

Architecture of a harmonized model of the growing pig for the determination of dietary net energy and protein requirements and of excretions into the environment (IMS Pig)

D. M. Green and C. T. Whittemore

University of Edinburgh, Agriculture Building, The King's Buildings, West Mains Road, Edinburgh EH9 3JG, UK

† E-mail : Darren.Green@ed.ac.uk

Abstract

The model incorporates, amongst its novel components, variable efficiency coefficients in the simulation of the responses of growing pigs to nutrient inputs, and thereby increases the accuracy and efficacy of control of feeding and nitrate excretion. The model determines (rather than is presented with) net energy and required amino acid level and balance. The estimation of protein turn-over as a function of rate of protein retention, protein mass and the maturity of the pig was found to be central to both the energy (ATP) and protein economy. Protein turn-over varied from around 0.14 to 0.08 of the protein mass depending upon the size of the pig. Efficiencies of energy yield from lipid, starch (and sugar), protein and (fibre-derived) volatile fatty acids were calculated to be 0.98, 0.86, 0.56 and 0.58 for ATP production and 0.90, 0.70, 0.50, and 0.44 for lipid retention, respectively. The maximum efficiency of use of ileal digestible amino acids was determined as around 0.85. The energy cost of protein synthesis was equivalent to 4.2 MJ metabolizable energy (ME) per kg, and the efficiency of use of ME for protein retention varied from 0.55 to 0.40 depending on the protein mass of the pig. The components of the model and the biochemical drivers are described in detail, and proof of principle of the main elements is presented. The model is different in its architecture to other published simulation models, and is considered to add to the present knowledge base in this discipline.

Keywords: energy, growth, mathematical models, pigs, protein.

Introduction

The paradigm of animal nutrient use and excretion can be divided into three closely connected elements. These are: (i) the yield of nutrients from diet substrate, (ii) the requirements for growth and body functions, and (iii) the construction of models that connect supply to requirement. Given such connections, it is possible to determine outcomes in terms of the rate and composition of growth, and in terms of excretions into the environment. This paper describes innovative structures for the essential architecture of models to deal with the third element. The proposals, which follow from new knowledge and methods of deduction, intend to bring increased understanding of the science and increased adaptability in industrial use. Both come from releasing fixed coefficients into variable format, and deriving the algorithms from deeper within the biochemical system. The scientific justification of the

particular model here presented is largely drawn from the reviews of Whittemore *et al.* (2001a, b and c)

The provenance and construct of various models relating to the responses of pigs to nutrient inputs has been recently reviewed elsewhere (Black *et al.*, 1986; Moughan *et al.*, 1995; Kyriazakis, 1999; McNamara *et al.*, 2000; Knap, 2000; Whittemore *et al.*, 2001a, b and c; Birkett and de Lange, 2001a, b and c). Models that effectively determine nutrient retentions will, with minimal amendment, also inform as to optimum nutrient provision within the context of the needs of environmental protection. The proposed model (IMS Pig) is a product of consortium members of the research programme 'Integrated Management Systems for Pig Nutrition Control and Pollution Reduction'. IMS Pig is novel in its usage of the information base and in the constructs used in the model architecture. *Inter alia*, it:

(a) links diet-derived primary nutrient substrates (amino acids, starch, non-starch polysaccharide, lipid) to tissue retention via algorithms that model mainstream biochemical processes and their interactions;

(b) uses a unified driver for the model, allowing compatible calculation of (i) the nutrient costs of energy and protein cycling, (ii) the interaction between the nutrient costs of maintenance and tissue retention, and (iii) the interactions between energy and protein usages;

(c) predicts the rate and composition of tissue retention during growth, and the cost of thermoregulation, from frugal model parameterization;

(d) reverses conventional model input values such that they become out-turn values [such as (i) the metabolizability of energy, (ii) the ideality of protein and the efficiency of use of ileal digested ideal protein, (iii) the efficiency of utilization of energy (k) for maintenance (k_M), for protein retention (k_{Pr}) and for lipid retention (k_{Lr})];

(e) replaces inflexible k_{Lr} , k_M and k_{Pr} values with a combination of stoichiometrically derived k_s values ($k_{s(0)}$ for lipid retention and $k_{s(m+p)}$ for maintenance and protein retention) and experimentally derived k_t values (accounting in terms of ATP for the residual efficiency loss due to process and transfer costs);

(f) allows catabolism of body lipid for the support of protein retention, and subsequent compensatory recovery of lipid;

(g) facilitates both the diagnosis and the treatment of response shortfalls by effective simulation and response prediction. This mode of employment is essential for a closed loop approach to the integration of a management system (IMS) for the control of nutrient provision and the reduction of pollution from faecal and urinary excretions.

Dietary substrates

A general diagrammatic layout is given in Figure 1. The IMS Pig model takes as its energy and protein sources those moieties truly digested in the foregut anterior to the terminal ileum (starch and sugar (see

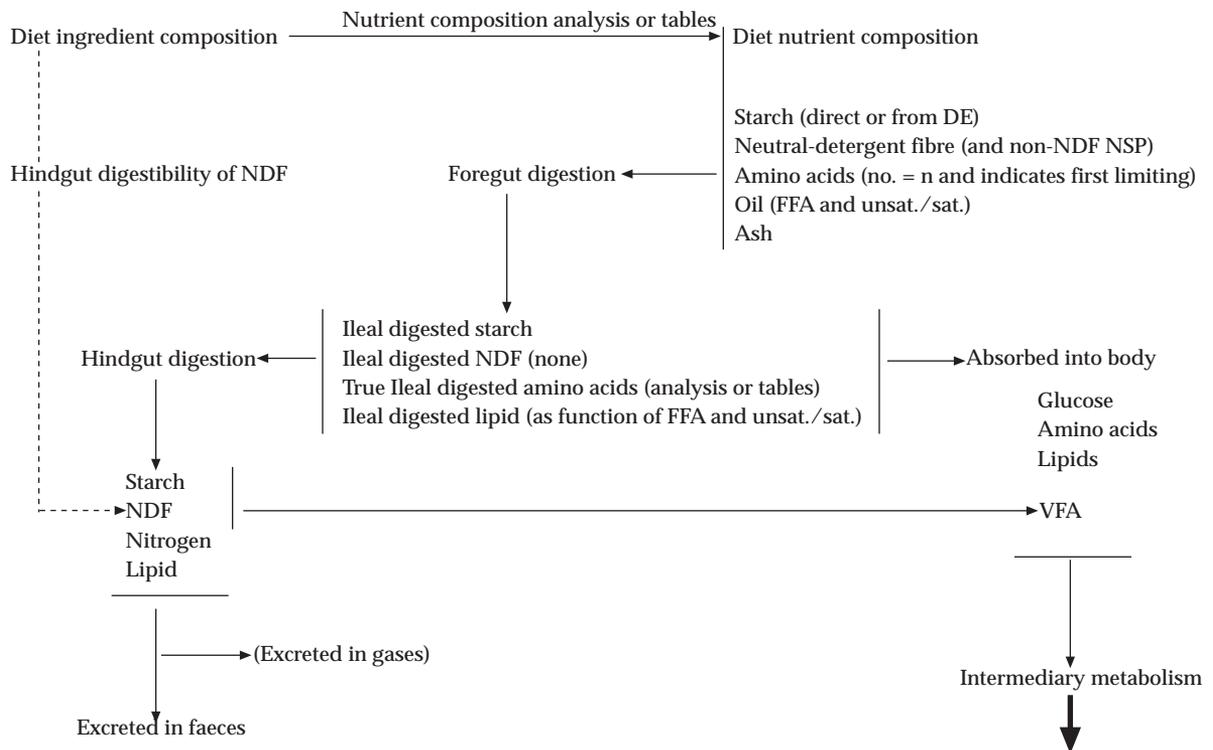


Figure 1 Diagrammatic depiction of the framework for calculating the yield of substrates from diet. DE = digestible energy, NDF = neutral-detergent fibre, NSP = non-starch polysaccharides, FFA = free fatty acids, VFA = volatile fatty acids.

also **Appendix 1**); amino acids; lipids), and the absorbed volatile fatty acid end-products of the hindgut fermentation of the remaining organic matter (non-starch polysaccharide (NSP); starch resistant to enzymic digestion). There will be some fermentation of NSP within the foregut (de Lange and Fuller, 2000), but for operational purposes of identifying end products, the model counts this as for the hindgut. The text here presented will offer default values for various parameters; in the presence of superior information these default values may be overridden.

Energy required for growth and maintenance in the IMS Pig model is sourced *via* ATP; input of diet digestible energy is not required. The model simulates individually the passage of each of the 20 amino acids from diet to usage; therefore input of 6.25N crude protein (CP), or ideal protein (indicating the amount of amino acids that are balanced with respect to requirement) is not required.

NSP includes primarily cellulose, hemicellulose and pectins. Together with lignin these make up the dietary fibre. The addition of the fructans and the oligosaccharides to NSP gives an estimate of fermentable carbohydrate. Starch and simple sugars are digested ileally. For cereal grains it is assumed that analysis for neutral-detergent fibre (NDF) measures cellulose, hemicellulose, pectin, and lignin, and will provide equivalence for NSP (Moughan *et al.*, 1999; Chesson, 2000). However, for other ingredients (and therefore for mixed diets), especially protein-rich extracted legume seeds such as soya-bean meal, NDF underestimates the cell wall (foregut indigestible) component. Chesson (2000) suggests that it may be sufficient to assume that in normal pig diets the (small) non-NDF NSP fraction is digested. This allows simplification of the model when food inputs carry only analysis for starch and NDF. However, for some foodstuffs, such as those derived from roots and legumes, the NSP fraction not counted within NDF may be significant. Non-NDF NSP fraction could be presumed as a remainder;

$$\text{non-NDF NSP (g/kg)} = 1000 - (\text{starch} + \text{sugar}) - \text{NDF} - \text{oil} - \text{protein} - \text{ash}$$

although such a difference estimation would be highly error prone. In the presence of an estimate of both NSP and NDF (and therefore non-NDF NSP), it may be prudent to assume less than complete absorption and energy provision. Jorgensen *et al.* (1996) have suggested that the overall digestibility of NSP may be as high as 0.6 to 0.8, but that this value

is highly specific to ingredient and to fibre level; that is to the level of non-NDF NSP. In the absence of further data, a default mid-range value of 0.66 is tentatively forwarded for the proportion of non-NDF NSP disappearing in the foregut; the remainder passes to the hindgut, where it is digested with the same efficiency as NDF.

The ileal digestibility of starch and sugar is assumed (as default) to be 0.99, the remainder to disappear in the hindgut and be dealt with in common with other energy sources arriving there.

The IMS Pig model assumes that the digestibility of NDF in the foregut, to yield glucose, is zero. The proportional disappearance from the hindgut is problematic in its quantification, but from the prediction equation for digestible energy (DE) of Morgan *et al.* (1987) it would appear that 1000 g of NDF may contribute 2.5 MJ DE which implies a digestibility of 0.14 (2.5/17.5). In the absence of better information, a default value for NDF digestibility is taken to be 0.22, derived from the above *net* 0.14 figure, and stoichiometric energy ratios, outlined later below. The fermentation of fibre is modelled as having a conversion of energy efficiency of $0.79 \times 0.8 = 0.63$. The quotient of 0.14 and 0.63 is 0.22. Digestibility of NDF will be higher for foodstuffs such as sugar beet, and lower for cereal husk. The model can accept particular digestibility values for the diet NDF where these are known.

With respect to protein, the IMS Pig model operates on the basis of the sum of the component amino acids. The error associated with the '6.25 multiplier' for protein mass as a multiple of nitrogen mass (range 5.7 to 6.4 depending on the amino acid composition of the protein; but for pig diets certainly less than 6.25), is thus avoided. True ('standardized') digestibility (Seve and Hess, 2000) values for diet ingredients at the terminal ileum are utilized. These may, in the absence of diet-specific analysis, be taken from data bases such as AmiPig (2000), or the equivalent. In the presence of information relating to only some of the amino acids, the total complement is estimated on the basis of a normal expectation for a pig diet. (Default values (g/kg diet) used were: lysine 1.14, threonine 0.74, methionine 0.27, cysteine 0.35, tryptophan 0.22, isoleucine 0.63, valine 0.77, leucine 1.29, phenylalanine 0.93, tyrosine 0.46, histidine 0.55, arginine 1.16, alanine 0.76, aspartic acid and asparagine 1.59, glutamic acid and glutamine 3.76, glycine 0.84, serine 0.92, proline 1.07.) Information provided from the ingredient list or diet analysis must minimally be sufficient to identify the rate of ingestion of the first limiting amino acid.

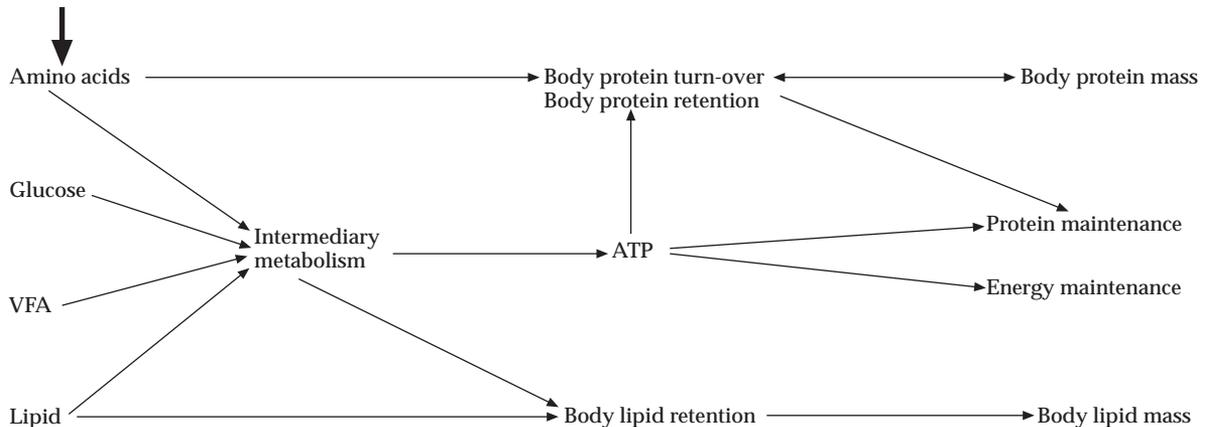


Figure 2 Diagrammatic depiction of the framework for calculating the usages of substrates absorbed into the body.

The proportion of dietary lipid (excluding the indigestible materials additionally determined by acid hydrolysis) that is absorbed anterior to the terminal ileum is much dependent upon the quality of the dietary source. The expected digestibility is therefore important knowledge for presentation to the model. Vegetable oils that have a high inclusion of unsaturated and long chain fatty acids and human grade tallow may approach 1.0 in their digestibility (Morgan *et al.*, 1984), while that for feed grade and spent oils may be substantially diminished (Whittemore, 1998; see also **Appendix 1**). The digestibility of lipid included in the diet may be specified as a model input.

Energy costs of maintenance (E_M), protein turn-over and protein retention (E_{Pr})

Presently, many operational models for the simulation of growth response to energy supply are driven by the energy costs of maintenance (E_M) expressed as a function of live weight, and the energy costs of protein retention driven through k_{Pr} (plus lipid retention through k_{Lr} , discussed later). These parameters are frequently used as if they were of fixed value, and modellers see their correct and compatible selection as seminal to the efficacy of their models. A number of shortcomings in this approach are evident from the review of Whittemore *et al.* (2001b).

(a) There is a wide range of empirical measurements for both E_M and k_{Pr} available from experimental reports. Whittemore *et al.* (2001b), Knap (2000) and Noblet *et al.* (1999) report E_M equations varying from $0.4 \times W^{0.75}$ to $0.6 \times W^{0.75}$ MJ, with k_{Pr} values varying from 0.434 to 0.62

(b) Part of the energy costs of protein retention are shared with part of the energy costs of maintenance, as both are involved in protein turn-over.

(c) Protein retention and turn-over rates are dependent upon protein mass (Pt), but maintenance is usually measured as a function of live weight (W); the ratio between W and Pt is variable.

(d) The value for k_{Pr} may not be a single value, because it is likely to be a function of the rate of protein retention (Pr) and the proportion of maturity of protein mass (Pt) attained by the animal (Pt_{max}/Pt). If, as suggested by Knap (2000) in confirmation of Whittemore (1983), relative turn-over rate varies across organs, then overall turn-over rate must vary as body composition changes with pig size. Variable turn-over rate implies a variable cost of protein synthesis, and thus a variable efficiency.

(e) The types of nutrient sources involved in the generation of ATP used for protein metabolism necessarily influence the efficiency of energy use (k_{Pr}), as ATP is delivered with different efficiency from different energy sources.

The turn-over of body protein in the pig can be divided into two processes: protein turn-over as a part of maintenance, and protein turn-over associated with the retention of new protein and the concomitant reorganization of body tissues (Figure 2). As the processes of maintenance operate even in the absence of any retention of body protein, there is a baseline rate of protein turn-over that will occur in the young but non- or slow-growing pig. Whittemore *et al.* (2001b) indicate that this minimum rate of protein turn-over at maintenance can be described by the equation

$$P_{x_m} = 0.05 \times P_t$$

where P_x is protein turn-over, and P_t is the current protein mass of the pig.

Estimates of protein turn-over are reviewed by Whittemore *et al.* (2001b). If, as suggested, protein turn-over rate is dependent upon both the degree of maturity of the pig, and the rate of retention of new protein, then the following equation could be used to determine protein turn-over rate:

$$P_x = P_r \times (1/z) \times P_{t_{max}} / (P_{t_{max}} - P_t)$$

where $P_{t_{max}}$ is the protein mass of the pig at maturity, and the asymptote of the protein retention curve considered below. Whittemore and Fawcett (1976) estimated z as 0.23. In the absence of another, this value is used as the default. The validity of this proposition can be examined by fitting values for z and P_r , and comparing the solution with measurements of turn-over reported elsewhere. Higher values of z will be appropriate for genotypes which show a lower degree of recycling of body protein at a given proportion of mature protein mass.

The maximum protein retention rate of a pig ($P_{r_{max}}$) may be described as a constant, or by a linear or curvilinear function (Whittemore and Green, 2002). If a Gompertz function is used:

$$P_{r_{max}} = P_t \times B \times \ln(P_{t_{max}}/P_t).$$

The above equations may be combined to determine protein turn-over rate where nutrient supply is not limiting;

$$P_{x_{max}} = P_t \times B \times \ln(P_{t_{max}}/P_t) \times (1/z) \times P_{t_{max}} / (P_{t_{max}} - P_t).$$

Expressed as a proportion of total body protein mass (that is the proportion of total body protein mass that is turned over on a daily basis) this becomes:

$$P_{x_{max}}/P_t = B \times (1/z) \times \ln(P_{t_{max}}/P_t) \times P_{t_{max}} / (P_{t_{max}} - P_t).$$

Figure 3 shows output from this equation. For pigs with body weights of 20 and 120 kg, the turn-over proportion is 0.13 and 0.07. These estimates are in satisfactory agreement with the reported experimental data, which suggest that the proportion of protein that is turned over daily in growing pigs is in the region of 0.10 to 0.14 (Riis, 1983; Whittemore *et al.*, 2001b). Lower values for z will result in higher predicted rates of protein turn-over. The shape of the curve for protein turn-over rate as a function of pig mass, but not its locus, is similar to that suggested by Danfaer (2000);

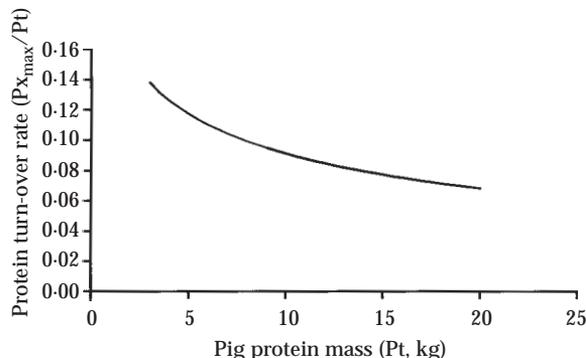


Figure 3 Predicted daily turn-over rate of protein mass (expressed as a proportion of total body protein) as a function of total body protein mass [$P_{x_{max}}/P_t = B \times (1/z) \times \ln(P_{t_{max}}/P_t) \times P_{t_{max}} / (P_{t_{max}} - P_t)$]. $P_{t_{max}} = 40$, $B = 0.012$, $z = 0.23$.

$$P_x = 6.72 + 19.8 \times \exp(-0.799 \times P_t).$$

If the level of protein turn-over predicted, minus any protein retention occurring, is less than the minimal level required for maintenance ($P_{x_m} = 0.05 \times P_t$), then this minimum is returned. Thus the following inequality stands:

$$P_x - P_r > 0.05 \times P_t.$$

Generally, P_r will be of such a magnitude that P_x will exceed this minimum.

These propositions for the IMS Pig model are frugal in their resources (see Figure 2). $P_{r_{max}}$ is defined by P_t . The Gompertz function requires B and $P_{t_{max}}$ to predict $P_{r_{max}}$, and $P_{r_{max}}$ is also required for the determination of P_x . P_x requires in addition only parameterization of z . E_M , discussed later, is determined as a function of P_t , and this single base is an appropriate means for accommodating the overlap between the energy usages of maintenance and turn-over. The veracity of this approach is tested in **Appendix 2**. Given the differing derivation of the proposed estimations from turn-over (footnote 11 in **Appendix Table 2.1**) and those from empirical measurement (footnotes 14 and 17), the out turns from the proposed innovative and more beneficial methodologies (as described above) are considered satisfactory and valid for inclusion in the new IMS Pig model.

In IMS Pig, the energy requirement for protein retention is calculated using ATP as the energy currency. The formation of 1 mol of peptide bonds is considered to require 4 mol of ATP together with a further 1 mol for transport across membranes, making 5 mol (van Es, 1980). After calculating the

number of moles of peptide bonds in the protein concerned, the ATP cost of protein retention and turn-over can be determined. If the average relative molecular mass of protein amino acid residues were 110, then the cost of protein turn-over would be 45.5 mol ATP per kg protein. In the model, the average molecular mass of the amino acids used to construct the protein is calculated from the appropriate amino acid composition.

The expression of maintenance should not be dependent solely on total protein turn-over, as the latter is driven in part by Pr, and the possibility of Pr being limited by restricted nutrient supply must be accommodated within the model. The expression of the energy costs of maintenance as a function of protein mass (Pt) is well supported by the literature (Whittemore *et al.*, 2001b), and the equation $1.85 \times Pt^{0.78}$ MJ ME per day is forwarded here. This value has an empirical source and includes that portion of the energy costs of maintenance which arise from protein turn-over occurring at maintenance, suggested here as $0.05 \times Pt$. When placed in the model on the net side of the energy transfer algorithm, the 'fasting metabolism' paradigm is more appropriate, and a multiplication factor of 0.81 is employed (Agricultural Research Council (ARC), 1981).

If the maintenance energy measurement is determined during fasting and therefore emanating from body lipid resource, then the 1.85 MJ constant is equivalent to 24 mol ATP (lipid yield is 39.6 MJ/kg or 514 mol/kg ATP). Including the 0.81 correction factor, the following is obtained:

$$E_M \text{ (mol ATP)} = 0.81 \times 24.0 \times Pt^{0.78}.$$

This value for E_M is then adjusted according to the level of activity of the pig and the degree to which it is diseased, both activity and disease being considered as draws upon the pig's energy

$$E_M' = (1 + F_{\text{Disease}} + F_{\text{Activity}}) \times E_M.$$

The default parameters for this function are considered to be those that apply to pigs with moderate activity and a normal level of immune challenge in intensive production units; that is, the conditions under which the empirical measurement of the requirement for maintenance might be made. The default value for F_{Activity} is taken as 0.1. That for F_{Disease} awaits the outcome of reviews of the energy and protein costs of immunity and disease presently in hand at this and other laboratories. The review of Black *et al.* (1999) suggests disease (in general) to (a) reduce food intake by up to 100%, (b) increase maintenance energy requirement by up to 30%, and (c) decrease protein retention rate by up to 90%,

depending on severity and duration. Disease may have specific components in addition to the general; thus enteric syndromes will reduce diet digestibility. It is not the purpose of IMS Pig to model the effects of overt clinical disease states, but it *is* evident that the cost of disease and the support of an active immune system differ between different production units, and account must be taken. Independently of gross food intake effects, the account would involve *inter alia* (a) maintenance energy expenditure, (b) turn-over protein loss, (c) a rise in core body temperature, and (d) a reduction in the digestibility of ingested nutrients.

Protein requirements for maintenance and protein retention

Accurate provision of the dietary protein requirement is pivotal to the optimization of growth and the minimization of pollution. Dynamic management needs flexible models but present models use constant functions for the efficiency of use of ideal protein for maintenance and protein retention. As widely reported (Whittemore *et al.*, 2001c), it has proved difficult to deduce the efficiency of use of ileal digested ideal protein (IP), which theory suggests should approach unity when not supplied in excess, but which does not do so. This has usually resulted in the necessary but unsatisfactory use by modellers of empirical factors representing best estimates of v , the efficiency of use of ileal digested ideal protein for protein retention when ideal protein is not supplied in excess. The review of Whittemore *et al.* (2001c) suggests that the value for v is usually proposed as lying between 0.75 and 0.95; de Lange *et al.* (2001) suggest on the basis of threonine studies 0.75. But there is presently no methodology for the deduction of the correct value. Resolution of these shortcomings is addressed with the hypothesis that the inefficiency of use of ileal digested ideal protein for both maintenance and protein retention is a consequence of losses in the course of protein turn-over. Such a hypothesis will also provide a common modelling base (Figure 2) for the interaction of utilization of dietary energy and protein.

The efficiency of resynthesis of turned-over protein is taken as 0.94, for a pig with a normal disease challenge, so of the protein that is broken down during turn-over, 0.06 is deaminated and not reused (Whittemore and Fawcett, 1976). Since at maintenance, the level of turn-over is taken as $0.05 \times Pt$, the loss of protein destined for deamination at maintenance is $0.003 \times Pt$.

As shown earlier, total protein turn-over (Px) is given by

$$Px = Pr \times (1/z) \times Pt_{\max}/(Pt_{\max} - Pt)$$

where $Px - Pr > 0.05 \times Pt$. This value for Px includes protein retention, Pr , and maintenance protein turn-over, $Px_m = 0.05 \times Pt$. Thus, the requirement of ideal protein for retention and turn-over is given by:

$$0.06 \times Px + Pr.$$

The energy costs of retention of turned-over protein within (Px_m) and outwith ($Px - Px_m$) maintenance, and of deposited protein (Pr) differ as they have different amino acid profiles (see **Appendix 3**).

The energy cost of the turn-over of maintenance protein (Px_m) is included in E_M and not counted again here. Due to the different amino acid profiles involved in portions of turn-over, the requirement for individual amino acids will vary in its amino acid balance according to the ratio between maintenance, turn-over, and retention of protein.

In addition to protein turn-over, there are two further drains upon the amino acid pools of the model: endogenous faecal losses and losses from the integument. These will appear as inefficiencies set against protein retention. Losses from the integument may be estimated as 0.1 g protein per $W^{0.75}$. The amino acid profile of integument losses is shown in **Appendix 3**.

Where, as properly in the IMS Pig model, the supply of amino acids is expressed in terms of true, or standardized, ileal digested amino acids (de Lange and Fuller, 2000; Seve and Hess, 2000; AmiPig, 2000), the requirement must provide for the endogenous faecal losses. These may be estimated as 0.57 g protein daily per $W^{0.75}$, for digestive secretions (with an amino acid profile shown in **Appendix 3**), plus 20 g protein (of the amino acid composition as found in the diet) per kg of food ingested for physical food effects if the diet is not abnormally high in fibre (Moughan, 1999).

The consequences of this approach are expanded in **Appendix 4**. Values that are returned in **Appendix 4**, including those for v , the efficiency of use of ileal digested ideal protein for protein retention when ideal protein is not supplied in excess, are considered to support the calculation of protein requirement by means of the presently proposed new methodology, and the incorporation of these innovations into the IMS Pig model. It may be noted that the efficiencies of use of both energy and protein are sensitive to, and linked together by, the value ascribed to the coefficient z . This is therefore a potential controller for the simultaneous adjustment of both the energy and the protein systems, and the interactions

between the two. z indicates the magnitude of protein turn-over for a pig of a given maturity.

Vector notation can be used to summarize the amino acid flow during protein turn-over and retention. This is shown in **Appendix 4**.

Energy costs of lipid retention

Where Lt and Pt are the total amounts of lipid and protein in the body of the pig, the achieved rate of lipid retention will relate to (a) the satisfaction of a minimum preferred ratio of lipid to protein in the pig's body [$(Lt : Pt)_{\text{pref}}$], and (b) the level of energy supplied in excess of the needs of maintenance and protein retention.

The concept of a preferred ratio of total lipid to total protein in the body $(Lt : Pt)_{\text{pref}}$, as demonstrated by Kyriazakis and Emmans (1992a) and further argued by Whittemore (1995), is accepted by IMS Pig as being reasonable, and likely to be dependent upon pig type. During normal growth, where maximum fatness for a given protein weight is not attained, and lipid retention is therefore desired by the pig, lipid retention (Lr) will target the achievement and subsequent maintenance of this ratio as a priority;

$$Lr_{\text{desired}} = Pt \times (Lt : Pt)_{\text{pref}} - Lt.$$

The model operates such that when the animal has an adequate nutrient supply for desired rates of protein retention, but $(Lt : Pt) < (Lt : Pt)_{\text{pref}}$, then the retention of lipid will be given priority over the retention of protein such as to limit Pr and achieve in the daily gain a ratio of $Lr : Pr$ that is set as the same ratio as is set for $(Lt : Pt)_{\text{pref}}$. Thus when $(Lt : Pt) < (Lt : Pt)_{\text{pref}}$ subsequent daily growth in energy limiting circumstances will be of the preferred ratio, but the total body will not attain the preferred ratio until energy is available above the requirements of maintenance and protein retention. Once $(Lt : Pt)_{\text{pref}}$ has been attained, the IMS Pig model will facilitate the exceptional circumstances that can occur in periods of nutrient shortage, when fat over and above $(Lt : Pt)_{\text{pref}}$ may be catabolized to join the general energy pool in the interests of optimizing protein retention. The maximum rate of catabolism of body lipid allowed in such circumstances is arbitrarily set to 0.009 kg lipid per $W^{0.75}$ daily, this being determined from knowledge that lipid can be catabolized at least at the rate required of fasting metabolism. Assuming an E_M requirement of 0.444 MJ per $W^{0.75}$ (National Research Council (NRC), 1998) and an efficiency, k_M of 0.81 (ARC, 1981), with energy sourced from lipid at 39.6 MJ/kg, then catabolism, C , can operate at least at the rate;

$$C = (0.444 \times 0.81) / 39.6 = 0.0091 \text{ kg/day per } W^{0.75}.$$

In extremis, a pig may become less fat than indicated by $(Lt : Pt)_{pref}$, but this may be taken as indicative of an abnormal, and not a growth, state. This may often occur however post-weaning, and thus in early life the growing pig will usually be seeking to attain $(Lt : Pt)_{pref}$. The achieved rate of lipid retention above $(Lt : Pt)_{pref}$ will be a function of the amount of energy remaining in the energy pool after the needs of all other functions have been met. No upper limit is set for Lr.

High quality dietary lipid can be directly incorporated into newly formed body lipid. But although in most circumstances the propensity for lipid retention will exceed the supply of lipid directly from dietary sources, there is an upper limit of perhaps 0.85 to the proportion of lipid retention achieved in this way (Lizardo *et al.*, 2000). This limit is dependent upon the diet and may vary from 0.5 to 1.0 (Whittemore *et al.*, 2001b). Accordingly, in the model it is tentatively assumed that no more than 0.8 of newly formed body lipid can arise directly from appropriate dietary lipid absorbed from the small intestine; the remainder of the new body lipid retention requires *de novo* manufacture.

Dietary lipids considered 'appropriate' for direct incorporation into body lipid are high quality vegetable, fish or pig oils of first-hand and natural origin with at least 50% long chain (> C14) unsaturated fatty acids. It is considered unlikely that all the 'appropriate' fatty acids will be used for direct incorporation into body lipid, so again an upper limit of 0.8 is set. The remaining 0.2 of 'appropriate' digested dietary lipid, together with 'inappropriate' dietary lipid is broken down and joins the pool of energy-containing compounds originating from lipid sources (primarily acetyl co-A). As such, it may be used for the purposes of fuelling maintenance, protein retention or indeed lipid retention (with a stoichiometric efficiency of 0.89). Insufficient is understood of lipid turn-over to allow algorithms of the type used for protein retention, but costs are in any event taken to be small. The efficiency of synthesis of body lipid from appropriate dietary lipid is high at 0.94, and the efficiency of turn-over of body lipid is likely to be similar.

Determination of energy yields from dietary substrates

Putative net energy yield from metabolites delivered at the location of the target tissue may be determined from the stoichiometry of the various biochemical processes involved. The determination of the overall efficiency of energy yield from the various nutrient substrates from digestion to the final point of

expenditure requires in addition to the stoichiometric calculation of energy available from absorbed dietary nutrients (k_s), the accommodation of the rather less determinable process and transfer costs (k_t). These are evidenced in the form of the efficiency differences between the stoichiometric estimate and empirical measurement. The overall efficiency is the product of k_s and k_t .

The IMS Pig model receives energy substrates in the form of digested starch, absorbed lipid, deaminated digested protein and digested dietary fibre. The starch (17.5 MJ/kg) is counted in terms of its glucose (15.7 MJ/kg) yield. (The mass ratio of glucose:glucose residues in starch is taken as 180:162). C18 fatty acids are assumed, and an energy value of 39.6 MJ/kg employed. Protein is counted in terms of the individual amino acids, which have widely differing yields (the stoichiometric calculation indicates some 4.9 MJ/kg from glycine and some 16.6 MJ/kg from isoleucine). For the purposes of comparisons in the present report (but not in the dynamic of the model) an average value will be used which assumes the conventional amino acid mix and a molecular weight of 110 g/mol. In this report (but not in the model), average values are taken for energy cost of deamination, and energy losses in the urine and an energy value of 14 MJ/kg is ascribed to 'protein-derived' ME (Whittemore *et al.*, 2001b). In the model, gross energy yields and energy loss through deamination are calculated from the blend of individual amino acids used as an energy source (and their nitrogen content), and thus these figures are dependent upon the diet and the destination to which amino acids are channelled by the model pig. The digested dietary fibre is presumed to yield volatile fatty acids through the medium of fermentation in the large intestine. This process is energy demanding on the part of the microbial population, and is energy wasteful through gaseous losses. IMS Pig assumes VFA yield in the form of acetate, propionate, lactate and butyrate, and assumes the gaseous losses to be as methane. The present report assumes that one mole of 'fibre-derived' glucose can be converted to either 2 mol of acetate, 2 mol of propionate or lactate; or 1 mol of butyrate, and that the remaining carbon is lost as CO₂. If the ratio of acetate:propionate:butyrate:lactate is 2:1:1:0, then 1 kg of fermented fibre will be converted to 0.74 kg of mixed VFA. Where the energy contents of fully digestible fibre and VFA are 17.5 and 18.7 MJ/kg, this represents an energy conversion efficiency of 0.79. Energy losses, in the form of methane, involved in the process of microbial fermentation of the fibrous fraction itself, in the absence of a more definitive value, are taken as

Table 1 Calculations for the efficiency of energy yield in the form of ATP for purposes of maintenance and protein synthesis

Substrate	Energy (MJ/kg)	ATP yield (mol/kg)	ATP yield (mol/MJ)	Scaled ATP yield (lipid = 1)	Observed efficiency‡	Estimate for k_t
Lipid (C18)	39.6†	514	13.0	1.00	0.94	0.94
Starch (glucose)	15.7§	211	13.5	1.04	0.83	0.80
Protein (ME)	14.0	209	14.9	1.15		
Protein (GE)	23.6	209	8.86	0.683	0.54	0.79
VFA (2: 1 ac: prop: but)	18.7	231	12.4	0.952		
Fibre-derived VFA	17.5	136	7.76	0.599	0.58	0.96

† In the presence of more detailed information concerning the fatty acids given in the diet, the algorithm for calculating ATP yield for fatty acids in **Appendix 1** could be used.

‡ Noblet *et al.* (1993).

§ Mass conversion of starch to glucose = 11.1

|| The 'VFA' row considers the energy yield from a starting mass of volatile fatty acids (VFA); however, the 'Fibre-derived VFA' row considers the energy yield from a starting mass of fibre, converted to usable energy via VFA intermediates. The net yields of the individual VFAs are shown in **Appendix 1**.

20% of the available energy, and a conversion factor of 0.8 is used. This efficiency is calculated from values reviewed by Whittemore *et al.* (2001b), which includes ARC (1981) and Bakker (1996). The model calculates the yield from a particular blend of VFAs at run-time. The default acetate : propionate : butyrate : lactate conversion ratio is set at 10 : 5 : 3 : 2.

For the calculations that follow, the enthalpy of hydrolysis of ATP is taken in this report as 50 kJ/mol (the model does not use this figure). This value is a variable as it is dependent upon cell function (values ranging between 40 and 70 are possible). Table 1 presents the calculations for the efficiency of energy yield in the form of ATP for purposes of maintenance and for the energy-expending element of protein synthesis. As both these systems are similarly requiring of ATP from the available pool, they are analogous with regard to their utilization of substrate energy and may be taken together. Stoichiometric calculation of k_t for maintenance and

protein synthesis ($k_{s(m+p)}$) is given in terms of mol ATP yield per MJ substrate energy (column 3), and this is scaled to lipid = 1 (column 4) as fasting metabolism energy is assumed to be dependent upon the catabolism of body lipid. Reported values of the efficiency of use of ME from various dietary substrate sources for maintenance are therefore assumed to be relative to that of body lipid. The ratio between $k_{s(m+p)}$ (column 4) and empirical determinations of the efficiency of use of energy for maintenance or for protein synthesis (column 5) allows determination of k_t (column 6).

Assuming 50 kJ/mol, the stoichiometrically determined energy yield in the form of ATP (mol/kg) suggests energy yields of 25.7 MJ/kg from lipid, 10.6 MJ/kg from glucose, 10.5 MJ/kg from deaminated protein, and 11.6 MJ/kg from VFA. Per kilogram of fermented fibre (not counting gaseous losses), the energy content of the resultant VFA is 6.8 MJ. These may be compared with the values for

Table 2 Calculations for the efficiency of energy yield for purposes of lipid synthesis

Substrate	Mass conversion (kg/kg)	$k_{s(l)}$ (MJ/MJ)	Observed efficiency (k_L)	Estimate for k_t
Lipid (direct)	0.94	0.94	0.98†	1.04
Lipid (resynthesized)	0.89	0.89	0.74‡	0.83
Starch (glucose)	0.34	0.86	0.73†	0.85
Protein (GE)	0.37	0.61	0.52†	0.85
VFA	0.35	0.74		
Fibre-derived VFA	0.20	0.46	0.43–0.67§	0.93–1.46

† Noblet and Henry (1991).

‡ Black *et al.* (1986).

§ ARC (1981).

|| See footnote comment so marked in Table 1. In the absence of evidence to the contrary, k_t for fibre-derived VFA is assumed to be close to unity.

Table 3 Calculation of IMS Pig model $k_t \times k_s$ efficiency of energy yield

	k_t	$k_{s(l)}$	$k_t \times k_{s(l)}$	Observed efficiency	$k_{s(m+p)}$	$k_t \times k_{s(m+p)}$	Observed efficiency
Lipid†	0.97	0.93	0.90	0.93	1.01	0.98	0.94
Starch (glucose)	0.83	0.85	0.70	0.73	1.04	0.86	0.83
Protein (GE)	0.82	0.61	0.50	0.52	0.68	0.56	0.54
Fibre-derived VFA‡	0.96	0.46	0.44	0.50	0.60	0.58	0.58

† Direct retention : resynthesized retention of 80:20.

‡ See footnote comment marked || in Table 1.

'physiological energy' given by Boisen and Verstegen (2000) of 26.6 for oleic acid and 18.0 for glycerol, 10.5 for glucose, 10.4 for CP (average source), 8.6 for acetate, 12.7 for propionate, and 15.9 for butyrate.

Table 2 presents efficiencies for the retention of lipid. The stoichiometric determination of the efficiency of transfer from mass of substrate to mass of deposited lipid is shown in column 1. The direct lipid-to-lipid value assumes a close relationship between ingested and deposited fatty acids. Calculated $k_{s(l)}$ values (column 2) are compared with those measured empirically (column 3) for the efficiency of use of energy for lipid retention. The resultant residual efficiency, k_r , is given in column 4.

Comparison of the k_t values for the substrates from Tables 1 and 2 show reasonable agreement between the two methods of calculation. Table 3 shows the average k_t values together with the k_s stoichiometric efficiencies for maintenance and protein synthesis and for lipid retention. The product of these two values represents the overall efficiency as employed in the IMS Pig model.

In IMS Pig therefore, the inflexibility of k_{Lr} , k_M and k_{Pr} values is superseded by a combination of experimentally-derived k_t values and stoichiometrically-derived $k_{s(l)}$ and $k_{s(m+p)}$ values. The k_t values are viewed as the inefficiency related to transfer costs, measured in terms of ATP, as shown in Table 4. Table 4 represents for the model the effective

Table 4 ATP cost of k_t

	k_t	Energy cost of k_t (MJ/kg)	ATP cost of k_t (mol/kg)
Lipid	0.97	2.0	15.4
Starch (glucose)	0.83	3.0	35.9
Protein	0.82	4.2	37.6
Fibre-derived VFA†	0.96	0.7	9.2

† See footnote comment marked || in Table 1.

outcomes of Tables 1, 2 and 3. Note that for fibre digestion, 20% of the energy yield is lost as methane, but this is not counted as an energy requirement on the part of the pig. The energy cost of the inefficiency of energy transfer is calculated as $(1 - k_r)$ multiplied by the energy content of the substance concerned. The equivalent ATP cost of transfer is calculated as $(1 - k_r)$ multiplied by the number of moles of ATP per kg obtained for that substance (as shown in Table 1).

The energy requirement for the synthetic element of the retention of 1 kg of protein (i.e. for protein turnover, Px, not counting the energy contained within the amino acids themselves) is suggested by Knap and Schrama (1996) to be 3.92 MJ/kg. This is based upon the assumption that one mole of peptide bonds requires 5 mol of ATP for their synthesis, which is the mode of operation of the present model. However, this includes 1 mol of ATP for transport of metabolites into the cell. As transport is included within k_t values, the model uses a value of 4 mol of ATP required per mol of peptide bonds formed. Most other estimates for this parameter are not based on such net energy yields, and are higher (for example : Whittemore and Fawcett (1976) suggest 5.6 to 9.1 MJ/kg, and elect 7.3). As evidenced above, this value may not be properly expressed as a constant, but will be dependent upon the proportional delivery of substrates, and is a variable that can now be accommodated by the IMS Pig model. This value may be estimated from the presently proposed methodology, using the calculated values of k_t together with the stoichiometrically determined values for the ATP yield from the various dietary substrates. **Appendix 5** shows the outcome of the estimates for the energy cost of protein synthesis for a standard diet, using various estimates of k_r . The IMS Pig delivers, by means of the above methodology, values for the energy cost of protein synthesis that are entirely consistent with expected and published values.

The model pig is assumed to channel its different energy resources into those processes where they can be used most efficiently. Thus dietary lipid is channelled as a priority into lipid retention, whereas dietary starch and glucose is used primarily for satisfying the demand for ATP.

Should the ATP requirement exceed that which can be supplied from the diet, the model will use body lipid as an energy source. Lipid so used does not accrue an associated cost of digestion, but otherwise is modelled as dietary lipid. Should the lipid mass of the pig drop below 5% of empty body weight, the pig will similarly use body protein as an energy source in preference to further lipid.

The order in which metabolites are consumed to provide ATP is as follows: VFA, glucose (from all sources), deaminated amino acids, dietary lipid, catabolized body lipid. Lipid retention is dealt with by the model after the satisfaction of ATP requirement, and thus has its metabolites delivered automatically with reversed priorities.

Nitrogen catabolism

All dietary amino acids not retained, and those amino acids from turned-over tissue that are not recycled are deaminated and the nitrogen excreted. As individual amino acids are modelled, the amount of nitrogen contained within the amino acids can be calculated explicitly, without need of a crude 6.25 multiplier. The net ATP yield of mixed amino acids is also calculated. The energy yield of the deaminated moieties from amino acids (E_N) is calculated according to the following equation, using the nitrogen content of the amino acids (N), as a correction factor to the standard enthalpy of combustion of the amino acids ($Q_{\text{combustion}}$). It is assumed that a standard protein with a nitrogen ratio of 6.25 will have a urinary energy content of 7.2 MJ/kg.

$$E_N = Q_{\text{combustion}} - N \times 7.2/6.25.$$

$Q_{\text{Combustion}}$ is calculated from the enthalpies of the amino acids and their relative abundances.

There are three exit routes from the pig for nitrogenous waste: (a) from the integument, (b) faecal losses from both ileal indigestible amino acids and endogenous losses, and (c) urinary losses through deaminated protein. There is no allowance made in the model for ammonia derived from hind-gut fermentation flow through the animal, or other similar recycling of nitrogen products.

Algorithms for lipid retention

Retained lipid (FA_{Lr}) is derived (a) directly, from 'appropriate' fatty acids (FA_{direct} , from the pool of dietary fatty acids, FA_{pool}), (b) from fatty acids that are broken down and resynthesized ($FA_{\text{turn-over}}$), and (c) from other sources (FA_{other}).

$$FA_{\text{other}} = FA_{\text{VFA}} + FA_{\text{protein}} + FA_{\text{glucose}}$$

$$FA_{\text{direct}} = FA_{\text{pool}} - FA_{\text{turn-over}}$$

The efficiency of conversion of mass of substances into lipid has already been considered in the previous section. The equation for lipid retention (FA_{glucose}) as derived from a blood glucose source ($glucose_{\text{pool}}$) is

$$FA_{\text{glucose}} = glucose_{\text{pool}} \times k_{s(l)glucose} \times GE_{\text{glucose}}/GE_{\text{lipid}}$$

$$Q = glucose_{\text{pool}} \times (1 - k_{s(l)glucose}) \times GE_{\text{glucose}}$$

Lipid retention is associated with the heat loss (Q), due to the imperfect conversion of gross energy, GE. The equations for lipid retention from fatty acids (direct and resynthesized), protein, and VFAs are similar. The lipid retention algorithm is the final algorithm in the model, and all remaining energy moieties in the pools are channelled into it. In the case of protein, the efficiency factor $k_{s(l)protein}$ pertains to gross energy (GE, $Q_{\text{combustion}}$ in the above equation), but the heat output to GE less the energy contained within urea and other excreted nitrogenous compounds (E_N above).

Total lipid retention (FA_{Lr}) can be given by:

$$FA_{Lr} = FA_{\text{other}} + k_{s(l)direct} \times (FA_{\text{pool}} - FA_{\text{turn-over}}) + k_{s(l)turn-over} \times FA_{\text{turn-over}}$$

As mentioned earlier, only 0.80 of retention can come direct from diet sources, and only 0.80 of diet lipid can be used for retention (Lizardo *et al.*, 2000).

$$0.8/(1 - 0.8) \times (FA_{\text{other}} + k_{s(l)turn-over} \times FA_{\text{turn-over}}) \geq k_{s(l)direct} \times (FA_{\text{pool}} - FA_{\text{turn-over}})$$

$$0.8/(1 - 0.8) \times FA_{\text{turn-over}} \geq FA_{\text{pool}} - FA_{\text{turn-over}}$$

Energetic response to environmental temperature

The thermoregulatory algorithms for the IMS Pig model are drawn from the comprehensive review of Whittemore *et al.* (2001b). The flow of heat from the IMS Pig model is constrained to lie within a range of defined limits determined by physical and environmental factors (see also Whittemore, 1998). When cold the pig will increase its heat output, and *vice versa*. When the pig achieves thermoneutrality the environmental temperature will be within the comfort temperature range, and no further metabolic response is asked of the pig. A major route for the

accommodation of excess heat production is through reduction of food intake, but this is not relevant where intake is defined or known. Some reduction in heat output is achieved through reduction in activity, and the model allows the achieved activity factor (maintenance energy multiplier), F_{Activity} to vary from its default value down to zero in order to achieve thermoneutrality.

Increase in heat output is achieved by the oxidation of energy-containing metabolites (cold thermogenesis). Nutrients that would otherwise be directed to protein and lipid retention are diverted to the generation of heat. Responses to both environmental heat and environmental cold are economically unfavourable. The source of metabolites for extra thermal energy is the same as that for ATP production. In the model, extra thermal heat production is considered as a drain upon the ATP pool; it is denoted by E_T and measured in moles of ATP.

Calculated heat production arises from only three sources in the model: first, from food consumed to provide energy in the form of ATP (maintenance, transfer costs [k_i] and the energy requirement for protein synthesis); second, from microbial fermentation in the hindgut; and third, from inefficiencies in the conversion of metabolites into retained lipid. In the first case, the heat output is given (for a single metabolite) by the equation shown below. Q is heat production (MJ), E_x is the heat energy content of substance x (MJ/kg), ATP_{req} is the ATP required for metabolic processes (mol), and ATP_x is the ATP yield of substance x (mol /kg).

$$Q = E_x \times ATP_{\text{req}} / ATP_x$$

The amount of substance x (kg) needed to satisfy the ATP requirement is given simply by ATP_{req} / ATP_x .

The relevant energy contents and ATP yields of substances are as described earlier. For protein, the heat lost is the GE minus the energy contained in the urine, i.e. 16.4 MJ/kg for a protein of 'standard' amino acid composition. Since ATP yield as a function of gross energy varies according to substrate, the heat output associated with metabolism depends upon the processes concerned, the components of the diet, and the order of precedence in ATP energy production.

During the microbial fermentation of fibre to VFA, energy is lost as chemical energy in excreted methane, and as heat. Methane loss is taken as 0.20 of the fibre mass/energy. Of the remaining fibre, there is some loss of CO_2 associated with VFA production, and concomitant loss of energy as heat.

For the 2 : 1 : 1 acetate : propionate : butyrate diet used earlier, the efficiency factor is calculated as 0.79, in terms of energy. Thus, for this diet, heat loss during fermentation of fibre is given by

$$Q = 0.80 \times (1 - 0.79) \times 17.5 \times \text{fibre}$$

which equates to 3 MJ/kg of fibre (NDF) digested. The heat production associated with the synthesis of lipid has already been described above.

Metabolites used for cold thermogenesis are taken by the model after the requirements of protein retention are satisfied and before the calculation of lipid retention is completed. If the needs for cold thermogenesis result in there being insufficient energy for lipid retention to satisfy the minimum ratio of lipid to protein, then protein retention rate is written down *pro rata*.

The bounds of the thermoneutral zone

The heat output of the model pig, Q , is constrained to lie between the upper and lower bounds of possible heat output, Q_{max} and Q_{min} , as determined by its physiology, behaviour, and environment. The algorithms for determining these bounds are largely derived from those used by Bruce and Clark (1979), Black *et al.* (1986), and Knap (2000), with some modifications. At Q_{min} , pigs may huddle in groups of size Pen_n ; at Q_{max} , pigs do not huddle: Pen_n is set at one.

The equation for overall heat flow from the pig is taken from Black *et al.* (1986), as are the equations for external thermal resistance, R_a , the resistance of the floor, R_f , and the tissue thermal resistance, R_t . An initial R_f value is calculated assuming a value of 0.15 for A_f/A (the proportion of skin in contact with the floor). For Q_{max} , if R_f exceeds R_a , then A_f/A is set at 0.1, else at 0.2. For Q_{min} the conditions are reversed. The equation for Ac/A (the proportion of skin in contact with other pigs) is taken from Black *et al.* (1986).

The system of equations to calculate evaporative heat loss was also obtained from Black *et al.* (1986). The total, Q_{sl} , is determined as the result of the equations for $Q_s + Q_l$ in hot and cold conditions, and the correction factor X_H determined to account for humidity. In cold conditions, Q_{sl} is divided equally between Q_s and Q_l (i.e. evaporative heat losses from the skin and lungs, respectively). In hot conditions, Q_l is set to two-thirds of the figure for Q_{sl} . The heat loss through the skin, Q_s , is then set to the Black *et al.* (1986) figure for evaporative losses from wet skin, H_e , subject to a minimum of one-third of Q_{sl} .

Prior to calculation of Q, Ts, the skin surface temperature, is set according to the following system of equations:

$$R_{\gamma} = R_t$$

$$R_{\delta} = 1 / [(Af/A)/R_f + (1 - Ac/A - Af/A)/R_a]$$

$$T_s = T_b - (T_b - T_a) \times R_{\gamma} / (R_{\gamma} + R_{125}).$$

Here, R_{δ} is the average resistance of the skin surface (resistors placed in parallel have additive conductance), and the skin is treated as lying between the tissue and surface resistances, R_{δ} and R_{γ} (resistors placed in series have additive resistance). Initial values for T_s of 32°C and 39°C are used for cold and hot pigs respectively.

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Appendix 1

Incomplete dietary information

In the absence of a starch analysis, starch may be estimated as

$$\text{starch (g/kg)} = 52.6 \times \text{DE (MJ/kg)} - 1.02 \times \text{oil} - 0.69 \times \text{NDF} - 1.25 \times \text{CP}$$

which is derived from the data of Morgan *et al.* (1987). The root mean square (RMS) for this equation was 44 g, and the constant term was removed, lending weight to the suggestion that the fraction of the NSP not accounted for by NDF determination may not be important other than for unusual diet mixtures. Where an estimate of DE is not available for effective solution of the above equation, either for the mixed diet or for the component ingredients, the relationship

$$\text{DE (MJ/kg)} = 17.5 - 0.015 \times \text{NDF} + 0.016 \times \text{oil} + 0.008 \times \text{CP} - 0.033 \times \text{ash}$$

of Morgan *et al.* (1987) for energy may be employed.

Moughan *et al.* (1999) suggest (perhaps rather unsafely) that the quality of feed grade fats could be estimated from the content of free fatty acids (FFA, g/kg), and

$$\text{DE (MJ/kg)} = 37.9 - 0.005 \times \text{FFA} - 8.20 \times e^{(-0.52 \times \text{U/S})}$$

where U/S is the ratio of unsaturated to saturated fatty acids. Using a similar model, Powles *et al.* (1995) proposed for growing pigs

$$\text{DE (MJ/kg)} = 36.9 - 0.0046 \times \text{FFA} - 7.33 \times e^{(-0.906 \times \text{U/S})}$$

The digestibility coefficient can then be taken as DE/39.6. The above equations may have utility where the level of FFA does indeed measure quality, but this is not always the case. The default values for this equation are FFA = 0, and U/S = 1.0 (a 50 : 50 ratio of saturated : unsaturated fatty acids).

Net energy (NE) yields of individual volatile fatty acids (VFAs)

Appendix Table 1.1, below, shows the net yields of the four VFA species, these values are weighted averaged to give values used for the calculations in Tables 1 and 2 (in main text).

Appendix Table 1.1 Net energy yields of individual VFAs

Metabolite	ATP yield (mol/mol)	RMM†	ATP yield (mol/kg)	NE (MJ/kg)‡	Reported NE (MJ/kg)	Lipid mass conversion (kg/kg)
Acetate	10	60	167	8.33	8.6	0.287
Propionate	21	74	284	14.2	12.7	0.300
Butyrate	27	88	307	15.3	15.9	0.530
Lactate	18	90	200	10.1		0.351

† Relative molecular mass (g/mol).

‡ Based on an estimated ATP hydrolysis enthalpy of 50 kJ/mol.

ATP yield of fatty acids

In the presence of information concerning the fatty acid profile of the diet, the following algorithm can be used to calculate the ATP yield of fatty acids. A single molecule of palmitate yields 129 mol ATP and has a relative molecular mass (RMM) of 256 units.

Adding a C₂H₄ unit yields an extra 17 mol ATP and 28 mass units.

Adding a single double bond deducts 2 mol ATP and 2 mass units.

For an (x: y) fatty acid, (where x indicates the length of the carbon chain, and y the number of double bonds) therefore:

$$\begin{aligned} \text{ATP yield (E, mol)} &= 8.5 \times x - 7 - 2 \times y \\ \text{RMM (mass units)} &= 32 + 14 \times x - 2 \times y. \end{aligned}$$

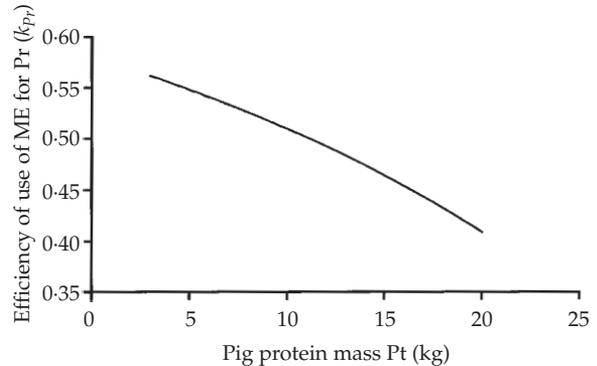
Thus, 1 kg of fatty acid provides an ATP yield of (mol/kg)

$$(1000/\text{RMM}) \times \text{E.}$$

Appendix 2

Appendix Table 2.1 gives the energy costs that may be deduced from the characterization of protein turn-over, together with equivalent values determined empirically by others. The purpose of **Appendix Table 2.1** is to test the likely veracity of the newly proposed IMS Pig methodology, and it is presumed that Pr was not limited by nutrient supply. Values for B and Pt_{max} for the Gompertz function determining Pr are set for pigs of good genetic merit.

For the purpose of verification of the protein turn-over engine (but not use in the dynamic model itself), the energy cost of synthesizing/re-synthesizing 1 kg of body protein, in the course of the turn-over of existing tissue and the retention of new, is taken from van Es (1980) and Knap and Schrama (1996), and assumed to be 3.92 MJ ME per kg protein synthesized. In operational mode IMS Pig calculates this value *de novo* as a function of the nutrient substrates supplied.



Appendix Figure 2.1 Efficiency of use of metabolizable energy when used for protein retention (k_{Pr}), plotted against total body protein mass.

Appendix Table 2.1 Energy costs determined from protein turn-over characteristics for pigs growing from 20 to 120 kg live weight (from Whittemore et al., 2001b)

	Protein mass (Pt, kg)				
	4	8	12	16	20
Protein retention (Pr, kg/day) ¹	0.111	0.155	0.173	0.176	0.166
Total protein turn-over (Px, kg/day) ²	0.534	0.840	1.08	1.27	1.45
Px / Pt ³	0.133	0.105	0.090	0.080	0.072
Energy cost of Px (MJ ME per day) ⁴	2.09	3.29	4.22	5.00	5.67
Efficiency of use of ME for Pr (k_{Pr}) ⁵	0.55	0.53	0.49	0.45	0.41
Maintenance element (MJ ME per day) ⁶	0.784	1.57	2.35	3.14	3.92
E_M (MJ ME per day) ⁷	5.45	9.37	12.9	16.1	19.1
Maintenance element/ E_M ⁸	0.14	0.17	0.18	0.19	0.21
Energy cost of Pr (MJ ME per day) ⁹	4.70	6.94	8.31	9.15	9.60
Corrected E_M (MJ ME per day) ¹⁰	4.67	7.80	10.6	13.0	15.2
Total M + Pr (MJ ME per day) ¹¹	9.37	14.7	18.9	22.2	24.8
From Quiniou <i>et al.</i> (1996)					
Energy cost of Pr (MJ ME per day) ¹²	5.35	7.47	8.33	8.48	8.00
E_M (MJ ME per day) ¹³	5.39	8.99	11.5	13.6	15.6
Total M + Pr (MJ ME per day) ¹⁴	11.3	16.5	19.8	22.1	23.6
From NRC (1998)					
Energy cost of Pr (MJ ME per day) ¹⁵	5.82	8.13	9.07	9.23	8.71
E_M (MJ ME per day) ¹⁶	4.96	8.35	11.3	14.0	16.6
Total M + Pr (MJ ME per day) ¹⁷	10.8	16.5	20.4	23.2	25.3

¹ $Pr_{max} = Pt \times B \times \ln(Pt_{max}/Pt)$; B = 0.012, $Pt_{max} = 40$.

² $Px_{max} = Pt \times B \times \ln(Pt_{max}/Pt) \times (1/z) \times Pt_{max}/(Pt_{max} - Pt)$; z = 0.23.

³ $Px_{max}/Pt = B \times (1/z) \times \ln(Pt_{max}/Pt) \times Pt_{max}/(Pt_{max} - Pt)$.

⁴ (Px \times 3.92).

⁵ $(Pr \times 23.6) / ((Px \times 3.92) + (Pr \times 23.6))$.

For pigs of lesser protein growth potential with B = 0.010 and $Pt_{max} = 30$, values of 0.55, 0.50, 0.45, 0.39 and 0.32 were returned.

⁶ $(0.05 \times Pt) \times 3.92$ (k values are not used here, so the 5 mol ATP per mol of peptide bonds paradigm is required).

⁷ Energy cost of maintenance calculated independently of turn-over when Pr > 0 from $E_M = 1.85 \times Pt^{0.78}$.

⁸ Proportion of maintenance that can be attributed to the energy cost of protein turn-over occurring at maintenance (Pr = 0).

⁹ Total energy expended in achieving protein retention. (Px \times 3.92) + (Pr \times 23.6).

¹⁰ E_M (?) - Maintenance element (⁶).

¹¹ Sum of corrected energy cost of maintenance and energy cost of protein retention.

¹² $k_{Pr} = 0.49$ (Quiniou *et al.*, 1996).

¹³ $E_M = 0.860 \times W^{0.60}$; W = Pt \times 6.25 (Quiniou *et al.*, 1996).

¹⁴ Sum of energy cost of maintenance and energy cost of protein retention (Quiniou *et al.*, 1996).

¹⁵ $k_{Pr} = 0.45$ (NRC, 1998).

¹⁶ $E_M = 0.444 \times W^{0.75}$ (NRC, 1998).

¹⁷ Sum of energy cost of maintenance and energy cost of protein retention (NRC, 1998).

Out-turn values calculated for k_{pr} (⁵) are also shown in **Appendix Figure 2.1** and diminish with increasing Pt over a range of values consistent with those measured empirically and reported in the literature (Whittemore *et al.*, 2001b). The efficiency of use of energy for the retention of protein (k_{pr}) is sensitive to the value ascribed to z ; lower values reduce the efficiency (when Pt = 4, and $z = 0.18$, then $k_{pr} = 0.49$). Estimates for the energy expended in the retention of protein (⁹) may be compared with those that would result from the use of $k_{pr} = 0.49$ (¹²) as determined by Quiniou *et al.* (1996), and from $k_{pr} = 0.45$ (¹⁵) as favoured by NRC (1998). Similar comparisons may be made for energy expended in relation to maintenance (¹⁰) with (¹³ and ¹⁶).

Because of the difficulty in differentiating the energy costs of protein retention and of maintenance, an informative comparison may be between the totals (¹¹) with (¹⁴) and (¹⁷). Model output (¹¹) is in agreement with these predictions at high values for Pt, but lower at low Pt. However, the agreement is sensitive to the level of protein retention: in the table shown it is considered as maximal. At maintenance (Pr = 0), model output reduces to E_M only, which over most of the range of Pt is higher for (⁷) than (¹³) and (¹⁶).

Appendix 3

Appendix Table 3.1 Amino acid profiles for various purposes of replacement/retention†

Purpose	Amino acids										
	Lys	Thr	Met	Cys	Trp	Ile	Val	Leu	Phe	Tyr	His
Protein retention	72	38	18	10	8	35	47	75	38	25	30
Integument losses	43	32	10	45	9	24	36	50	29	18	12
Endogenous gut losses	54	46	23	31	23	36	63	60	40	56	21
Maintenance turn-over	65	98	18	62	17	49	44	45	33	46	21
Non-maintenance turn-over	66	38	19	13	10	34	45	75	38	25	28

† Values are derived from the review of Whittemore *et al.* (2001c). For protein retention, these values are derived from the equations of Kyriazakis *et al.* (1993), evaluated at a protein mass of 9.6 kg (approx. 60 kg live weight). All numbers refer to proportions of the form g/kg. Non-essential amino acids are assumed to be retained in the following profile: arginine, 67; alanine, 64; aspartic acid and asparagine, 87; glutamic acid and glutamine, 136; glycine, 92; serine, 42; proline, 68. These values were derived from Kyriazakis *et al.* (1993), as above. Where, in the above profiles, the values for Arg-Pro are absent, these are interpolated from the profile for protein retention.

Appendix 4

Appendix Table 4.1 uses the protein turn-over characteristics identified for **Appendix Table 2.1**.

For a diet protein of typical composition, the IMS Pig model, based upon the characterization of protein turn-over, returns estimates for maintenance [$P_{X_m} = 0.05 \times Pt$] (³) that are similar to those suggested elsewhere (Whittemore *et al.*, 2001b and demonstrated by Carr *et al.*, 1977 (¹²)). The amount of total amino acid required to support turn-over at maintenance may be expressed as $0.003 \times Pt$, which takes account of protein losses consequent upon maintenance protein turn-over and gives requirements that are some 0.15 greater than for Pr alone (⁴). The maximum efficiency of use of ileal digested ideal protein, v_{max} (⁵) is therefore 0.85, which pertains when there is no excess amino acid supply. This efficiency is consistent with maximum values reported in the literature (Whittemore *et al.*, 2001c). Reduction in the value ascribed to z in the equation [$P_x = Pr \times (1/z) \times Pt_{max}/(Pt_{max} - Pt)$] will reduce the maximum efficiency possible for the conversion of ileal digested ideal protein to body protein (if $z = 0.18$, values for v_{max} of around 0.80 are returned). Losses in skin and hair, and endogenous faecal losses are estimated as described above (⁶), and allow the determination of the total requirement (⁸) for ileal digested amino acids (expressed in the table as ideal protein) when standardized values are used for the characterization of the ileal digestibility of amino acids in foodstuffs. If, for purposes of present comparisons, ideal protein is assumed to contain 70 g/kg of lysine, then the lysine requirement and the lysine energy ratio can be determined (^{9,11}), using the energy requirement previously calculated in **Appendix Table 2.1**. These values exclude any concomitant energy costs of lipid retention. Kyriazakis and Emmans (1992b) working with pigs growing to 30 kg concluded that the efficiency of use of ileal digested ideal protein was energy dependent and has a maximum value of 0.82. They forwarded the equation for efficiency $v_{max} = 0.0012 \times ME/CP$ (where ME denotes metabolizable energy [MJ/kg food] and CP digested CP [kg/kg food]). This reaches a value of 0.82 in the calculated region of 1.3 g lysine per MJ ME.

Vector notation for amino acid flow

$$\begin{aligned}
 \mathbf{A}_{prod} &= (P_x - P_{X_m} - Pr) \times \mathbf{A}_{Pxt} + P_{X_m} \times \mathbf{A}_{Pxm} \\
 \mathbf{A}_{req} &= Pr \times \mathbf{A}_{Pr} + (P_x - P_{X_m} - Pr) \times \mathbf{A}_{Pxt} + P_{X_m} \times \mathbf{A}_{Pxm} \\
 E_{P_x} &= Pr \times E(\mathbf{A}_{Pr}) + (P_x - P_{X_m} - Pr) \times E(\mathbf{A}_{Pxt}) \\
 E(\mathbf{i}) &= 1000 \times \sigma / (\mathbf{RMM} \cdot \mathbf{i})
 \end{aligned}$$

In the above, \mathbf{A}_{req} is a vector containing the masses of amino acids required for the resynthesis and retention part of turn-over, \mathbf{A}_{prod} describes the amino acids produced during the desynthesis part of turn-over. \mathbf{A}_{Pr} , \mathbf{A}_{Pxt} and \mathbf{A}_{Pxm} are respectively vectors containing the proportions of each amino acid that make up newly retained protein, turned-over protein, and maintenance turn-over protein. E_{Px} is the total energy requirement (mol ATP) of protein turn-over, and \mathbf{RMM} is a vector containing the relative molecular weights of the amino acid residues. σ is the number of moles of ATP required to form a peptide bond, taken as 4. E_{Px} does not contain a term for the energy cost of maintenance protein turn-over, as this is already included in the empirically derived maintenance energy, described elsewhere.

Appendix Table 4.1 Protein requirements determined from protein turn-over characteristics for pigs growing from 20 to 120 kg live weight

	Protein mass (Pt, kg)				
	4	8	12	16	20
Protein retention (Pr, kg/day) ¹	0.111	0.155	0.173	0.176	0.166
Total protein turn-over (Px, kg/day) ²	0.534	0.840	1.08	1.27	1.45
IP for maintenance (IP _m , kg/day) ³	0.012	0.024	0.036	0.048	0.060
IP for Pr (IP _{Pr} + IP _{PTO} , kg/day) ⁴	0.131	0.181	0.202	0.204	0.193
Efficiency of use of IP for Pr (v_{max}) ⁵	0.85	0.86	0.86	0.86	0.86
Losses in skin and hair (kg/day) ⁶	0.001	0.002	0.003	0.003	0.004
Endogenous gut losses (kg/day) ⁷	0.027	0.045	0.061	0.076	0.089
Total requirement (kg/day) ⁸	0.171	0.252	0.302	0.331	0.346
Lysine requirement (kg/day) ⁹	0.0120	0.0176	0.0211	0.0232	0.0242
Energy costs for M + Pr (MJ ME per day) ¹⁰	9.37	14.7	18.9	22.2	24.8
Lysine: energy ratio (g lysine per MJ ME) ¹¹	1.28	1.19	1.12	1.05	0.98
IP _m (kg/day) ¹²	0.011	0.018	0.024	0.030	0.035

¹ $\text{Pr}_{\text{max}} = \text{Pt} \times B \times \ln(\text{Pt}_{\text{max}}/\text{Pt})$; $B = 0.012$, $A = 40$.

² $\text{Px}_{\text{max}} = \text{Pt} \times B \times \ln(\text{Pt}_{\text{max}}/\text{Pt}) \times (1/z) \times \text{Pt}_{\text{max}}/(\text{Pt}_{\text{max}} - \text{Pt})$; $z = 0.23$.

³ $0.003 \times \text{Pt}$.

⁴ $(0.06 \times \text{Px} - 0.003 \times \text{Pt}) + \text{Pr}$.

⁵ $\text{Pr}/((0.06 \times \text{Px} - 0.003 \times \text{Pt}) + \text{Pr})$. The maximum efficiency of use of ileal digested ideal protein for purposes of the retention of protein, and when protein is not supplied in excess of requirement (v_{max}).

⁶ $0.0001 \times (\text{Pt} \times 6.25)^{0.75}$.

⁷ Where food intake is $0.09 \times W^{0.75}$; $0.020 \times (0.09 \times W^{0.75}) + 0.0006 \times W^{0.75}$.

⁸ Sum of (^{3,4,6,7}).

⁹ Assuming 0.07 kg lysine per kilogram ideal protein.

¹⁰ Sum of corrected energy cost of maintenance and energy cost of protein retention (**Appendix Table 2.1**).

¹¹ For purposes of protein retention plus maintenance only, that is assuming lipid retention is zero. (⁹)/(¹⁰) $\times 1000$.

¹² From Carr *et al.* (1977). $0.94 \times (\text{Pt} \times 6.25)^{0.75}/1000$.

Appendix 5

Appendix Table 5.1 shows comparative values for the energy cost of protein synthesis. The diet entered into this example calculation comprised 400 g/kg starch, 200 g/kg protein, 150 g/kg NDF, and 40 g/kg lipid (calculated ME content, 14.0 MJ). The calculation assumes all the protein is deaminated.

Appendix Table 5.1 Energy cost of the synthesis of protein

	$k_{\text{t(starch)}}$	$k_{\text{t(lipid)}}$	$k_{\text{t(protein)}}$	$k_{\text{t(fibre)}}$	Net ATP yield (mol/kg)	Energy cost of protein synthesis (MJ/kg)†
Maximum efficiency	1.00	1.00	1.00	1.00	177	3.60
Noblet <i>et al.</i> (1993)	0.80	0.94	0.79	0.96	147	4.32
Noblet and Henry (1991)	0.85	1.04	0.85	0.96‡	156	4.07
Knap and Schrama (1996)						3.92
IMS Pig	0.83	0.97	0.82	0.96	152	4.19

† As for Px. See footnote 4 to **Appendix Table 2.1**.

‡ Noblet *et al.* (1993).