) gives (4) below. The response in nitrogen retention (NR , g/kg body weight^{0.73} per d) per unit starch intake (S , g/kg body weight^{0.73} per d) was related to the intakes of both starch and nitrogen through:

$$dNR/dS = \varepsilon \times \exp(-q S) \times (1 - A \times \exp(-rN)) \quad (4)$$

where N is the scaled nitrogen intake (g/kg^{0.73} per d) and ε , q , A and r are parameters. The values of the parameters, and hence the efficiency of protein utilisation, were said to depend on animal factors including genotype, sex, age and nutritional history.

Rule 4. Black *et al.* (1986) proposed that protein retention was a linear function of metabolisable energy intake (MEI , MJ/d) when MEI was less than that required for PR_{max} . The equations presented were equivalent to:

$$PR = b \times (MEI - (c \times ME_m)) \quad (\text{g/d}) \quad (5)$$

$$b = X_{\text{sm}} \times ((n \times \exp(-yW)) + z) \quad (\text{g/MJ}) \quad (6)$$

where ME_m is the amount of metabolisable energy needed for maintenance. The rate of response, b , depended on W through (6). The values of the parameters n (0.7), y (-0.0192) and z (0.65) were assumed constant across genotypes, sexes, environments and degrees of maturity. Their biological meaning, if any, is not clear. The parameter c is discussed below. The value of X_{sm} depended only on genotype ranging from 0.68 to 1.2. The value of LR was calculated on the grounds of energy balance.

Equation 6 was modified by NRC (1998) to include the effects of different values of the parameter called $MPAR$, the 'mean protein accretion rate over the range of 20 to 120 kg W ' and ambient temperature (T). In addition, the parameters of equation 6 are now related to digestible energy intake, DEI (MJ/d), rather than MEI (hence b' rather than b). The revised equation is:

$$b' = ((17.5 \exp(-0.0192 W)) + 16.25) \times (MPAR/125) \\ \times (1 + (0.015(20 - T))) \quad (\text{g/MJ DE}) \quad (7)$$

The equation is only for energy-limiting foods, but no definition is given of such foods.

Rule 5. Kyriazakis & Emmans (1992a,b) proposed a model that made protein retention, subject to $PR < PR_{\text{max}}$, a function of the ideal protein supply above maintenance (equation 8). The slope of protein retention on ideal protein supply above maintenance is the marginal material efficiency of ideal protein retention, e_p . This was made a linear function of the ratio of energy to protein in the feed (equation 9), subject to an upper limit of e_p^* .

$$PR = e_p \times (IP - IP_m) \quad (8)$$

$$e_p = \mu \times (MEC/DCPC) \quad (9)$$

MEC and $DCPC$ are the contents of metabolisable energy (MJ/kg) and digestible crude protein (kg/kg) in the food used. The values of μ (0.0112) and e_p^* (0.814) were assumed to be constant for all genotypes and degrees of maturity.

Rule 6. de Greef & Verstegen (1995) proposed that, when energy is in short supply, protein is 'adequate' and $PR < PR_{\text{max}}$, an increase in energy supply (DEI , MJ DE/d) is partitioned between marginal increases in protein and lipid retention using a constant marginal ratio (MR). The primary equations are:

$$PR = a + b' \times DEI \quad (\text{g/d}) \quad (10)$$

$$LR = c + d \times DEI \quad (\text{g/d}) \quad (11)$$

From which follows the definition of MR as:

$$MR = d/b' \quad (12)$$

The values of the parameters (a and c , g/d) and (b' and d , g/MJ DE) were seen as varying with genotype and live weight (de Greef & Verstegen, 1995). It is important to note that MR is not a parameter in its own right but is calculated from the values of b' and d .

Rule 7a. van Milgen & Noblet (1999) proposed a model where retention of protein and lipid are calculated from the metabolisable energy supply, when protein is assumed to be non-limiting. The data used for the analysis were assumed by the authors (J van Milgen, personal communication) to come from experiments where the animals were limited only by energy, and not by protein supply. Each extra MJ of metabolisable energy above maintenance is partitioned so that X_i MJ/d goes to protein and $(1 - X_i)$ MJ/d goes to lipid retention (equations 13 and 14). The value of X_i is made a function of live weight (equation 15) with the values of the parameters c_i and d_i , dependent on genotype.

$$PR = k_p \times X_i \times (ME - ME_m) \quad (\text{g/d}) \quad (13)$$

$$LR = k_f \times (1 - X_i) \times (ME - ME_m) \quad (\text{g/d}) \quad (14)$$

$$X_i = c_i + d_i \times (W - 20) \quad (15)$$

The energetic efficiencies with which metabolisable energy is used for protein and lipid retention are k_p and k_f and these may be affected by the nutrient source (van Milgen *et al.* 2000), although it has not been stated how. The values of these two parameters are assumed constant across genotypes and live weights. It is further assumed that at maintenance no protein or lipid is either retained or lost.

Rule 7b. The model defined by Rule 7a was modified by van Milgen *et al.* (2000) to produce Rule 7b. In this model, the parameters that determine the rates of retention of protein and lipid are k_p , k_f , ME_m , PR_{max} and a new parameter, F . F was defined as the (MEI/ME_m) value at which $PR=PR_{max}$. The full set of equations proposed in the Appendix of van Milgen *et al.* (2000) is complex and the equations are not reproduced here. The authors used a set of parameters, different from that used for Rule 7a, for estimation from an extensive set of data on three kinds of pig. The set included k_p , k_f and ME_m as before. The additional parameters were: PR_{max} at both 100 and 150 d of age, B (the Gompertz growth rate parameter), F_{100} (MEI as a multiple of ME_m required to attain PR_{max} at 100 kg of body weight) and dF (the change in F due to a change of 1 kg in body weight). A consequence of the change from Rule 7a to Rule 7b is that PR and LR are now both curvilinear functions of MEI until $PR=PR_{max}$, rather than linear ones.

Qualitative assessment of proposed rules

In this section, the rules will be challenged in turn to identify any conceptual weaknesses. The intention is to identify those areas where rejection is not possible on qualitative grounds. Reasons for qualitative rejection include: dietary protein is not considered in the energy only models; food protein is inadequately described; lipid loss is not possible; the values of many parameters are needed. A partitioning rule that has fewer parameters is preferred to one with more, other things being equal. This is a version of the criterion widely used in science called Occam's Razor (Forster, 2000). Where the number of parameters is large a rule will be rejected for this reason alone. Quantitative tests are in the accompanying paper (Sandberg *et al.* 2004).

Rule 1 uses a description of food protein that is now generally seen as inadequate. The parameter Z predicts a reduction in the *gross efficiency* of protein utilisation, without distinguishing between protein requirements for maintenance and protein retention. While an important first step in the modelling of pig growth it is now only of historical interest and is acknowledged as such by its authors (Whittemore *et al.* 2001).

Rule 2a extends Rule 1 to consider the protein supply as ideal protein and makes the efficiency with which it is used a function of the degree of maturity. The efficiency is still the gross rather than the marginal efficiency. The new proposal of a minimum ratio of lipid to protein in the gain does not permit lipid to be lost while there is a gain in protein. There is strong evidence (Dividich *et al.* 1980; Stamataris *et al.* 1991; Kyriazakis & Emmans, 1992a,b; Bikker, 1994) that this can occur. Therefore Rule 2a (and by implication that of Moughan *et al.* 1987 and de Lange, 1995) are not considered for quantitative analysis.

Whittemore (1995) rejected Rule 2a. He changed from a

ratio of lipid to protein in the gain, to ratios of lipid to protein in the body as a possible constraint to PR to produce Rule 2b. Green & Whittemore (2003) applied the revised approach to a model that also had a maximum allowable rate of lipid loss. The implementation of the rule is, however, such that it becomes, at least in part, the same as that of Rule 2a by setting a minimum ratio of lipid to protein in the gain. Green & Whittemore (2003) state that when the actual ratio of L to P is below that which the pig prefers $(L:P)_{pref}$ 'then the retention of lipid will be given priority over the retention of protein such as to limit PR and achieve in the daily gain a ratio of $LR:PR$ that is set to the same ratio as is set for $(L:P)_{pref}$ '. In addition, Green & Whittemore (2003) have a lower limit for the L to P ratio (D Green, personal communication), which is less than the value of $(L:P)_{pref}$ described by Green & Whittemore (2003) as a limit 'below which the animal was not prepared to go'. The concept of a desired ratio of lipid to protein in the body that may change with degree of maturity (Emmans, 1988), and the lower limit of the ratio of lipid to protein in the body, are shown in Fig. 1.

Green & Whittemore (2003) raised an important issue: what is the maximum *rate* of lipid loss that an animal could undergo at the expense of growing body protein, before protein retention would become penalised in some way? It is widely recognised (Black, 1974; Whittemore, 1995; Emmans & Kyriazakis, 1997; van Milgen & Noblet, 2003) that pigs may lose lipid, while gaining protein. van Milgen & Noblet (2003) stated that the pig is prepared to lose lipid for only a short period of time but do not state what this is. Wellock *et al.* (2003), and Whittemore (1995), set a minimum value for the ratio of protein to lipid in the body. A necessary consequence is that lipid can be lost only when the ratio of L to P exceeds this minimum. Black *et al.* (1986) also recognised that pigs might not want to lose lipid 'indefinitely'. Where a model allows lipid to be lost, which is necessary, it should also set a minimum value for the ratio of L to P .

Rule 3 considers the protein and the energy, as starch, supplied by the diet, but it does not clearly account for

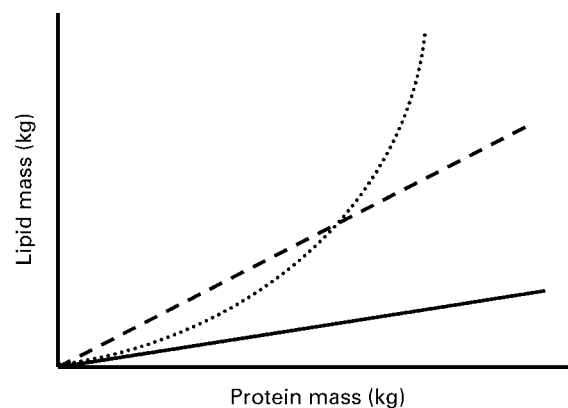


Fig. 1. Possible relationships between protein (P) and lipid (L) masses in pigs. Desired fatness (.....) is described by $L_{des}=a \times P^b$ (Emmans, 1988). The preferred fatness (---) is described by $L_{pref}=(L:P)_{pref} \times P$ and the minimum fatness (—) by $L_{min}=(L:P)_{min} \times P$ (Whittemore, 1995).

maintenance requirements for either protein or energy. However, it raises an interesting issue, as was done by Miller & Payne (1961), that the efficiency of using protein for maintenance might be a function of the energy to protein ratio of the food. In addition, Rule 3 implies that the relationship between any additional amount of energy as starch and the efficiency of protein utilisation is curvilinear, rather than rectilinear as suggested by Kyriazakis & Emmans (1992a,b). While Rule 3 initially calls for the values of only four parameters in order to solve its important equation, these values were stated to be affected by genotype, state, live weight and nutritional history. The practical consequence of this is that each experiment needs to be carried out across all of these factors, possibly in all combinations, in order for the rule to be able to be applied in any given case. An enormous amount of information is needed therefore and, on this ground alone, Rule 3 is not taken forward for quantitative testing.

Rule 4 defines the metabolisable energy needed for a zero rate of energy retention as ME_m . When $ME/ME_m=c$ (Equation 5) then $PR=0$ while LR is negative. No mention is made of any effect of food composition on the value of c , taken as being constant at 0.55. The rule states that the marginal increment in protein retention per extra MJ of metabolisable energy supplied falls with increasing live weight. To apply the rule to any particular genotype needs evaluation of the parameter X_{sm} (Equation 6). As only one parameter is affected by genotype the model cannot be rejected on the grounds of complexity. While the model of NRC (1998) is slightly more complex than that of Rule 4 we did not feel able to reject it for this reason.

Rule 5 takes into account protein for maintenance and the CPC , d_i , v and energy values of the diet. The rule allows the prediction of the transition from the 'protein-limiting' to the 'energy-limiting' phase of protein retention as illustrated by the data of amongst others Campbell *et al.* (1985) and Bikker (1994). The plateau in PR predicted to occur when energy is limiting at high protein intakes is below PR_{max} . The rule predicts this effect by making e_p decline as the $(ME/DCPC)$ value of the diet declines. When the diet is such that lipid retention is predicted to be negative, no upper limit is set either for the rate of lipid loss or to the total loss that can occur. If the model is to be made dynamic then certainly the second of these conditions needs to be changed. This was done by Wellock *et al.* (2003) who set a minimum to the ratio of L to P . Rule 5 asserts that there is no effect of genotype (including sex) or live weight on the values of its parameters. The resulting simplicity means that it cannot be rejected on the grounds of complexity.

The use of the marginal ratio in Rule 6 has, along with Fuller & Crofts (1977), a high parameter requirement. No systematic relationship between the values of the parameters and live weight is proposed. The rule also only deals with the protein content of the food in a way that is poorly defined (see de Greef & Verstegen, 1995). Figure 2 illustrates the concept of the marginal ratio, and is typical of a linear plateau system. It is not possible using Rule 6 to predict whether particular foods or food allowances would be limiting in protein. For this reason, it is not considered further.

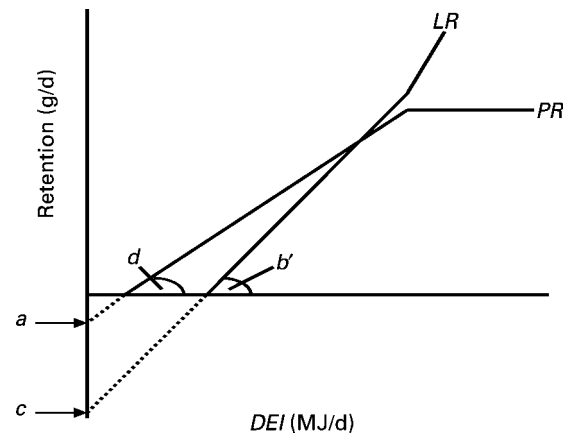


Fig. 2. The relationship between the rates of retaining protein (PR) and lipid (LR) and digestible energy intake (DEI) partitioned according to the marginal ratio (MR) rule; $MR=d/b'$ (de Greef & Verstegen, 1995).

Rule 7a predicts that an animal eating an allowance that provides MEI that equals its maintenance requirement for energy does not lose or gain any lipid or protein. This is inconsistent with the observation that animals often lose lipid at substantial rates while gaining protein (e.g. Dividich *et al.* 1980; ARC, 1981). The rule does not consider protein supply explicitly. The values of the parameters c_i and d_i , which depend on genotype and sex, are used to relate X_i , the partitioning parameter (Equations 13 and 14) to W . The relationship between X_i and W is shown in Fig. 3 for different genotypes and sexes.

The data used to quantify Rule 7a for seven different kinds of pig came from a single level of feeding, 'close to *ad libitum*' of a single food except that two of the genotypes had some extra protein. This must limit the use of the equations in a dynamic model to predict growth for different food allowances with varying concentrations of protein and energy. As the model deals neither with the protein content of the food nor with different levels of feeding (because of the nature of the data used) it will not be discussed further.

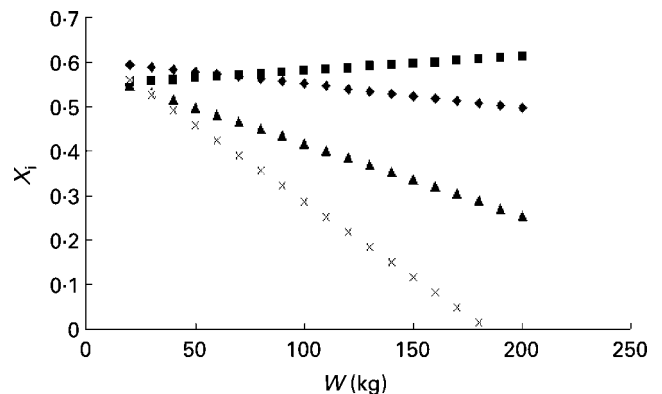


Fig. 3. The relationships between the parameter X_i and live weight (W) for four different genotypes, calculated from the genotype specific values of the parameters given by van Milgen & Noblet (1999): $X_i=c+d_i(W-20)$. The four genotypes are: Synthetic male (\blacklozenge), Pietrain male (\blacksquare), Large White male (\blacktriangle) and Large White female (\times).

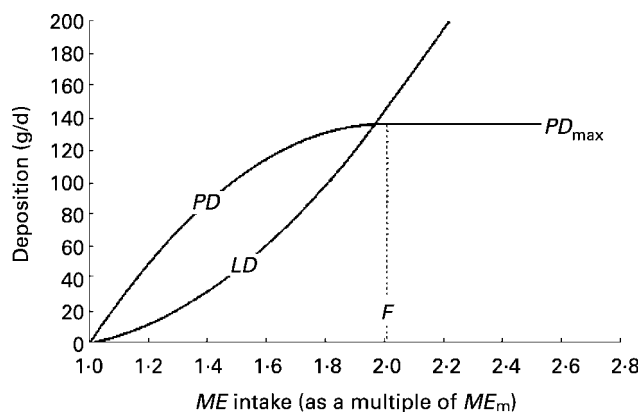


Fig. 4. The relationships between protein deposition (*PD*) and lipid deposition (*LD*) and metabolisable energy intake (*MEI*) as a multiple of that required for maintenance (ME_m), as described by van Milgen *et al.* (2000). *F* is the value of MEI/ME_m at which PD_{max} is reached.

The information needed to use the model described by van Milgen *et al.* (2000), here called Rule 7b, is very considerable. The response in *PR* and *LR* to *MEI* is now different from that shown in Fig. 2 (see Fig. 4).

To describe a kind of pig it is necessary to feed it at different levels at each of several body weights and to measure the rates of lipid and protein retention. The data collected, at least in principle, can then be analysed to yield estimates of the parameters of the model. van Milgen *et al.* (2000) used 145 energy and N balances to estimate the values of the twenty-seven parameters in their full model. The full model was simplified by assuming that the values of three of the parameters were the same for the three genotypes used, leading to a model with twenty-one parameters. The authors do not discuss the fit of the model nor if there were any patterns in the residuals. The values of some of the important parameters were not well estimated. The standard errors of the maintenance coefficients were 25% of the estimates themselves; the standard errors of the Gompertz growth rate parameters were 35% of the estimates of the coefficients.

The information needed to use Rule 7b for any particular genotype, existing in the future, is unlikely ever to be available. The authors state that the *concepts* of Rule 7b may be employed, and adapted, to deal with more complex situations, including disease. However, it would be difficult to take Rule 7b forward, partly because of the information needed and partly because the supply of protein is not explicitly considered; it is not considered further.

Conclusions

The rules of partitioning considered here are usually components of more comprehensive pig growth models (Whittemore, 1983; Black *et al.* 1986, 1995; Moughan *et al.* 1987; Emmans, 1988; Ferguson *et al.* 1997; NRC, 1998; van Milgen & Noblet, 1999; Knap, 2000; Green & Whittemore, 2003; Lovatto & Sauvant, 2003; Schinckel *et al.* 2003; Wellock *et al.* 2003). Models have increased in size and complexity since those of Whittemore &

Fawcett (1974, 1976). Partitioning rules in the literature are now considered.

Rules 1, 2a, 7a and 7b were found to be inadequate, although on different grounds, and will not be considered further. It was not possible to reject the concepts put forward by Rules 2b, 3, 4, 5 and 6 on qualitative grounds. They all raise the issue of the factors that may affect the net marginal efficiency of protein retention. These include live weight, genotype, including sex, and the composition of the food. It is important to establish whether the effects of the animal and the food composition variables are independent of each other, or not.

The position with Rule 6 (de Greef & Versteegen, 1995) is the same in that although only four parameters need to be evaluated initially these are also said to depend on genotype and live weight. Again, an enormous amount of information is needed. As there are other rules that do not appear to have such high requirements for information Rules 3 and 6 will not be quantitatively assessed in the next paper.

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