Partitioning of limiting protein and energy in the growing pig: testing quantitative rules against experimental data

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Literature solutions to the problem of protein and energy partitioning in the growing pig are quantitatively examined. Possible effects of live weight, genotype and food composition on the marginal response in protein to protein and energy intakes, on protein and energy-limiting foods are quantified. No evidence was found that the marginal response in protein retention to ideal protein supply, when protein intake is limiting, is affected by live weight, genotype or environmental temperature. There was good evidence that live weight does not affect the marginal response in protein retention to energy intake when protein intake is not limiting. Limited data for different genotypes suggested no effects on this response. A general quantitative partitioning rule is proposed that has two key parameters; e_p* (the maximum marginal efficiency for retaining the first limiting amino acid) and R* (the maximum value of R, the energy to protein ratio of the food, MJ metabolisable energy (ME)/kg digestible crude protein (DCP), when e_p* is just achieved). When $R < R$* the material efficiency of using ideal protein is $(e_p*/R*) \times R$. The value of e_p* was determined to be 0·763 (SE 0·0130). There was no good experimental evidence that e_p* is different for different amino acids. The best estimate of R* was 67·9 (SE 1·65) MJ ME/kg DCP. Live weight, genotype and temperature did not affect the values of either parameter. A more general understanding of partitioning, including the effects of 'stressors' such as disease, may be achieved by using the preferred rule as a starting point.

Swine: Growth: Partitioning: Protein: Energy

Nutrient partitioning in the growing animal is the distribution of absorbed protein and energy to protein (*PR*) and lipid (*LR*) retention once the requirements for maintenance have been met. In a companion paper, Sandberg *et al.* (2005) described solutions that have been proposed to the problem of the partitioning of scarce resources and criticised these qualitatively. Quantitative tests of the rules that withstood qualitative criticisms (Black *et al.* 1986; Kyriazakis & Emmans, 1992*a,b*; Whittemore, 1995; National Research Council, 1998) are presented here. Black *et al.* (1986) and Kyriazakis & Emmans (1992*b*) deal with the marginal response in protein retention to both energy and protein intake, whichever is scarce. Black *et al.* (1986) proposed that there are effects of live weight and genotype on these responses; Kyriazakis & Emmans (1992*a,b*) proposed that there were not. National Research Council (1998) made the marginal response in protein retention to energy intake depend on body weight (following Black *et al.* 1986), potential rate of protein retention and temperature. Whittemore (1995) proposed a minimum ratio of lipid to protein in the body at which the partitioning rule of an animal may change to conserve body lipid. The value of this minimum ratio, and the factors that might affect it, are also considered here.

The marginal efficiency with which dietary protein supply above maintenance is retained (e_p) is central to the prediction of the rates of retention of both protein and lipid as shown in Fig. 1.

Whittemore *et al.* (2001) recently concluded that the evidence '…would point empirically to a value of [the maximum marginal efficiency, e_p*] of 0·75 to 0·85 but gives scant guidance as to how the prevailing value in any given circumstance may be determined'. It will be shown that the values of e_p and e_p* for particular conditions of food, animal and environment, and estimates of their errors, can be experimentally determined. The work presented here extends the work of Birkett & de Lange (2001) and van Milgen & Noblet (2003) to produce a general partitioning rule for growing pigs.

Protein retention in relation to energy and protein intakes

The response in protein retention to energy intake

Kyriazakis & Emmans (1992*a,b*) made the marginal efficiency of retaining ideal protein (e_p) a function of the
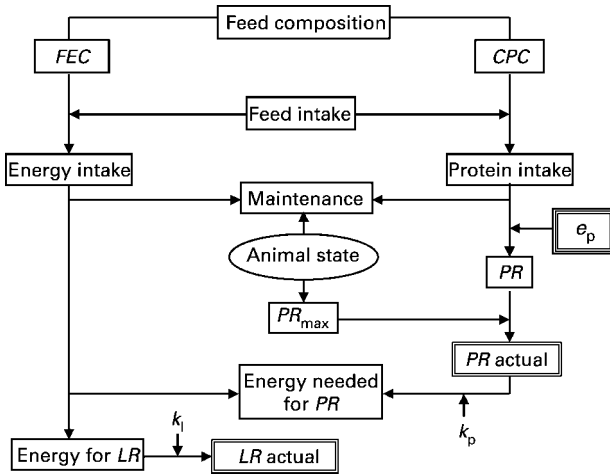

Fig. 1. A schematic representation for predicting actual protein (*PR*) and lipid (*LR*) retentions for a pig eating a food containing energy (*FEC*, MJ/kg) and protein (*CPC*, kg/kg). Energetic efficiencies for *PR* and *LR* are k_p and k_l respectively. The state of the animal determines its maintenance requirements for energy and protein and its maximum rate of protein retention, PR_{max}.

ratio of the metabolisable energy content (*MEC*, MJ/kg) to the digestible crude protein content (*DCPC*, kg/kg) of the food, *R* (MJ metabolisable energy (ME)/kg digestible crude protein (DCP). The proposed relationship was $e_p = \mu R$ with a maximum value for e_p of e_p^* when *R* was above a specific value, R^*. The value of R^* was calculated as 72·55 (SE 1·53), with $e_p^* = 0·814$ and $\mu = 0·0112$ (SE 0·00022). The minimum value of e_p was calculated as 0·2, when all of the energy came from protein. In support, Fuller & Crofts (1977) predict a value of 0·17 for the net protein utilisation when all of the energy comes from protein. The strong assumptions made by Kyriazakis & Emmans (1992*a,b*) were that the values of e_p^* and μ, and hence R^*, were independent of live weight and genotype, including sex. Black *et al.* (1986, 1995), Fuller *et al.* (1995) and de Greef & Verstegen (1995), amongst others, disagree with this position and expect effects of live weight and genotype.

The partitioning rule of Black *et al.* (1986), which is also used by Schinckel & de Lange (1996), NRC (1998) can be summarised as the two equations in Sandberg *et al.* (2005):

$$PR = b \times (MEI - (c \times ME_m))(\text{g/d}) \qquad (1)$$

$$b = X_{sm} \times ((n \times \exp(-yW)) + z)(\text{g/MJ}) \qquad (2)$$

MEI is metabolisable energy intake and ME_m the amount needed for maintenance, MJ/d. The rate of response, *b*, depends on both live weight, *W*, and genotype through the value of the parameter X_{sm}. The values of the other parameters *n* (0·7), *y* (−0·0192) and *z* (0·65) were assumed constant across live weights, genotypes, including sex and environments. Equation 2 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 2 are now related to digestible energy intake, *DEI* MJ/d, rather than *MEI* (hence

b' rather than *b*). The revised equation is:

$$b' = ((17·5 \ \exp(-0·0192W)) + 16·25)$$
$$\times (MPAR/125) \times (1 + (0·015(20 - T)))) \qquad (3)$$
$$(\text{g/MJ DE})$$

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

Where it is the case that $e_p = \mu R$ and $R \leq R^*$, but only then, the two positions described above, one where *PR* is made a function of energy intake and the other where *PR* is made a function of *R*, can be shown to be equivalent (Kyriazakis & Emmans, 1992*a,b*). The second position becomes:

$$PR = b \times MEI - a \qquad (4)$$

The linear coefficient *b* can be shown to be equal to μv, where *v* is the quality (the proportion of digested protein that is ideal) of the dietary protein. Therefore, when in later sections testing the effects of live weight and genotype, including sex on *b*, the value of of μ is also being tested given assumptions about *v* (see below). The supply of energy is here considered as *MEI* as it is consistent with the rules of Black *et al.* (1986) and Kyriazakis & Emmans (1992*a,b*).

The response in protein retention to protein supply

The methodology used in analysing the data for protein (or amino acid) supplies and retentions, are described below. Both the independent variable (intake) and the dependent variable (retention) need clear quantitative descriptions, before a value for e_p can be determined. In addition, the different descriptions of protein (or amino acid) retention and protein (or amino acid) supply also need considering.

Protein retained as a function of the ideal protein supply. The ideal protein supply, *IP* (g/d), is that defined by Moughan (2003). It is calculated as:

$$IP = FI \times CPC \times d_i \times v \qquad (5)$$

FI (kg/d) is the food intake, *CPC* (kg/kg) is the crude protein content, d_i is the ileal digestibility and *v* is the quality of the protein. Ileal digestibility is preferred to faecal digestibility estimates, but may need correction for any endogenous flow of amino acids (Moughan, 2003). The ratio of the first limiting amino acid in the digestible protein, relative to its concentration in the reference protein is *v*.

There is large variation in the estimates of the amino acid composition of the reference protein, which is used to calculate *v* (Table 1). Part of this variation may reflect analytical problems. Moughan (2003) pointed out that 'Modern amino acid analysis is capable of providing data with a within-laboratory repeatability of 5 % or less and a reproducibility between laboratories of around 10 %, but to achieve such results requires careful attention to detail'. A further problem is that the amino acid composition of the reference protein can change with increasing supplies of the particular amino acid (Batterham *et al.* 1990).

Table 1. The amino acid composition of pig body protein from different sources: the consequence of the variation on the calculation of the maximum marginal efficiency of amino acid retention (e_p*) is shown, together with the values of e_p* proposed by Heger et al. (2002, 2003)

	Amino acid composition of pig protein (g/kg crude protein) from different sources†													e_p* calculated from the N retention data of Heger et al. (2002, 2003)‡			Values of e_p* proposed by Heger et al. (2002, 2003)‡
	1	2	3	4	5	6	7	8	9	10	Min	Mean	Max	Min	Mean	Max	
Cystine (C)	–	13	12	9	16	–	10	9	–	13	9	11·7	16	–	–	–	–
Histidine	24	35	27	32	27	26	28	28	36	22	22	28·0	36	0·86	1·09	1·40	1·17
Isoleucine	21	29	37	31	28	32	33	35	37	30	21	31·9	37	0·47	0·72	0·86	0·81
Leucine	56	76	74	67	68	68	74	65	75	71	56	69·5	76	0·69	0·86	0·94	0·81
Lysine	55	60	65	64	63	60	70	66	73	60	55	64·2	73	0·70	0·82	0·94	0·91
Methionine (M)	–	19	19	19	22	–	18	20	–	20	18	19·6	22	–	–	–	–
M + C	–	32	31	28	38	31	28	30	31	33	28	31·5	38	0·78	0·88	1·06	0·85
Phenylalanine (P)	–	39	38	35	36	–	38	35	–	36	35	36·7	39	–	–	–	–
Tyrosine (T)	–	28	25	25	25	–	26	25	–	25	25	25·6	28	–	–	–	–
P + T	49	67	63	60	61	62	64	59	72	–	49	61·9	72	0·55	0·70	0·81	0·67
Threonine	30	39	40	38	34	36	38	36	39	34	30	36·9	40	0·67	0·82	0·93	0·83
Tryptophan	–	7	8	–	–	8	8	–	11	12	7	9·1	12	0·59	0·77	1·01	0·66
Valine	36	40	51	41	41	44	47	44	50	44	36	44·2	51	0·67	0·82	0·95	0·82

† Sources: 1, Siebrits et al. (1986); 2, Moughan & Smith (1987); 3, Campbell et al. (1988); 4, Batterham et al. (1990); 5, Kemm et al. (1990); 6, Chung & Baker (1992); 7, Kyriazakis et al. (1993); 8, Bikker et al. (1994a); 9, Mahan & Shields (1998); 10, Wu et al. (1999).
‡ Heger et al. (2002, 2003) presented linear regression equations of responses of N retention to increasing amino acid supply. The value of e_p* was calculated as ((slope × 6·25)/1000) × proportion of amino acid in pig protein.

The marginal material efficiency, e_p, is defined as:

$$e_p = PR/(IP - MP) \qquad (6)$$

In the cases where e_p was calculated rather than determined by regression of PR on IP the ideal maintenance requirement (MP) was calculated as $0.004P$ where P is the protein weight of the pig calculated as $0.16W$.

The response in inferred amino acid retention to amino acid supply. For the ideal protein concept to be valid, all amino acids have to be used with the same efficiency, when they are first limiting. Boisen et al. (2000), who recently reviewed the definitions and applications of the ideal protein concept, did not mention this necessary assumption. It has been challenged by Heger et al. (2002, 2003), who proposed that amino acids were retained with different efficiencies, when first limiting. Whittemore et al. (2001) agreed with the above view that 'there may be differences in the efficiencies of utilization of amino acids'.

Heger et al. (2002, 2003) did not measure the retention of each amino acid, but calculated it indirectly from the measured nitrogen retention. It was assumed that all protein retained had the amino acid composition reported by Bikker et al. (1994a), except for tryptophan where the value was taken from Kyriazakis et al. (1993). The amino acid composition of whole body protein has been reported by several authors as shown in Table 1. The variation between authors is substantial. The data of Heger et al. (2002, 2003) for amino acid supply and protein retention were combined with the amino acid compositions of body protein shown in Table 1 to estimate a possible range in e_p*.

The values for e_p* calculated by Heger et al. (2002, 2003) fall within the range presented, and agree on average with the mean (0·83) across the amino acids (Table 1). However, for any one amino acid the uncertainty about its value for e_p* is substantial. Given this uncertainty, which arises from the different estimates of the composition of body

protein, it is not justified to use the data of Heger et al. (2002, 2003) to conclude that the maximum efficiency of amino acid retention is different for different amino acids. It may therefore be possible to use a single overall efficiency for all amino acids whichever is first limiting, and this is discussed further below.

Testing the rules with experimental data

The effect of live weight, genotype and environmental temperature on the marginal response in protein retention for protein- ($R > R$*) and energy- ($R \le R$*) limiting foods are now considered. This definition of protein- and energy-limiting foods was chosen, as it was the only quantitative one present in the literature. For example, de Greef & Verstegen (1995) recognise the necessity of defining 'protein adequate foods' but do not give a quantitative definition.

Preferred tests would be experiments that consider defined protein and energy supplies across live weights, genotypes and environments. Foods with a wide range of protein concentrations given at several allowances would be needed. The experiments in the literature that most closely matched these conditions for protein- and energy-limiting foods are now considered in turn.

The marginal response in protein retention to protein supply in protein-limiting foods

Effects of live weight. Black & Griffiths (1975) concluded that there was no difference in the marginal response in nitrogen retention to nitrogen intake of liquid-fed lambs at live weights between 5 and 25 kg. The response in pigs was estimated from PR and crude protein intake (CPI) CPI g/d the data of Campbell et al. (1984), 45–90 kg, and Campbell et al. (1985a), 20–45 kg. The regression equations presented by the authors were $PR = 0.382\,CPI - 11.15$, for the 20–45 kg pigs, and $PR = 0.425\,CPI - 17.8$, for the 45–90 kg pigs.

The lower value of the slope for the smaller pigs can be attributed to the fact that only the protein retained in the carcass was analysed. If 0·9 of total protein is in the carcass then it would be expected that the coefficient for the whole body would be 0·382/0·90=0·424, which is not different from that found for the 45–90 kg pigs. These data thus give no reason to suggest that the marginal response will change with live weight.

Other experiments also suggest that live weight does not have an effect on the marginal response of protein retention to a limiting protein supply. de Lange *et al.* (2001) investigated the marginal response in threonine retention to ileal digestible threonine intake and found no difference at live weights of 40 and 75 kg. The retention of threonine was inferred from the assumed threonine composition of protein retention (determined in a sub-set of the animals on trial). The value of the net threonine efficiency was calculated as 0·734 (SE 0·0111).

Mohn *et al.* (2000) found no effect of live weight (45 and 70 kg) on the marginal response in inferred lysine retention to ileal digestible lysine intake. The efficiency was stated as 0·75 with no estimate of error. The combined data of the two experiments of Bikker *et al.* (1995, 1996) for 20–45 kg and 45–85 kg pigs do not reject the idea that live weight affected the marginal efficiency. Susenbeth (1995) also concluded that the marginal response in protein retention to limiting protein supply was not affected by live weight.

Campbell & Dunkin (1983a) found a high response in nitrogen retention to nitrogen intake ($R > R*$) for pigs from 1·8 to 6·5 kg, the lowest range possible for postnatal animals. The regression equation of nitrogen retention on nitrogen intake had a slope of 0·880 (SE 0·05). However, this high estimate is an exception. Campbell & Dunkin (1983b) used pigs from 7 to 19 kg, after weaning. Their marginal response was a lot lower at 0·616 as was its standard error of 0·011. It is possible that technical difficulties in measuring nitrogen balance in very small pigs, and the presence of the disease (rotavirus) reported by the authors, led to the high estimate found by Campbell & Dunkin (1983a). It alone is not seen as sufficient to reject the findings of the other experiments that live weight does not affect the marginal response in protein retention when $R > R*$.

Effects of genotype including sex. Kyriazakis *et al.* (1995) used entire male Large White × Landrace and pure Chinese Meishan pigs. The estimated values of e_p* were 0·785 and 0·760, respectively (SED 0·032). Fuller *et al.* (1995) used different breeds including Duroc, purebred Large White and the three sexes of a commercial hybrid, over the 40–85 kg weight range. Two foods with either 149·1 or 206·1 g crude protein/kg food were given in three allowances. The data of Fuller *et al.* (1995) where $PR < PR_{max}$ are shown in Fig. 2.

Fuller *et al.* (1995) concluded that 'the results indicate that an animal's superiority may result from a greater efficiency of protein utilisation or a higher lean growth potential but that these two characteristics are not simply related'. A different interpretation of Fig. 2 is possible. There is one data point for the commercial hybrid female that cannot be explained and is clearly indicated on the graph; it was omitted from the analysis here. The slopes
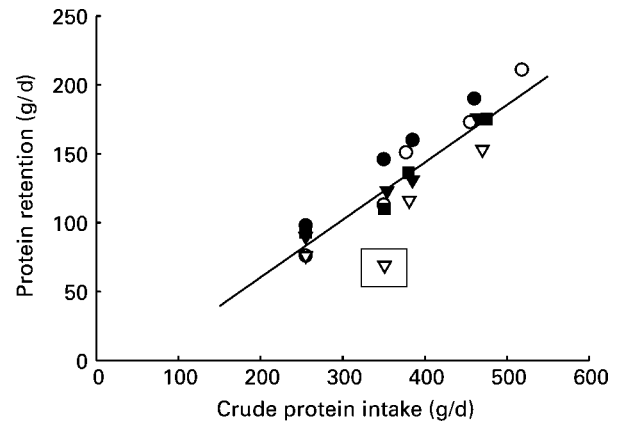

Fig. 2. Protein retention (*PR*, g/d) is plotted against crude protein intake (*CPI*, g/d), for the five kinds of pig: Duroc (●), Large White males (○), commercial hybrid males (▼), commercial hybrid females (▽) and commercial hybrid castrates (■) used by Fuller *et al.* (1995). Data points that were clearly part of a plateau were omitted; an outlier is shown in the square box. The regression line is $PR = 0.417(CPI - 55.4)$, which has the common slope and the average intercept.

for the five genotypes were not significantly different ($P > 0.1$). The common slope, shown in Fig. 2, was 0·417 (SE 0·025). The conclusion of Fuller *et al.* (1995) may thus be challenged.

In support of no effects of genotype is the experiment of de Greef *et al.* (1992) who gave a commercial (S1) and a sire (S2) strain of pigs the same, one limiting level of protein from a food where $R > R*$. The pigs retained 42 and 43 g protein/d, respectively. The experiment does not support the idea that pigs with greater PR_{max}, which was determined in the experiment as 187 g/d for S1 and 153 g/d for S2, have different values for e_p*.

There is evidence that different sexes of pigs use a limiting protein supply with similar efficiency. Campbell *et al.* (1984, 1985b) found no difference in e_p* between entire males and females. The genetic maximum for protein retention was greater for males in agreement with Black *et al.* (1995). The data of Batterham *et al.* (1990) are shown in Fig. 3; they lend strong support to this conclusion. Kyriazakis & Emmans (1992a,b) did not find any effect of sex on e_p*.

It would appear safe to conclude from the above experiments that different genotypes (including sex) do not use a limiting protein supply, with different marginal efficiencies, when $R > R*$.

Effect of temperature. Models of growth that consider environmental temperature, e.g. Black *et al.* (1986) and Wellock *et al.* (2003a), assume that temperature does not have an effect on the marginal response in protein retention on protein-limiting foods. No evidence is presented in support of this assumption. Campbell & Taverner (1988) grew pigs from 9 to 20 kg at 14 and 32°C. The slopes of protein retention on crude protein intake were 0·524 (SE 0·013) and 0·485 (SE 0·013), respectively, which are not significantly different ($P > 0.2$). Ferguson & Gous (1997) grew pigs fed *ad libitum* from 13 to 30 kg on foods with 93–230 g crude protein/kg at 18, 22, 26 and 30°C. The data (Fig. 4) show clearly that the marginal response in protein
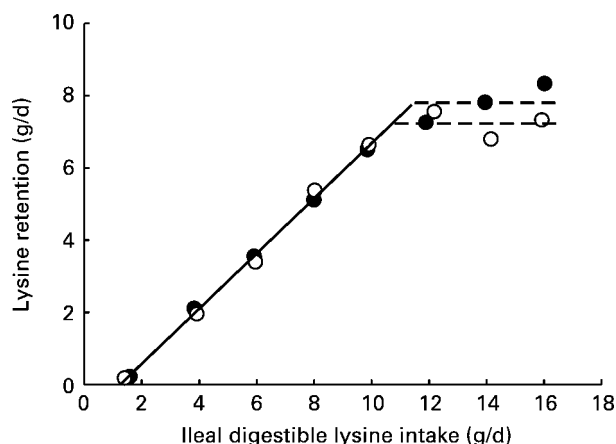
Fig. 3. Response in lysine retention (R_{lys}, g/d) to ileal digestible lysine intake (I_{lys}, g/d): the regression line is $R_{lys}=0.763(I_{lys}-1.245)$ for the combined data of male (●) and female (○) Large White (20−45 kg) pigs used by Batterham *et al.* (1990). Separate plateaux for males and females are shown.

retention, 0·525 (SE 0·015), was not affected by temperature when $R > R^*$.

In support of these experiments is that of Berschauer *et al.* (1983) who kept young pigs at 22°C and then 10°C and did not find an effect on the marginal response in nitrogen retention to nitrogen intake. Hence, it would appear safe to conclude that temperature does not affect the marginal response in protein retention when the protein supply is limiting.

The marginal response in protein retention on energy-limiting foods

The following sections consider the effects of genotype, live weight and temperature on the response in protein retention to energy intake for foods where $R \le R^*$. The conclusions of Mohn & de Lange (1998) are considered first.

Mohn & de Lange (1998) presented a table (their Table 5) with twenty estimates of b (where $PR=b \times MEI - a$)
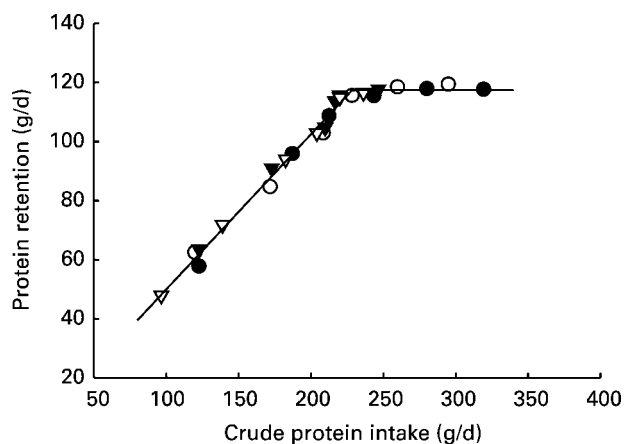

Fig. 4. The response in protein retention to crude protein intake for pigs fed *ad libitum* foods that were limiting in protein at four different temperatures: 18°C (●), 22°C (○), 26°C (▼) and 30°C (▽) as found by Ferguson & Gous (1997). The solid line is described by $PR=0.525(CPI-4.92)$ until the plateau of 117·4 g/d is reached.

across different genotypes and live weights. Although it cannot be guaranteed that all experiments that they analysed had values of $R \le R^*$, a necessary condition for $b=\mu v$, their mean value of b was 6·2 (SD 2·3) g protein/MJ ME. In none of the three experiments where the effect of live weight was directly estimated (de Greef & Verstegen, 1993; Quiniou *et al.* 1995; Mohn & de Lange, 1998) was there any indication of systematic change in the value of b with live weight. Across the twelve experiments on males (from their Table 5) the correlation between b and W was $r=0.23$ ($P=0.465$). There was an indication, across experiments, that the mean value for castrates (3·97, n 3) was lower than that for females (5·16, n 5), which was lower than that for males (7·17 (SE 0·64), n 12). With μ estimated as 0·0112 (Kyriazakis & Emmans, 1992a,b) the value of b would be expected to be 7·84, when $v=0.70$, and 10·08 when $v=0.90$.

The rule of Black *et al.* (1986) predicts that b will reduce with live weight towards an asymptotic value that is dependent on genotype. Black *et al.* (1986) presented values for the genetic partitioning parameter X_{sm}, which is defined in equation 2: 'X_{sm} has a value of 1·2, 1·0 and 0·78 for entire males, females and castrates of the fast growing genotype and corresponding values of 1·0, 0·85 and 0·65 for a slow growing genotype'. When the value of the genetic parameter $X_{sm}=1.2$ the value of b falls from 10·0 ($W=1$ kg) to 5·0 ($W=250$ kg) g protein/MJ ME. With $X_{sm}=0.65$ the equivalent change in b is from 5·4 to 2·7 g protein/MJ ME.

NRC (1998) adapted the approach of Black *et al.* (1986) and made the response of PR to energy intake depend on genotype, through the value of $MPAR$ and W (equation 3). Across four genotypes ($MPAR=100, 125, 150, 175$ g/d), and W varying between 20 and 120 kg, the predicted mean estimate of b was 5·94 g protein/MJ ME. The experiments that are relevant tests of the effects of live weight, genotype and temperature on the value of b are now considered.

Effect of live weight. Quiniou *et al.* (1995) performed nitrogen balances at 45, 65, 80 and 94 kg. The pigs were given four levels of feeding, all of which provided a constant high supply of protein (420−450 g crude protein/d). The treatments may be viewed either as measuring the response in PR to MEI or as a means of seeing how e_p varies with R. The common slope b across live weights was 8·85 (SE 0·63). Fitting a model that allowed different slopes (7·39, 8·88, 10·23 and 8·23 at 45, 65, 80 and 90 kg, respectively) at each weight gave no statistical improvement ($P>0.5$). In a similar experiment (48, 64, 79 and 94 kg) on three kinds of pigs, Quiniou *et al.* (1996) concluded, 'the stage of growth had no significant effect on [b]'.

Mohn *et al.* (2000) gave pigs six levels of energy intake at two levels of protein at both 45 and 75 kg. Protein retention is plotted against MEI in Fig. 5 with the two highest levels of MEI excluded in all four cases because PR could have reached PR_{max} on these treatments. The common slope for the two weights was 7·18 (SE 0·53) g protein/MJ ME. Allowing different slopes did not improve the fit of the model ($P>0.5$).

Dunkin & Black (1985) presented estimates of b, for pigs of a range of live weights (30, 46, 74 and 90 kg) that were fed eight levels of an energy-limiting food. The values of b were
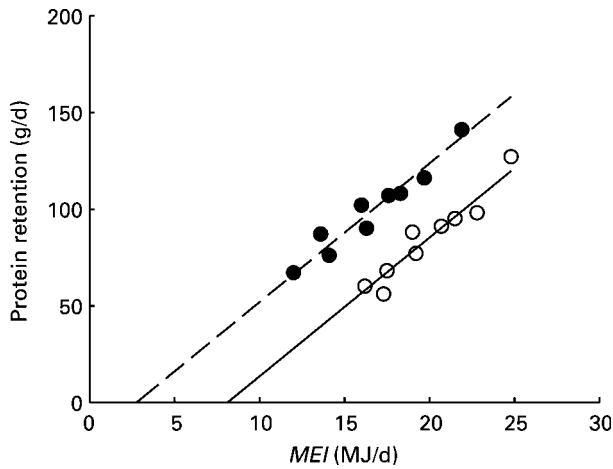
Fig. 5. The response in protein retention (*PR*, g/d) to metabolisable energy intake (*MEI*, MJ/d) at two live weights (● 45 and ○ 75 kg) as found by Mohn *et al.* (2000). The regression lines were fitted with a common slope and different intercepts: $PR = 7.18(MEI - 2.77)$ for the 45 kg pigs (− −) and $PR = 7.18(MEI - 8.12)$ for the 75 kg pigs (—).

presented as g nitrogen retention/MJ ME without estimates of error. Expressed as g protein/MJ ME the slopes were 8·25, 6·44, 5·75 and 6·75, respectively. These estimates do not support a systematic change in the value of *b* with increasing live weight as is suggested by Black *et al.* (1986) and NRC (1998). Campbell & Dunkin (1983*a*) performed an experiment with very small pigs (1·8–6·5 kg). The food can be seen as energy limiting with $R = 56.3$ MJ ME/kg DCP. The value of *b* was determined here by regression as 7·61 (0·31), which is not different from the value for the 90 kg pigs of Dunkin & Black (1985) or that for the 75 kg pigs of Mohn *et al.* (2000). The evidence, taken as a whole, is thus consistent with the view that the marginal response in protein retention on energy-limiting foods does not vary with live weight.

Effect of genotype including sex. Kyriazakis *et al.* (1994) gave pure Chinese Meishans and Large White × Landrace pigs a high protein basal food that was diluted with starch to different extents to give a range of values of *R* (33–119 MJ ME/kg DCP). The allowances were such that *PR* was below PR_{max} for both genotypes. The authors concluded that 'the calculated efficiency of protein utilization, e_p, was found to be directly proportional, up to a maximum value, to the ME:DCP ratio of the diet for both breeds...'. The overall constant of proportionality was

0·0108 (SE 0·00024), the value of which did not differ significantly between the two breeds. The values of *b*, determined here by linear regression from three treatments where a linear response to additions of starch (energy) was observed, were 9·93 (SE 2·55) and 9·65 (SE 0·16) for the Large Whites and Chinese Meishans. These did not differ significantly ($P > 0.4$).

The experiment of Quiniou *et al.* (1996) used three genotypes, boars (bPPx) and castrates (cPPx) of a Large White × Pietrain breed and castrates of a Large White breed (cLW). The response in *PR* (determined by nitrogen balance) to four levels of energy intake at a constant high protein intake was considered at four live weights. Quiniou *et al.* (1996) concluded that the response in protein retention to increasing supplies of metabolisable energy intake above maintenance, ME_p (MJ/d), was independent of live weight, but did depend on genotype. The values of *b* for the bPPx, cPPx and cLW pigs were 6·0, 4·0 and 3·4 (g/MJ), respectively, with no standard errors given.

However, in the regressions of Quiniou *et al.* (1996) of *PR* on ME_p the intercept was fixed by the authors at 64 g/d for all three genotypes. Here a model with a common slope that allowed different intercepts for the three genotypes was also tested. It is not possible to distinguish between the two models from a formal statistical point of view as is shown in Table 2. The variation seen in this data set may partly be attributed to different foods being used for each genotype.

When considering the data where *PR* is plotted against ME_p it is difficult to decide whether a particular point belongs to a positive response or to the plateau. This problem is present in the data of Quiniou *et al.* (1996) and J van Milgen (personal communication). The data for the individual Pietrain castrates are in Fig. 6, in which the linear regression is shown. The value of the regression coefficient, estimated assuming that there was no plateau, was 4·223 (SE 0·648). Using the method described below the same data were used to estimate the values of the parameters of the linear–plateau model that is also shown in Fig. 6. The linear–plateau model gave a better fit, but not significantly so. The value of the linear coefficient was 4·815 (SE 0·862), which was 1·14 times as great as the estimate where no plateau was allowed.

Effects of temperature. Neither the model of Black *et al.* (1986) nor that of Wellock *et al.* (2003*a*), who consider the effects of temperature, assume that temperature has any effect on the marginal response in protein retention to

Table 2. The response in protein retention, *PR* (g/d), to the metabolisable energy available for production, ME_p (MJ/d)†

Model	df	RSS	RMS		*b*	SE		*a*	SE
I	141	48125	341	cPPx	3·81	0·38		85·5	6·05
				(cPPx − bPPx)	1·61	0·24			
				(cPPx − cLW)	−1·07	0·22			
II	141	48030	341		4·06	0·38	cPPx	80·90	6·83
							(cPPx − bPPx)	24·36	3·80
							(cPPx − cLW)	−17·67	3·80

df, residual degrees of freedom; RSS, residual sums of squares; RMS, residual mean square.
† The regression is $PR = a + b \times ME_p$. Two different models were fitted to the data of Quiniou *et al.* (1996), for three pig genotypes (cPPx, bPPx and cLW). Model I, used by Quiniou *et al.* (1996), fitted a common intercept but allowed different slopes for each genotype. Model II used a common slope that allowed different intercepts for each genotype. The differences in the slopes (Model I) and intercepts (Model II) compared to cPPx are shown here.
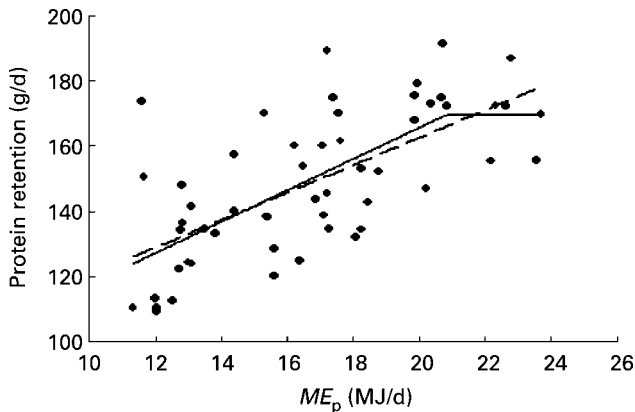
Fig. 6. The response in protein retention (*PR*, g/d) to metabolisable energy intake above maintenance (*ME*$_p$, MJ/d) for the individual Pietrain castrate pigs (Quiniou *et al.* 1996; J van Milgen, personal communication). The linear regression (– –) and the linear–plateau model (—) are both shown.

energy intake on protein-adequate foods. However, NRC (1998) states that the marginal response to energy intake on protein-adequate foods falls as temperature increases (equation 3). The argument follows from the experiment of Close *et al.* (1978). There are two problems. The first is that the food used was probably limiting in protein (*R*=86·6 MJ ME/kg DCP). The second is that, even when interpreted as an energy experiment, the data are far from persuasive that the response varied with temperature (Fig. 7).

There appears to be no experiment where *MEI* has been varied at different temperatures, using energy-limiting foods (*R* < *R**). In the absence of any evidence to the contrary it is provisionally concluded that there are no effects of temperature on the marginal response in protein retention to energy-limiting foods. An experiment to test this conclusion is warranted.

The testing performed here supports the view that there are general partitioning rules where the marginal response in protein retention to protein- or energy-limiting foods is independent of live weight, genotype and temperature.
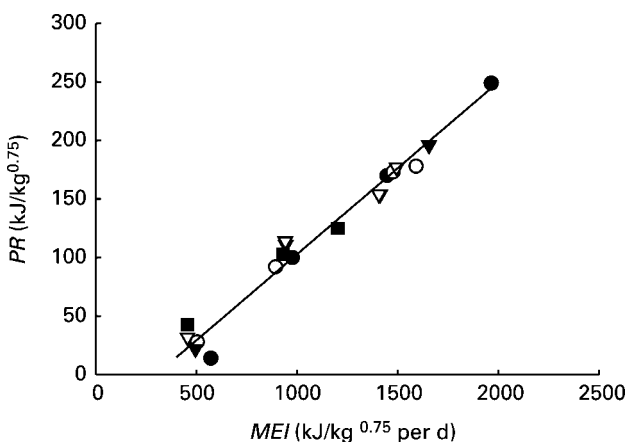

Fig. 7. The response in protein retention (*PR*, kJ/kg$^{0.75}$ per d) to metabolisable energy intake (*MEI*, kJ/kg$^{0.75}$ per d) for pigs given different allowances of the same food at five different temperatures from Close *et al.* (1978): 10°C (●), 15°C (○), 20°C (▼), 25°C (▽), 30°C (■). The regression line for all the data is *PR*=0·147 (0·0062)*MEI* − 44·07 (7·58).

The questions that remain from the testing are considered in the discussion. Attempts are now made to determine the values of the key partitioning parameters.

The estimation of the values of the parameters e_p^*, μ and R^*

The general rule $e_p = \mu R$ requires two of its three partitioning parameters to be determined, from which the third can be calculated. The statistical methodology for determining R^* and e_p^* is first described, after which the parameter estimates are given.

Statistical methodology

Two kinds of regression were performed. The response in protein or amino acid retention to protein or amino acid intake was examined by eye. Where it was judged to be linear over the range below any visible plateau, set either by energetic or genetic limits, a standard linear regression was performed. The other regression used was for a continuous linear–plateau model. This was used to describe the relationship between e_p and R (equation 8).

A linear–plateau model for e_p has a constant derivative for $e_p < e_p^*$ and 0 for $e_p > e_p^*$. Fitting such a function in a statistical software package is not straightforward. However, the important parameter R^* needs determining with estimates of its error. For this reason the derivative of the plateau model was approximated by the continuous function:

$$A(e_p) = 0.5\,\mu \times (1 + \tanh \times [w(R - R^*)]) \qquad (7)$$

For large values of w, $A(e_p)$ converges to μ for $R < R^*$ and to 0 for $R > R^*$. This equation can be integrated to yield equation 8, which is a good approximation of the linear–plateau model.

$$e_p = e_p^* + 0.5\,\mu R - 0.5/w \times \mu(\ln(\cosh(w \times R^*)) + \ln(\cosh(w(R - R^*)))) \qquad (8)$$

The continuous approximation of a linear–plateau model (equation 8) was fitted in the statistical software Sigmaplot version 7·0 (SPSS Inc., Chicago, IL, USA). This permitted estimation of the values of the slope (μ), the break point (R^*) and the maximum marginal efficiency (e_p^*) with their errors. Sigmaplot uses the Marquardt–Levenberg algorithm for least squares estimation of the parameters (Marquardt, 1963). The parameters are assigned initial estimates from which the best estimates are determined by the least squares method from 100 iterations. The larger the value of w the more abrupt the transition between the linear part and the plateau part of the relationship. This approach is preferred to an alternative approach, piecewise, linear regression, where again the slope of the second phase is constrained to zero (Hudson, 1966).

Parameter values

The determination of the value for e_p^* in some experiments has relied by necessity on assumptions about digestibility, protein quality and protein requirements for maintenance.

The approach to determine e_p* with a minimum amount of assumption is done by regressing determined ileal digestible amino acid intake on determined amino acid retention when $R > R$*. This assumes that the ileal digestibility is representative of the 'truly' available amino acid.

Surprisingly few experiments were found in pigs that considered the response in ileal digestible amino acid intake to a large range of amino acid supplies, where above-mentioned dimensions were measured. The experiments that are used here to estimate the value of e_p* are those of Batterham *et al.* (1990), Chung & Baker (1992) and Bikker *et al.* (1994*b*). The response of Chung & Baker (1992) was at three levels of methionine intake, while Batterham *et al.* (1990) used eight levels of lysine and Bikker *et al.* (1994*b*) used fifteen levels of lysine. The results of the regressions of amino acid retention on ileal digestible amino acid intake are presented in Table 3.

The determined values for e_p* in Table 3 are overall lower than that proposed for e_p* by Kyriazakis & Emmans (1992*a,b*) of 0·814. The slightly lower value for methionine may be because Chung & Baker (1992) took the ileal digestibility of methionine to equal unity from a companion experiment and the authors did not give any estimate of error of the parameter estimates. The residual of Bikker *et al.* (1994*b*) is much higher than that of Batterham *et al.* (1990).

The estimate of Batterham *et al.* (1990) is taken as the best with a value of e_p* of 0·763 (SE 0·0130). The lower estimate of Bikker *et al.* (1994*b*) of 0·699 (0·0384) was not as well estimated and is not significantly different. The experiments of de Lange *et al.* (2001) considering threonine (e_p*, 0·73 (SE 0·011)) and Mohn *et al.* (2000) considering lysine (e_p*, 0·75) are in support of this estimate. In addition, the value for e_p* determined by the continuous linear–plateau regression for the combined data of Kyriazakis & Emmans (1992*a,b*) and Kyriazakis *et al.* (1994) for two genotypes and two sexes was 0·783

(SE 0·0112), not significantly different from the value of Batterham *et al.* (1990). The values of μ, R* and e_p* for these experiments are shown in Table 4.

The value of R* from the continuous linear–plateau regression of the combined data (Table 4) is similar to the above values and was equal to 67·9 (SE 1·65). Then, taking the best estimate of e_p* from the experiment of Batterham *et al.* (1990), permits calculation of the slope μ as 0·763/67·9 = 0·0112.

Therefore, the best parameter estimates are: e_p* = 0·763 (SE 0·0130) and R* = 67·9 (SE 1·65) with the subsidiary parameter μ estimated as 0·0112. These estimates are seen as applying across live weight, genotype (including sex) and temperature. Partitioning rules, which permit loss of lipid, require another parameter that sets the lower limit to the pigs' lipid content.

The lower limit to body fatness in pigs

It is a necessary condition for a partitioning rule that permits loss of lipid when protein retention is positive to have some lower limit for the amount of lipid that can be lost (Sandberg *et al.* 2005). Whittemore (1995) stated that 'there may be postulated a value for $(L:P)_{min}$, a crisis value below which the metabolic system may experience trauma'. A value for $(L:P)_{min}$ of 0·5 was proposed. However, it was recognised that the value could be lower (Whittemore, 1995). Green & Whittemore (2003) state that the value of $(L:P)_{min}$ is likely to be dependent on genotype, but did not give the values. Green & Whittemore (2003) also have an absolute minimum fatness defined as $0·05W$. Wellock *et al.* (2003*a*) stated 'that an animal cannot lose lipid that is not present, and must have some minimum lipid content (L_{min}) necessary for survival'. They proposed that the minimum value was $0·1P$, where P is the protein mass in the body, which is conceptually equivalent to $0·05W$ as proposed by Green & Whittemore (2003).

The lower limit to a pig's lipid content, of relevance to a partitioning rule, is the ratio of lipid to protein at which the pig reduces its rate of protein retention to maintain its lipid content. This may be due to the limit for the biological structures of the pig (Wellock *et al.* 2003*a*: $0·1P$) or some higher limit (Whittemore, 1995: $0·5P$). It is not clear whether these ratios depend on either live weight or genotype. Experimental data where the rates of retention of protein and lipid were measured at low body lipid to protein ratios would help to decide this point. The food would need to be sufficient in protein to ensure that the animal was only limited in energy.

Table 3. The regression of amino acid retention (g/d) on ileal digestible amino acid supply (g/d) from three sources (all diets had more than 83 MJ metabolisable energy per kg digestible crude protein)

Source†	Slope	SE	Intercept	SE	Residual SD (g/d)
1	0·763	0·0130	− 0·950	0·0850	0·121
2	0·699	0·0384	2·536	6·438	3·55
3	0·717		− 0·041		NA

† Sources: 1, Batterham *et al.* (1990) for lysine; 2, Bikker *et al.* (1994*a*) for lysine; 3, Chung & Baker (1992) for methionine.

Table 4. The response in the efficiency of retaining ideal protein, e_p, to the ratio of metabolisable energy to digestible crude protein (R, MJ ME/kg DCP) in the food, estimated by the continuous linear–plateau model†

Source‡	Genotype	n	R	μ	SE	e_p*	SE	R*	SE	Residual SD
1	Large White × Landrace	40, 44	43−125	0·0138	0·0015	0·795	0·0151	67·8	2·10	0·0566
2	Large White × Landrace	23	33−119	0·0103	0·0014	0·709	0·0185	64·8	3·30	0·0452
3	Chinese Meishan	25	33−119	0·0145	0·0013	0·822	0·0168	70·2	2·65	0·0443
All	Both	132	33−125	0·0131	0·0009	0·783	0·0112	67·9	1·65	0·0582

μ, Regression coefficient of e_p on R; e_p*, plateau value for e_p; R*, the value of R at which e_p reaches e_p*.
† For details of the continuous linear–plateau model, see p. 218.
‡ Sources: 1, Kyriazakis & Emmans (1992*a,b*); 2, Kyriazakis *et al.* (1994); 3, Kyriazakis *et al.* (1994).

Campbell & Dunkin (1983*a*) performed a similar experiment to that preferred. Pigs between 1·8 and 6·5 kg were given four allowances of a food that contained 359 g crude protein/kg DM and 25·4 MJ gross energy. At the lowest allowance of food, the pigs were retaining 24 g/d of protein, and the marginal response was linear in relation to the protein supply. The ratio of lipid to protein in the body was 0·29*P*. This suggests the estimate of Whittemore (1995) to be too high as an estimate of the minimum ratio of lipid to protein in the body.

Close & Stanier (1984) determined that newborn pigs (1·34 kg) had a ratio of 0·23*P* and stated that these pigs grew normally up to weaning. It is therefore not possible to reject the ratio of 0·1*P* proposed by Wellock *et al.* (2003*a*). The above values suggest that the minimum ratio may be less than 0·23*P*–0·29*P*. The question that remains is whether this ratio is different for genotype and/or live weight.

Discussion

The rules of partitioning proposed by Black *et al.* (1986), Kyriazakis & Emmans (1992*a*,*b*) and Whittemore (1995) withstood the qualitative criticisms in the companion paper (Sandberg *et al.* 2005). The problem raised is the marginal response in protein retention to limiting protein or energy supplies for different genotypes at different live weights (Black *et al.* 1986; Kyriazakis & Emmans, 1992*a*,*b*). In models which predict lipid loss coupled with protein gain it is necessary to define the ratio of lipid to protein in the body at which the pig reduces its rate of protein retention to maintain the lipid content (Whittemore, 1995).

It has been discussed here and elsewhere that *b*, the slope of *PR* on *MEI*, is equal to μv, given that $R < R^*$. The distinction between the approach where $e_p = \mu R$ and the approach where $PR = b \times MEI$, is made by R^*. This was not recognised by van Milgen & Noblet (2003) who stated in relation to $e_p = \mu R$ '…as this function intersects the origin, the approach is essentially similar to a linear–plateau function between energy intake and *PD* [protein deposition]'. The view that there is considerable real variation in the value of *b* (e.g. de Greef & Verstegen, 1995; Schinckel & de Lange, 1996; van Milgen & Noblet, 1999) can be explained, at least in part, by the variation in the energy to protein ratios of the food. In addition, some of the variation in *b* may be attributed to variation in calculating *v* from variation in amino acid compositions of food and pig proteins, which may either actually exist, or, may arise from differences in analytical methods (Moughan, 2003).

There is a significant amount of evidence suggesting that live weight does not have an effect on the marginal response in protein retention to protein- or energy-limiting foods. The evidence for no effect of genotype was not as abundant. The data reviewed here suggest that it is safe to assume that different genotypes have the same marginal responses to protein- and energy-limiting foods. Temperature does not appear to affect the marginal responses in protein retention to protein-limiting foods. In the absence of evidence no conclusions could be drawn for energy-limiting foods. The questions that remain unresolved and some possible experiments that could address these questions are considered below.

The overall conclusion of the analysis done here is that the rule of Black *et al.* (1986) and its modified form (NRC, 1998) does not agree as well with literature data as the general rule of Kyriazakis & Emmans (1992*a*,*b*). The parameters of the rule were determined as e_p^* (0·763 (SE 0·013)), R^* (67·9 (SE 1·65)) and μ (0·0112). For modelling purposes and future experiments, it is useful to identify general rules. The partitioning rule in this case is general as its parameters are independent of genotype, live weight and temperature, which increases the flexibility of using a rule within larger models. In addition, as the rule is seen as general it may be useful for investigating the partitioning of scarce resources during times of disease and/or social stress (as discussed below).

A difficulty in determining parameter values for models that aim to predict the response of an individual animal is that experimental data usually come from experiments on more than one animal. Even if a linear–plateau model correctly represents the response of any individual at a time, it is still possible that a population of animals will have a response that is curvilinear (Fisher *et al.* 1973) at a time. Curnow (1978) has described the underlying mathematics. Ferguson *et al.* (1997) and Pomar *et al.* (2003) have applied similar arguments to populations of growing pigs. In addition to the variation between individual pigs at a time possibly causing curvilinearity, there is also the effect of each of the individuals changing with time (Pomar *et al.* 2003). Fuller & Garthwaite (1993) attempted to describe the responses of individual pigs experimentally and presented parameter values for linear–plateau and exponential models for individual animals. The authors concluded that the exponential model was to be preferred, but there were problems with the statistical analyses and with the way in which protein retention was scaled to live weight, to take out period effects.

It may be useful to consider experimentally the marginal responses of different genotypes, at both very low and high live weights, to help to solve the problem raised by one set of data (Campbell & Dunkin, 1983*a*) on very small pigs. To determine the effect of live weight on the maximum efficiency of protein retention, the energy to protein ratio of the food would need to be greater than 67·9 MJ ME/kg DCP and it would be necessary to ensure that $PR < PR_{max}$ on all treatments. To assess the effects of live weight on R^* and μ a range of energy to protein ratios above and below 67·9 MJ ME/kg DCP would be needed.

There may be effects of temperature on the partitioning rule used by pigs for energy-limiting foods. This could not be assessed here, as suitable data were not identified. The effect of temperature should be assessed for pigs kept in environments that are cold, thermoneutral or hot for a pig of a particular genotype and state (Wellock *et al.* 2003*a*). The estimation of e_p^*, R^* and μ, and quantification of the parameters of the energy system used, would strengthen the test of any partitioning rule in such a situation.

The value of the maximum material efficiency of protein (amino acid) utilisation is a debated area (Whittemore *et al.* 2001). The assumption that has been made here is for the same value to be used for the material efficiency of using

all amino acids that constitute 'ideal' protein. There appears to be a lack of evidence of sufficient detail (such as Batterham *et al.* 1990) for the estimation of e_p^* for different amino acids in pigs. A large range of values for the maximum material efficiency of protein (amino acid) utilisation has been proposed for pigs ranging from 0·55 (Susenbeth, 1995) to 0·94 (Leibholz, 1985). However, in both these cases e_p^* was calculated using a number of assumptions. The experimental data from the poultry literature are in support of a much narrower range. Baker (1991) concluded from poultry and murine literature that different amino acids are used with different efficiencies. However, he also concluded that 'utilisation efficiency of individual dietary amino acids varies around the 76 % figure [taken from Velu *et al.* 1971], with slow-turnover amino acids such as lysine being used more efficiently (80 %) than fast-turnover amino acids such as isoleucine (61 %)'.

Recent experimental data in poultry suggest smaller differences. The values for e_p^* were lysine 0·76 (Edwards *et al.* 1999), valine 0·73 (Baker *et al.* 1996), threonine 0·82 (Edwards *et al.* 1997) and methionine 0·68 (Edwards & Baker, 1999). The methodology used was similar to that of Batterham *et al.* (1990), although the true digestibility of the crystalline amino acids used was assumed as 100 % from another experiment. The mean of the above estimates is 0·75, which is not different from our proposed best estimate, 0·763, and the central value of 0·76 proposed by Baker (1991).

There is not complete agreement for the estimates of e_p^* for the different amino acids from the pig and poultry literature. In pigs the estimate for threonine of 0·734 (de Lange *et al.* 2001) is very similar to that for methionine of 0·717 (Chung & Baker, 1992). In poultry the estimate for threonine of 0·82 (Edwards *et al.* 1997) was very much greater than that of 0·68 for methionine (Edwards & Baker, 1999). Rather than the difference between amino acids truly varying between species it is likely that all of these four estimates do not differ from each other. Their mean does not differ from 0·763 taken here for e_p^*. It may be useful to experimentally determine the maximum efficiency of amino acid utilisation in pigs (and poultry) using a standardised procedure. The standardised procedure would include attempts to minimise the variation of amino acid analysis (Moughan, 2003), ensure that $R > R^*$ and to implement a range of amino acid supplies that is similar to that of Batterham *et al.* (1990).

It is necessary for the chosen partitioning rule to have a complementary constraint to the loss of lipid to maintain positive protein retention. Wellock *et al.* (2003*a*) proposed a value of $0 \cdot 1P$ calculated on biological grounds of what the lowest amount of lipid in a biological structure may be. This is taken forward, but it is possible that this would be too low an estimate. The selection for lean genotypes at higher weights may have reduced the 'desired ratio' of lipid to protein in the body at a protein weight (Emmans & Kyriazakis, 2000). This may increase the likelihood that pigs of an improved genotype will meet the minimum ratio at a faster rate than those of an unimproved genotype. Experiments may be warranted to explore the value of the minimum ratio across different genotypes.

The general rule of Kyriazakis & Emmans (1992*a,b*) which considers both available protein and energy supplies is preferred to other rules of partitioning considered here and in the companion paper (Sandberg *et al.* 2004). The partitioning of scarce resources is of current interest in relation to stressors such as disease (Lochmiller & Deerenberg, 2000; Coop & Kyriazakis, 2001; Houdijk *et al.* 2001; Powanda & Beisel, 2003) and social stress (Wellock *et al.* 2003*b*). It is useful to have a general rule as a starting point to consider any effects of disease or social stress. The values of the key parameters e_p^* and R^* may be explored experimentally in relation to such stressors to further explore scarce resource partitioning. The particularly relevant stressor is that of pathogen challenges as there is a current lack of such information. Therefore, it may be useful to determine the value of e_p^* as done by Batterham *et al.* (1990) and R^* in relation to the exposure of pigs to different pathogens to further our understanding of resource partitioning in such circumstances. The pathogens considered should include bacteria, viruses and parasites of a range of challenge doses to permit comparisons to be made of these. Challenge with pathogens may increase body temperature, stimulate the immune response and require resources to be directed towards the repair of damaged tissues. In addition, challenge with a pathogen may reduce the voluntary food intake (Kyriazakis *et al.* 1998).

The purpose of this and the companion paper (Sandberg *et al.* 2005) was to describe the partitioning problem, identify solutions, and then criticise these qualitatively and quantitatively. It has been possible to choose a general rule which, when combined with an energy system, permits prediction of protein and lipid retention from protein and energy supplies. General rules are useful for models of growth as they permit models to expand and consider new areas of research. The work done here will contribute to future considerations of scarce resource partitioning and growth modelling in the pig. Future work will include quantitative descriptions of the infectious environment on scarce resource partitioning.

Acknowledgements

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