Technical review of the energy and protein requirements of growing pigs: protein

C. T. Whittemore[1]†, D. M. Green[1] and P. W. Knap[2]

[1]*University of Edinburgh, Agriculture Building, West Mains Road, Edinburgh EH9 3JG, UK*
[2]*PIC International Group, PO Box 1630, D-24826, Schleswig, Germany*

† E-mail: c.t.whittemore@ed.ac.uk

Abstract

A review of work reported in the literature was used to present quantitative descriptions of protein use in the growing pig. These are detailed in the text, which also points to preferred values, and to anomalies and lacunae. The review was prepared with the objective of allowing from its content the inclusive and quantitative modelling of amino acid requirement. Requirement was approached as the sum of the component factors: maintenance and protein retention. Ileal true digestible protein and amino acid requirements are presented in a form consistent with that forwarded for energy. Thus both energy and protein elements can be conceptualized within a single coherent framework. Priority uses for absorbed amino acids were assumed to be (a) to support endogenous protein losses resultant from the passage of food and incomplete re-absorption prior to the terminal ileum, (b) to replace lost hair and skin, and (c) to cover the basic maintenance losses which will occur as a result of minimal protein turn-over even when protein retention is zero. The bulk of the protein requirement was directly linked to the daily rate of protein retention, for which the linear-plateau response was accepted. For determination of the maximum rate of protein retention the Gompertz function was proposed, although the use of a single value throughout the growth period was not dismissed. The balance of amino acids for protein retention is specified as different from that for maintenance. Central to the approach was the proposal that the inefficiency of use of ileal digested ideal protein, even when not supplied in excess, was an expression of protein losses occurring as a result of protein turn-over. The requirement for the satisfaction of the losses from protein turn-over occurring as a consequence of protein retention, and therefore additional to the requirements for maintenance, was identified. Quantification was attempted with sufficient success to warrant its inclusion into requirement estimation. It was concluded that this element addressed previously inadequately explained protein utilization inefficiencies. Algorithms are presented based upon protein turn-over which appear to be consistent with empirical findings.

Keywords: *nutrient requirements, pigs, protein.*

Introduction

The gross utilization of nitrogen (N) by pigs in the European economy has recently been comprehensively reviewed by, amongst others, Dourmad *et al.* (1999). Two-thirds of the N consumed by pigs is excreted in faeces and urine. This is not only a measure of nutritional shortcomings, but also an embarrassment to the European Union target maximum application rate of 170 kg/ha (Whittemore, 1995) and the control of ammonia emissions into the atmosphere. More than a quarter of these losses may be attributed to a failure to maximize production and to optimize efficiency by the correct matching of dietary protein quantity and quality to that required by the pig as it grows.

The provision of nutrients to animals comprises three steps: the yield of nutrients from feedingstuff substrates, the animal's requirement for nutrients and the response of the animal in terms of nutrient

retention and excretion. This review addresses the middle of the three elements, nutrient requirement, with a view to approaching a methodology for the recommendation of nutrient allowance.

The ileal digestibility of protein and of amino acids is taken as the basis of protein supply to the body, because nitrogenous compounds absorbed posterior to the terminal ileum are considered as not contributing significantly to the protein economy of the pig (Seve and Hess, 2000). Substantial amounts of amino acids remaining in the tract posterior to the terminal ileum do disappear from the caecum and colon due to metabolism by the hind-gut flora. But there is no effective absorption of amino acids from the hind gut and the nitrogen (N)-containing moieties disappearing do so as simple compounds such as ammonia. So only those amino acids digested from the small intestine are taken as able to serve any useful purpose in the satisfaction of nutrient requirement. Absorbed but unusable N moieties, arising in the blood stream from the hind gut, do however create a demand for their active excretion.

As values for apparent digestibility of amino acids are affected by level of intake and by diet characteristics, and include the endogenous faecal losses which appear in the faeces together with the indigestible protein fraction, the apparent digestibilty values for dietary amino acids are unlikely to be additive. True, or 'standardized', ileal digestibility values are therefore likely to be the more useful descriptors of feedingstuffs (Boisen and Moughan, 1996; AmiPig, 2000; Boisen, 2000; Mosenthin *et al.,* 2000; Seve and Hess, 2000). The standardized ileal digestibility values will be higher than the apparent digestibility values, according to the levels of endogenous losses sustained. Employment of standardized (or true) ileal digestible values for foods necessitates that the endogenous losses of amino acids from the gut not remaining associated with the diet and accounted within the standardized digestibility value (that is, the most part) are fully accounted for in the estimation of requirement. The rate of endogenous secretion is itself dependent upon the amount of protein (and fibre) in the gut. Seve and Hess (2000) discuss the appropriate dietary conditions for the determination of levels of endogenous loss.

Proteins are manufactured by the pig from 20 amino acids. Nine of these cannot be synthesized within the body of the animal itself and are therefore designated as essential elements of the diet. The essential amino acids are; lysine, methionine, threonine, tryptophan, isoleucine, leucine, histidine, phenylalanine and valine. Given sufficient methionine, cysteine can be synthesized by the animal; and similarly for tyrosine in the presence of sufficient phenylalanine. Arginine is not essential for the growing pig above 20 kg, and the other non-essential amino acids which can be synthesized in the body of the pig are alanine, aspartic acid, asparagine, glutamic acid, glutamine, serine, glycine, and proline.

Losses occurring at maintenance

Protein requirements for maintenance arise from the need to make good losses from the gut tissue, from the skin, and in urine. These may be expressed in terms of the amounts of amino acids balanced in the manner required to make good the loss. This balance is termed 'ideal protein' (IP) and relates closely to the amino acid composition of the tissue lost but also takes into account any differential efficiency there may be amongst amino acids in either the processes of their excretion or of their replacement (Agricultural Research Council (ARC), 1981; Riis, 1983a). The relative importance of differential efficiency amongst amino acids remains unclear (Moughan, 1999) but would bring about differences between the amino acid composition of the 'product' for which ideal protein is required and the amino acid composition of the requirement for ideal protein. Total losses (IP_m) comprise the sum of losses from the gut (IP_g), skin (IP_s) and in urine (IP_u).

Some 100 to 350 g of endogenous protein may enter the gut of the growing pig daily and of this some 0·2 to 0·3 may escape re-absorption. Factors affecting the final losses of endogenous protein from the gut are reviewed by Nyachoti *et al.* (1997). According to Moughan (1999), losses from the gut surfaces arising as a result of the passage of food and escaping re-absorption are around 20 g protein per kg dry food ingested. This value is affirmed by Mosenthin *et al.* (2000) and the review of Black (2000). Fan *et al.* (1995) suggest a range of 10 to 30 g endogenous protein exiting the ileum per kg dry-matter (DM) intake. Nyachoti *et al.* (1997) indicate values of 12 to 52 g per kg DM intake. On semi-synthetic diets Tullis *et al.* (1986) recorded a lower value of 8·1 g. As endogenous secretions rise to the challenge of dietary protein and fibre, measurement with synthetic or depleted diets are likely to be faulted. Higher values result from more fibrous diets but, as the mechanisms are unclear, a regression function on the basis of diet fibre content appears unsafe.

Gut losses of protein of endogenous origin also arise from intestinal epithelium cells and secretions returned to the gut semi-independently of 'physical food effects' but connected with the digestive processes. Most of these elements will again be re-

Table 1 *Amino acid composition of protein (g amino acid per kg protein) lost from the gut (terminal ileum), skin, and in urine from basal turn-over at protein equilibrium (maintenance). Adapted from Moughan's (1999) review of various sources, and Mahan and Shields (1998). The final column is from the balance of amino acids to lysine = 100 given by NRC (1998) if 65 g lysine per kg protein is assumed*[*]

Amino acid	Moughan (1999) From gut	Moughan (1999) From skin and hair	Moughan (1999) From turn-over	Mahan and Shields (1998) In non-carcass tissues	Mahan and Shields (1998) In blood	NRC (1998) For maintenance
Lysine	54	43	66	66	90	65[*]
Methionine	23	10	19			18
Cysteine	31	45	13			
Methionine plus cysteine				29	23	80
Tryptophan	23	9	10	13	15	17
Histidine	21	12	28	28	56	21
Phenylalanine	40	29	38			33
Tyrosine	56	18	25			
Phenylalanine plus tyrosine				71	97	79
Threonine	46	32	38	36	37	98
Leucine	60	50	75	71	130	45
Isoleucine	36	24	34	35	13	49
Valine	63	36	45	49	90	44
Others	547	690	609			

absorbed in the course of normal digestion, but that which escapes has been calculated from various sources by Moughan (1999) to be 0·57 g protein daily per $W^{0.75}$, where W is live body weight, in kg. There are likely to be significant effects of intestinal disease upon the rate of endogenous loss but the level of the effect is unknown. The suggested balance of amino acids is given in Table 1. Endogenous protein losses are high in methionine, cysteine and threonine, and this argues for a greater proportion of these amino acids in the protein requirement for maintenance (Boisen *et al.*, 2000).

Moughan (1989) estimated losses from the outer surfaces of the pig in the form of skin and hair to be some 0·1 g protein daily per $W^{0.75}$. The suggested balance of amino acids is given in Table 1.

Losses occur as nitrogenous compounds in the urine primarily as a result of the inefficiency associated with the basal level of turn-over of body tissue protein occurring when the animal is in protein balance. (Urinary N output increases in the face of disease challenge, and it has been suggested that urinary losses may increase by the equivalent of 1 g protein per $W^{0.75}$ (N. S. Jessop, personal communication)). Fuller (1980), and Buttery and D'Mello (1994) suggest that at maintenance the daily turn-over of total protein in healthy animals is some 16 g per $W^{0.75}$. Whittemore and Fawcett (1976) working from Millward *et al.* (1974), and Riis (1983b) from a variety of sources, (and also see Reeds (1989)) indicate a value of around 0·05 of the total protein

mass (Pt). The efficiency of recapture is presumed high at 0·94; thus losses may be derived as 0·96 g protein per $W^{0.75}$ and 0·003.Pt daily for the two methods respectively. The estimate calculated by Moughan (1999) from this source is for 0·89 g protein per $W^{0.75}$. There is little difference in these three estimates for pigs of <60 kg but the use of the three-quarter power (rather than unity) reduces the value at higher live weights. Whittemore *et al.* (1978) and Tullis *et al.* (1986) measured 3·90 and 3·96 g N lost daily in the urine of 50-kg pigs maintained in N equilibrium. This is equivalent to a loss of 1·31 g protein per $W^{0.75}$. Interpretation of the data reviewed by Carr *et al.* (1977) gives 0·94 g protein daily per $W^{0.75}$. National Research Council (NRC, 1998) assumes for maintenance 0·036 g lysine daily per $W^{0.75}$. The requirement for lysine may be translated into that for the replacement of lost protein using the presumption of 65 g lysine per kg protein (Fuller *et al.*, 1989), giving a lower estimate of 0·55 g protein per $W^{0.75}$. As this paper will go on to place protein turn-over at the centre of protein requirement calculation, there may be justification for deriving maintenance need (additional to those at gut level) from protein turn-over. As discussed later, because the rate of turn-over is dependent upon the rate of protein retention, it will be necessary to differentiate between the minimum requirement for maintenance (at zero retention) and the effective requirement occurring during active growth.

In comparison to the amino acid balance suggested for protein retention, that for making good losses

occurring at maintenance is importantly elevated with respect to methionine plus cysteine, threonine, and perhaps tryptophan. For the balance of amino acids required to replace maintenance losses occurring as a result of tissue protein turn-over, the tissue analysis of Kyriazakis *et al.* (1993) (Table 3) is germane.

Description of the rate of protein retention from 20 to 120 kg live weight

The net requirement for balanced amino acids is the sum of the requirement for maintenance (IP_m) and for protein retention (IP_{Pr}). The target rate for protein retention (Pr) may be discretionary. More generally however, for the production of meat from growing pigs, it is presumed that target Pr will be the maximum available (Pr_{max}). The reason for this is that lean meat is both the most desirable and the most economical tissue to retain in the whole body growth. The level of protein retention attained in practice will inevitably fail to reach the potential (Pr_{max}). The shortfall will be dependent, *inter alia*, upon feeding and housing management, and (perhaps most importantly) upon the level of disease. Pr attained will therefore be highly farm specific (Morel *et al.*, 1993). The importance of disease in reducing food intake, reducing the attainable rate of Pr, increasing maintenance costs, and increasing excretion rates has been stressed (amongst others) by Black *et al.* (1995 and 1999). These authors suggest chronic disease to increase maintenance by proportionately 0·30 and reduce Pr_{max} by proportionately 0·10. However, what is most evident is the lack of quantitative data in this area.

It has been argued that Pr will increase linearly with increasing supply of IP in the presence of adequate energy (ARC, 1981), with no evident limit. The form of the response of protein retention to nutrient supply was revisited in a series of experiments reported by Bikker (1994). Kielanowski (1969) and Rerat (1972) proposed a maximum to the value for Pr, dependent upon sex and genotype. The presence of an upper limit (Pr_{max}) leads to the linear/plateau model of Whittemore and Fawcett (1976) for protein retention in response to increased nutrient supply. The linear/plateau model has been well supported by subsequently obtained experimental results, and is generally accepted for both the determination of nutrient requirement and the building of simulation models. This may be verified by (amongst others) the reviews of Black *et al.* (1986), Stranks *et al.* (1988), de Greef and Verstegen (1995), de Lange (1995), NRC (1998), Moughan (1999), Schinckel (1999), Quiniou *et al.* (1999), and van der Peet-Schwering *et al.* (1999). Kielanowski (1969) and Rerat (1972) proposed a single value for Pr_{max} over the 20-120 kg live weight

range. For purposes of practical nutrition this proposal has the present support of Mohn and de Lange (1998). However, linearity can not be generally applied, as values are necessarily infeasible for heavier pigs that must decrease their maximum rate of protein retention (ultimately to zero) as they approach mature size. A number of functions may be argued to describe the relationship between Pr (presumptively Pr_{max}) and the increasing live weight of the pig (Thompson *et al.*, 1966). These include: allometry (Huxley, 1932), quadratic and cubic polynomials (NRC, 1998); Bridges, Richards and augmented allometric equations (Schinckel and de Lange, 1996; Schinckel, 1999; Wagner *et al.*, 1999); and the Gompertz equation (Emmans, 1988; Whittemore *et al.*, 1988; Emmans and Kyriazakis, 1999). The present authors conclude that for purposes of predicting practical expectations for Pr_{max} as a function of live weight, the single value (linear) and the Gompertz functions are both suitable; although each not without significant limitations. The Gompertz can adequately describe both the phase of linear growth and the diminishment in potential protein retention as maturity is approached. In the case of the linear function; $Pr_{max} = a + b(W)$, the slope is presumed not significantly different from zero, and the constant expresses the daily rate of protein retention over the live-weight range. In the case of the Gompertz function, $Pr_{max} = W.B.\ln(A/W)$, A is the mature weight, W the present weight and B the growth coefficient. Pr_{max} varies as a function of live weight over the range, and is zero at maturity. The peak rate of protein deposition occurs at A/e, thus the curve rises more steeply in early life than it declines later. Significantly, van Milgen *et al.* (2000), in full knowledge of the alternatives available, opted to describe Pr_{max} as a Gompertz function of live weight. NRC (1998) recognized that, by definition, Pr_{max} could only be approached, and never measured, and recommended that nutrient requirement be calculated with respect to achieved rates for Pr as determined on farm. The notion of 'operational' on-farm values for Pr_{max} (and their means of measurement) had been forwarded earlier by Morel *et al.* (1993). The thinking of NRC (1998) in this regard is peerless, as discussed below. Unfortunately, the choice of the cubic polynomial as the curve to fit farm-collected data is faulted (Whittemore, 2000).

For the determination of the requirement for IP_{Pr} it now remains only to declare a single value for Pr_{max} in the case of the linear assumption, or values for A and B in the case of the Gompertz. It is assumed that for a given data set the single value for Pr_{max} by linear analysis will be similar to the highest value for Pr_{max} at A/e when the Gompertz is employed

Table 2 *With respect to the equation $Pr_{max} = Pt \cdot B_p \cdot \ln(A_p/Pt)$; values for B_p (the growth coefficient), A_p (the mature weight of protein tissue (Pt_{max}) in the whole live body), and $B_p.A_p/e$ (the highest value for Pr_{max} which occurs at 0·37 of mature protein weight), suggested by Whittemore (1998) for meat pigs*

		B_p	$A_p(Pt_{max})$	$B_p.A_p/e(Pr_{max})$
Utility	entire male	0·0105	37·5	0·145
	female	0·0100	35·0	0·130
	castrated male	0·0095	32·5	0·115
Commercial	entire male	0·0115	42·5	0·180
	female	0·0110	40·0	0·160
	castrated male	0·0105	37·5	0·145
Improved	entire male	0·0125	47·5	0·220
	female	0·0120	45·0	0·200
	castrated male	0·0115	42·5	0·180
Nucleus	entire male	0·0135	52·5	0·260
	female	0·0130	50·0	0·240
	castrated male	0·0125	47·5	0·220

(Whittemore *et al.,* 1988). Measured values for Pr_{max} presently range from 0·1 to more than 0·2 kg/day (for example, see Kielanowski, 1969; Whittemore *et al.,* 1988; Rao and McCracken, 1991; van Milgen *et al.,* 2000).

As is evident, the determination of the nutrient requirement for protein has at its kernel the declaration of a value for Pr_{max} (ARC, 1981; Stranks *et al.,* 1988; NRC, 1998). This value may be surmised from; results of experiments in which Pr was measured under unlimiting nutritional conditions, knowledge of performance of the genotype in question under controlled test conditions, or from use of an inverted model. The literature is well supplied with guideline values according to breed, degree of 'improvement', and sex (for example, see Table 2).

Such guidelines are useful for approximation, for tuition, and for the diagnosis of suspected performance failure in European 'white' pig types. They do not however form a proper basis for accurate and quantified provision of nutrient requirement in practice. For this, Pr should be measured directly. B_p values of 0·009 to 0·012 have been found recently in experimental pigs, and found to be sex and genotype dependent (see van Milgen *et al.,* 2000). The present authors therefore recommend the evaluation of Pr in nucleus breeding stocks by chemical analysis of the final carcass and the release of the values determined to those whose responsibility it is to provide for the nutrient requirement of the slaughter generation. For on-farm measurement, the approach of NRC (1998) is

recommended (but not their choice of equation), whereby carcass protein content is estimated from commercially available slaughter data.

Requirement for protein retention

The primary requirement is for balanced amino acids (IP) to resource the daily rate of protein retention (Pr). This requirement, IP_{Pr}, is conventionally taken to be similar in amino acid balance to that found in the retained tissue; there being little expectation of differential efficiency of retention in body protein amongst the amino acids. Pr and IP_{Pr} may also be presumed synonymous by definition, thus the satisfaction of Pr (kg/day) may be achieved by the provision of equivalent quantities of IP_{Pr}. While an essential amino acid is limiting, response to increasing increments of the limiting amino acid may be assumed to be linear, as was found by Susenbeth *et al.* (1999). The presumed balance of essential amino acids in ideal protein for protein retention according to a number of authorities is given in Table 3. A notable discrepancy is in level of phenylalanine + tyrosine suggested by Boisen *et al.* (2000) compared with the whole-body content determined by Kyriazakis *et al.* (1993). There may be differences in the amino acid profiles of different body parts, and of muscles deposited at different rates (see Moughan, 1999) but exact quantification is not yet feasible. It should not be assumed that the balance of the amino acids in retained protein is the same as that needed in the requirement for ideal protein to satisfy that retention, as there may be differences in the efficiencies of utilization of amino acids. Thus, for example, the suggested ratio of tryptophan to lysine

Table 3 *Amino acid composition of protein (g amino acid per kg protein) required for purposes of satisfying the daily rate of protein retention*

Amino acid	ARC (1981)	NRC (1998)[1]	Close and Cole (2000)	Kyriazakis *et al.* (1993)[3]	Mahan and Shields (1998)[4]	Boisen *et al.* (2000)
Lysine	70	70[2]	70[2]	72	76	70
Methionine	18	19	20	18		18
Cysteine				10		
Methionine plus cysteine	35	39	39		30	36
Tryptophan	10	13	14	8	11	12
Histidine	23	22	23	31	37	25
Phenylalanine	34	42	39	38		40
Tyrosine				26		
Phenylalanine plus tyrosine	67	65	81		68	80
Threonine	42	42	47	38	40	45
Leucine	70	71	78	74	71	80
Isoleucine	38	38	41	35	39	40
Valine	49	48	55	47	47	52
Arginine		34			65	

[1] Using the values of Fuller *et al.* (1989), together with various reports from Baker and his co-workers.
[2] NRC and Close and Cole give the balance in relation to lysine = 100. A value of 70 g lysine per kg protein is assumed (NRC, 1998).
[3] Composition of whole body protein in growing pig.
[4] Composition of the carcass.

approaches 0·2 in ideal protein, but is little more than half this in tissue. Empirically determined estimates of the amino acid composition of ideal protein may also differ from that deduced from the amino acid composition of the product; simply because the former, being empirical, is necessarily influenced by many interactions and variables occurring at the time of measurement.

Provision of IP_{Pr} will not satisfy the full requirement for ideal protein to achieve any given level of protein retention. Milligan and Summers (1986), Moughan (1989) and Knap (1995) present clear evidence from a number of sources (see also Reeds and Fuller (1983)) to the effect that there is a relationship between total body turn-over rate and the rate of protein retention. If this is accepted, then Pr will accumulate additional requirement to support losses from protein turn-over over and above those counted within the context of maintenance. This important argument is introduced into requirement estimation procedures by Moughan (1989) and further elaborated by Moughan (1999). Turn-over losses resulting from Pr (IP_{Pto}) will be expected to appear as urinary-N losses.

The provision for replacement of protein lost as a result of protein turn-over above maintenance (IP_{Pto}), is dependent upon a reasonable estimate of protein turn-over. Edmunds and Buttery (1980) estimated 0·465 kg of whole body protein synthesis in actively growing pigs of 25 kg live weight (approximately

4·0 kg total body protein) which were retaining 0·092 kg protein daily. The estimate of whole body protein turn-over may be divided between the more rapidly cycling viscera and the less rapidly cycling muscle mass. And although the ratio of these two fractions will change with pig weight, such sophistication would be unwarranted given present understanding, and whole body turn-over assumptions will be used. Riis (1983b) estimates the growing pig to turn over 0·14 of the total body protein mass (Pt) daily. The review of Reeds (1989) suggests some 0·10. As suggested above, some 0·05 may be associated with maintenance, leaving 0·09 if the Riis estimate is used. Of this remainder some 0·06 may fail to be reincorporated. Losses thus amount to 0·0054.Pt, or $IP_{Pto} = 0.0054.Pt$. This is about 17 g and 104 g daily for a 20 kg and 120 kg pig respectively. This calculation may be faulted in failing to take account of the inverse relationship between increasing size and/or maturity and turn-over rate (Millward *et al.,* 1976; Goldspink and Kelly, 1984). Reeds (1989) states that in growing animals protein synthesis relates to their rate of growth and that animal age has a significant effect on the contributions of the various tissues to whole body turn-over, and therefore the proportion of turn-over associated with growth (as opposed to maintenance). An inverse relationship between maturity and turn-over would give a greater constancy in the calculated daily rate of loss, as the increasing body mass turning over is offset by a reduction in the fraction of

the total body protein turned over daily. Neither does the above calculation take account of any effect there may be upon the rate of protein turn-over or the rate of protein deposition. Whittemore and Fawcett (1976), using derivations from the protein turn-over studies of Millward *et al.* (1974), proposed that protein turn-over (Px) could be estimated from the rate of protein retention and the degree of maturity. Their equation was; $Px = Pr/(0.23.(Pt_{max} - Pt)/Pt_{max})$, where Pt is the present protein mass, and Pt_{max} the mature protein mass. With an estimated 0·06 loss rate, 100 g of protein retention by a pig of 20 kg and 200 g by a pig of 120 kg would calculate to losses of 28 g and 84 g respectively. From these values should be deducted the turn-over losses already accounted in the maintenance value, taken above to be some 0·003.Pt. Adding a term for IP_{Pto} will therefore reduce the presumptive perfect efficiency of conversion of IP_{Pr} to Pr by some 10 to 30%, depending on Pt and Pr.

That the sum of IP_m and IP_{Pr} did not account for the realized efficiency of utilization of absorbed ileal digested ideal protein when provision was not in excess has long been appreciated, and is probably a function of both food type and animal effects (Batterham, 1993). Whittemore (1999) has reviewed the matter. Given the definitions of ileal digestibility and ideal protein, the theoretical efficiency of the use of ileal digested ideal protein (*v*) might appear necessarily to approach unity (Ferguson, 1988; Edwards and Campbell, 1993; Moughan, 1993). Rao and McCracken (1990) found an upper limit of 0·9 but also a progressive reduction with increasing level of diet supply. Upper limits for *v* of 0·9 to 0·95 were suggested by Fisher (1976) and Whittemore (1983). But utilization values as low as 0·6 have been measured, and as stated by Wiseman *et al.* (1991), the promise that the use of ileal digestibility values would substantially improve the precision of dietary protein supply has thereby not been wholly fulfilled. Estimates of efficiency of use of ileal digested amino acids imply that the measurement of ileal digestibility was accurate in the first place. This may not always be so as the determination is difficult, variable, and highly dependent on the degree of food processing (Batterham, 1993; Hodgkinson and Moughan, 2000a and b). Kyriazakis and Emmans (1992a and b) measured a maximum value for the net efficiency of utilization of ideal protein above maintenance of 0·81, and found the value dependant upon energy : protein ratio. Whittemore (1998) was unable to find measurements in practice above 0·85, and settled for *v* = 0·85 as an upper limit. De Lange (unpublished, University of Guelph) has determined 0·74. All of which would point empirically to a value for *v* of 0·75 to 0·85 but gives scant guidance as to how the prevailing value in any given circumstance may be determined.

Moughan (1995) approached the loss of efficiency of use of ileal digested ideal protein through the concept of 'inevitable catabolism'. From various sources he argued that inevitable catabolism could account for 0·1 to 0·4 of absorbed ideal protein; the rate of loss being positively related to the rate of protein absorption (and thereby protein deposition). Moughan (1999) presents unpublished data from his own laboratory showing a 0·15 shortfall in expected Pr, and goes on to interpret the results of Batterham *et al.* (1990) to show that inevitable catabolism will account for some 0·2 of absorbed ideal protein, and be linearly related to Pr.

It may be surmised that the estimation of IP_{Pto} and *v* separately represent deductive and empirical approaches to the identification of the same factor; the inefficiency of use of ileal digested ideal protein for purposes of protein retention that occurs even when supply is not in excess. The amino acid balance for protein required for this purpose is that already identified previously to make good losses from protein turn-over occurring at maintenance.

Protein : energy interactions

The interaction between protein and energy, and the consequences for the rate of growth and composition of the pig as it grows, is more an *outcome* of the provision of energy and protein, than a determinant of the requirement.

Protein is energy rich, but when the constituent amino acids are used for the production of retained body protein, energy is not released. Thus ingested protein contributes to the metabolizable energy (ME) input but that proportion which is retained makes no contribution to the available net energy. Whittemore and Fawcett (1976) identified energy in protein separately from the 'protein-free' energy, and divided the former into that which was retained (and therefore required energy) and that which was not. Non-retained protein (usually 0·5 or more of the total) was assumed to be deaminated, (and therefore contributed energy). Given an energy value of 23·6 MJ per kg digested protein, these authors subtracted an energy cost of 2·4 MJ ME per kg protein deaminated and a further 7·2 MJ/kg protein deaminated for the inevitable loss of energy in the urine coincident with the excretion of N-containing moieties. A rather similar value of 3·5 MJ/kg protein *ingested* has been determined by Le Bellego *et al.* (2000). The ME yield from protein substrate that is not used for retention was therefore estimated as 14 MJ ME per kg.

In the presence of sufficient energy, daily protein retention (Pr) will, according to the presumptions outlined earlier above, respond linearly to increasing supply of ileal digested ideal protein above maintenance; the slope of the response reflecting the material efficiency of use. A limit in energy supply will cause the response to plateau at the commensurate level (Black and de Lange, 1995). Ultimately response in the daily rate of protein retention to protein supply will cease when the plateau defined by Pr_{max} is attained.

The 'linear/plateau' model to describe the response of protein retention to nutrient intake which results from factorial analysis of nutrient requirement (Whittemore, 1979 and 1980), was not accepted by ARC (1981), who offered in addition both linear and curvilinear models. The linear model presumes Pr_{max} to be out of range of energy intake potential (appetite), while the curvilinear would likely result from analysis of a population of linear/plateau responses. The linear/plateau paradigm is now largely accepted for the purposes of construction of nutrient requirement models describing the response of protein retention in growing pigs to the dietary supply of energy (see Bikker, 1994; Moughan *et al.,* 1995; NRC, 1998; Kyriazakis, 1999; van der Peet-Schwering *et al.,* 1999). Mohn and de Lange (1998) confirmed recently that while energy is limiting the response of protein retention to increments of energy will be linear. The plateau (Pr_{max}) is taken to be sex and genotype dependent. The principle has been demonstrated experimentally by, amongst others, Campbell *et al.* (1985), Dunkin *et al.* (1986), Quiniou *et al.* (1995), Quiniou *et al.* (1996). However, van Milgen *et al.* (2000) recently re-examined the value of an assumption of a curvilinear regression of Pr on ME intake.

Recent reviewers (Black, 1995; NRC, 1998; Moughan, 1999) present a family of linear/plateau responses with the plateaux increasing with increasing pig weight up to around 80 kg and then decreasing. At all live weights the response in daily protein retention to increasing energy supply is linear, but the plateau is achieved at progressively higher energy intakes up to 100 kg. Table 4 presents the values shown by Black *et al.* (1986), which also form the basis of NRC (1998). The amount of energy associated with zero gain increases (as it must) with increasing live weight, and Black *et al.* (1986) and NRC (1998) take this to occur at 0·55 of the maintenance requirement. But the constancy of the slope of the response for different live weights and potentials for protein retention remains contentious. The regression of protein retention on ME intake depicted by Black *et al.* (1986), and reproduced by

others subsequently (Black, 1995; NRC, 1998; Moughan, 1999) show a diminishment in slope as the family of curves fan downwards with increasing live weight. The picture prepared by Black *et al.* (1986) was not, of itself, a representation of experimental results, although it was founded on the results of the Australian group (Black *et al.,* 1986). The same response is well addressed by Quiniou *et al.* (1999), using the empirical data sets collected at Institut National de la Recherche Agronomique in the past decade. The slope of protein retention on energy intake will be reflective of both the diversion of energy to lipid retention (which might be expected to increase at higher live weights) and the value pertaining for k_{Pr} (see above). The average value depicted by Black *et al.* (1986) is around 60 g Pr/MJ ME, while that measured by Quiniou *et al.* (1996) was around 45 g Pr/MJ ME. Black *et al.* (1986) suggest the slope to be a function of both sex and genotype, and the same could be inferred from Quiniou *et al.* (1996). NRC (1998) are sceptical, but suggest there may be a positive relationship with the achieved rate of protein retention. Black *et al.* (1986) state that the change in body N deposition with ME (G_{NBE}, g/MJ) when protein deposition is below its potential is;

$$G_{NBE} = (0{\cdot}7e^{-0{\cdot}0192W} + 0{\cdot}65)\, X_S$$

where W (kg) is body weight and X_S is a factor that allows for differences between strain and sex of pig. X_S 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 the slow growing genotype. The empirical parameterization of the slope of protein retention upon energy supply may however be sterile in view of the possibility that it may be better determined from its underlying causes, as indicated above. Van Milgen *et al.* (2000) describe most aptly the difficulties inherent in modelling at too high a level in the system's response hierarchy.

Table 4 *Relationship between maximum rate of daily retention of protein and energy intake for pigs of increasing live weight. Interpolated from Black* et al. *(1986)*

Empty body weight *(kg)*	Maximum rate of protein retention attained *(g/day)*	Intake of ME at point of termination of linear response and beginning of plateau *(MJ ME/day)*
5	55	7
25	120	18
50	150	26
75	160	32
100	155	35
150	130	34
200	75	26

Acknowledgements

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