

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

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Abstract

A review of work reported in the literature was used to present quantitative descriptions of energy dispositioning in the growing pig. These are detailed in the text, which points to preferred values, as well as to anomalies and lacunae. The review was prepared with the objective of allowing from its content the inclusive and quantitative modelling of energy requirement. Requirement is approached as the sum of the component factors; maintenance, protein retention and lipid retention. Conventional expressions of maintenance requirement, as some function of pig mass, were found unconvincing in their variety of expression of coefficients and exponents. The review concluded that maintenance is properly related to protein turn-over, and thereby requires at least to include elements of concomitant protein metabolic activity. It was also judged that maintenance costs might be farm-specific. The energy requirements for activity, gaseous losses and disease were identified as important, but unsatisfactory in their quantification. Exploration of the energy costs of uncomfortable ambient temperatures suggested that whilst the responses of the pig are open to sophisticated and relatively exact calculation, the description of comfort remained inexact. The efficiency of retention of lipid by direct incorporation was high and may comprise a substantial proportion of the dietary lipid supply. There was little evidence of variation in the efficiency of utilization of metabolizable energy from carbohydrate for lipid retention. The linear-plateau paradigm for protein retention was adopted. The efficiency of utilization of energy for protein retention measured by a variety of approaches was found to be highly variable, prone to error and the literature confused. It was concluded that the efficiency of use of metabolizable energy for protein retention would be a function of at least: (a) the absorbed substrate being metabolized for the synthesis of body protein, (b) the rate of total protein tissue turn-over associated with the retention of newly accreted protein and not already accounted in the estimate of maintenance, (c) the mass of protein tissue involved in turn-over, and (d) the degree of maturity attained, and any influence maturity may have upon the rate of turn-over of total body protein. Algorithms for energy requirement are presented based upon protein turn-over and these appear to have some consistency with empirical findings.

Keywords: energy, nutrient requirements, pigs.

Introduction

The utilization of nutrients by animals comprises three aspects: 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. A methodology for the recommendation of nutrient

allowance is approached through quantification of nutrient requirement for growing pigs at various levels of performance and within differing environmental conditions. The value of this approach to the optimization of pig production systems is affirmed by Jean dit Bailleul *et al.* (2000). Whilst the accommodation of varying performance level is essential to meaningful calculation of requirement, the present review does not attempt the

quantification of the components of growth; for which see Schinckel (1999) and Emmans and Kyriazakis (1999).

The proposition of Kielanowski (1965) for energy requirement (E , MJ metabolizable energy (ME) per day), whereby energy intake is regressed on protein and lipid deposition, has been the basis for many models representing energy utilization in growing pigs and serves as the 'point of departure' for this paper:

$$E = E_M + E_{Pr}/k_{Pr} + E_{Lr}/k_{Lr}.$$

This model states that energy (E) is used for maintenance (E_M), protein retention (Pr ; $E_{Pr} = 23.8Pr$ (MJ/kg)) and fat retention (Lr ; $E_{Lr} = 39.6Lr$ (MJ/kg)). The efficiencies of the latter two (k_{Pr} , k_{Lr}) are not the same, so the overall efficiency of use of ME will depend upon the ratio of each of the three functions E_M , E_{Pr} , E_{Lr} . An error in the estimate of any one parameter will result in a counterbalancing error in the others, as all must sum to a statement of the ME input. This implies that estimates reached independently of each other in different experiments and by different methodologies are liable to misuse when placed together. Rarely has there been compliance with this implication when estimates for E_M , k_{Pr} and k_{Lr} are put together in an attempt to predict the requirement for E (Agricultural Research Council (ARC), 1981; National Research Council (NRC), 1998). Despite usage to the contrary, the Kielanowski model makes no demand that E_M is independent of the rate of energy retention, nor that E_M is some function of live body weight, nor that the efficiencies (k) are fixed in value. For completeness, the model should include terms for the energy cost of cold thermogenesis (E_T), the energy cost of disease (E_D) and activity (E_A). Again despite common usage, the determined costs of E_T , E_D and E_A are unlikely to be independent of the general rate of heat output ($E_M + ((E_{Pr}/k_{Pr}) - E_{Pr}) + ((E_{Lr}/k_{Lr}) - E_{Lr})$). Conventionally, the heat output resultant from energy expenditure in the arrangement and deposition of minerals in growing bone, and the energy associated with the formation and storage of glycogen are rolled into E_M . The effective energy system of Emmans (1994) also counts as important separable elements in the usage of energy: those associated with nitrogen excretion, the elimination of faecal organic matter and the generation of gaseous escapes of E (E_{Gas}). This energy is used, but is not available for metabolism.

It is the intention of the paper to elaborate the variable, but inter-dependent, nature of present estimates for the energy requirement of protein retention, lipid retention and maintenance in the

growing pig. It is evident that some elements of energy usage are more advanced in their quantitative expression than others. This is reflected in the apportioning of the text but does not necessarily reflect relative importance. The consideration of energy requirement implies consideration also of food intake and this is addressed in the previous review of Whittemore *et al.* (2001).

Maintenance

Black and de Lange (1995) stated that the 'major energy-demanding processes for maintenance of an animal include those associated with blood flow, respiration, muscle tone, ion balance and tissue turn-over, those associated with activity and the ingestion of food, and those associated with the control of body temperature. The energy requirements of the first group of processes have been measured as the heat production of a fasting animal when lying recumbent.' In the Kielanowski (1965) model, maintenance is all the energy that is metabolizable but not directly attributable to protein or lipid growth. For the actively growing animal, however, the paradigms become incoherent as many energy using processes (including, but not only, protein turn-over) are common to, and interact with, both maintenance and production. Slower growing animals have lower maintenance requirements than faster growing ones, and (due to turn-over costs) animals with relatively greater visceral mass have a higher maintenance requirement (Koong *et al.*, 1983). Visceral mass will be influenced by quantity and type of diet.

Utilization of energy below maintenance, including the metabolism of body stores to generate ATP, is more efficient than that above maintenance. Blaxter and Boyne (1978) suggest the slope expressing the regression of energy retention on energy intake diminishes curvilinearly with increasing energy intake but ARC (1981) presumes linearity. Maintenance (E_M) may be estimated as the fasting heat production divided by the efficiency factor (k_M) and ARC (1981) suggests k_M to be 0.81. This loss in efficiency of 0.19 is the heat loss that follows from the consumption of food (its ingestion, digestion and metabolism) taking place between fasting and the achievement of maintenance (Noblet *et al.*, 1993a). There is no reason to seek k_M as a constant. It will vary according to energy source, in common with other coefficients involved in the shift from ME to net energy (NE). Noblet *et al.* (1993a) measured k_M , the efficiency of utilization of ME for the NE of maintenance in sows, to average 0.77. This average was the composite of k_M values of 1.00, 0.82, and 0.70 for dietary lipid, dietary starch and sugar, and dietary digested protein respectively. Noblet *et al.*

(1993a) also referred to their earlier work which found that for growing pigs k_M values were 0.94, 0.83, and 0.54 for digested lipid, digested carbohydrate and digested protein respectively. The same group identified a k_M of some 0.82 for products absorbed from the small intestine and some 0.56–0.59 for products (derived from cell wall non-starch polysaccharide (NSP)) absorbed from the hind gut. E_M is therefore affected by, and k_M can be calculated from, the diet composition. Thus Noblet *et al.* (1994b) suggested $k_M = 0.672 + 0.00066 \text{ lipid} + 0.00016 \text{ starch}$. The fermenting of carbohydrate (rather than enzymic digestion) leads to losses of some 0.2 of the available energy as methane and of some 0.06 as heat, and additional losses will accrue in the support of hind-gut bacteria. Further, energy generated from volatile fatty acid (VFA) is used some 0.15 less efficiently than that from other nutrient substrates (Bakker, 1996), due to less effective conversion into ATP upon oxidation. The k_M appropriate for the products of hind gut digestion remains speculative, a wide range of values having been determined in practice (Bakker, 1996).

It is accepted that the state of maintenance is physiologically highly unlikely, as energy balance will be associated with simultaneous lipid loss and protein gain (Whittemore *et al.*, 1981; van Milgen and Noblet, 1999). The following analysis, for simplicity in an arena already sufficiently complex, will therefore restrict itself to the maintenance energy usage in pigs whose state is above maintenance.

Maintenance requirement (E_M , MJ ME per day) is usually expressed as a function of live weight to the three-quarter power ($W^{0.75}$). It is logical to associate a substantial proportion of the costs of maintenance to the energy requirement of protein turn-over that will occur even when there is no protein accretion. Kielanowski (1972), Graham *et al.* (1974) and Whittemore (1983), noting the ability of the exponent to take out the effects of animals fattening as they grew bigger and the likely relationship between maintenance and the fat-free body mass, suggested an exponent of unity for animals which were lean. Certainly, it has long been noted that the appropriate exponent tends to fall as W increases (Whittemore, 1976), or put another way and as confirmed again recently by van Milgen *et al.* (1998), fasting heat production falls with increasing W when the 0.75 exponent is used. For the Large White breed, E_M was 0.626 MJ ME. $W^{0.75}$ at 28 kg and 0.533 MJ ME. $W^{0.75}$ at 60 kg. These workers also found a tendency for fasting heat production to be lower in pigs which were also fatter. Knap (2000) interpolated the classical data of Thorbek to show E_M (MJ ME) when expressed as a function of $W^{0.75}$ to decline

curvilinearly from some 0.750 at 20 kg to 0.550 at 40 kg, 0.450 at 60 kg, and 0.400 at 80 kg. A commonly used mean estimate for E_M is 0.444 MJ ME. $W^{0.75}$ (NRC, 1998); Knap (2000) favoured 0.504, Noblet *et al.* (1993a) 0.400. Regressing ME intake on $W^{0.75}$, E_{Pr} , and E_{Lr} , Noblet *et al.* (1999) determined E_M as ranging between 0.434 and 0.523. $W^{0.75}$, measured concomitantly with values for k_{Pr} and k_{Lr} of 0.43 and 0.91 respectively. The three-quarter power was not however the most appropriate exponent; 0.60 giving best fit. Using this value, E_M was determined as 0.917 to 1.081. $W^{0.60}$, measured concomitantly with $k_{Pr} = 0.62$ and $k_{Lr} = 0.84$. ARC (1981) had earlier found a line of better fit to be 0.719 MJ ME. $W^{0.63}$. Curvature in the ARC line is highly influenced by estimates of E_M for pigs of less than 20 kg W , and for pigs of 20 to 120 kg W a simplistic $E_M = 3.0 + 0.1W$ can be computed. On grounds that much of maintenance may be related to the turn-over of the protein mass, then where Pt is the protein mass of the pig, there is also some logic in the linear $E_M = 1.68 + 0.952Pt$ or the fitted curve $E_M = 1.85Pt^{0.78}$ of Whittemore (1983). Importantly, the work of Rao and McCracken (1991 and 1992) points to faster growing and leaner genotypes (and sexes) having higher requirements for maintenance (around 0.600 MJ ME. $W^{0.75}$), which adds to the rationality of expressing E_M as a function not of W , but of Pt .

The report of Quiniou *et al.* (1996) suggests Large White pigs to have a maintenance requirement some 10% higher than the Pietrain. Noblet *et al.* (1999), in a detailed and complete examination of pigs widely differing in fatness, concluded E_M to be influenced by breed, but not muscle mass or sex. Neither did NRC (1998) conclude any effect of sex *per se* from their review. Importantly, however, Black *et al.* (1986) take from the literature the conclusion that there is a sex and breed effect upon the requirement for maintenance. They attribute this to the influence of the proportion of the body mass that is protein, and it is this that largely influenced these authors to follow Whittemore (1983) and express maintenance as a function of protein mass. Tess *et al.* (1984a), in common with other reports in the literature, found that when expressed as a function of $W^{0.75}$ the estimate of fasting heat production fell with increasing pig weight. They argued that a relationship with protein mass was more plausible; especially given the contribution to heat production from the viscera. Their data appeared to be best fitted when fasting heat production was expressed as a function of lean mass using the exponent 0.84, but they also give, for fasting heat production in 17-week-old pigs, 1.68Pt^{0.79}. Van Milgen *et al.* (1998) stated that their data indicated no single coefficient (for either W or Pt) to be appropriate for the range of

pig types (breed/sex groups) studied. This illustrates the limitation of using simple mathematical relationships to represent maintenance energy requirements either as a function of body weight or total body protein mass.

Perhaps the most important consideration in the estimation of E_M is the great variation between experiments, and the substantial error associated with each. Experimental methodology (serial slaughter, calorimetry, statistical models used, range of live weights covered) has a substantial impact on variation in estimates of E_M . Food effects (including visceral mass), environment, activity and disease are but some of the inevitable further causes of variation between experiments. Luiting (1999) contributes to the complexity with the finding that efficiency in the use of energy for maintenance is not only variable, but heritable and therefore likely to be dependent upon genetic makeup and selection pressures. Knap (2000) asserts E_M to be not only a relevant component of breeding objectives but the most significant one, once fatness targets are satisfied.

Unsurprisingly, estimates of E_M and estimates of k_{Pr} are confounded, and the efficiency k_M may also be affected by the values attributed to other efficiencies, especially k_{Pr} (van Milgen and Noblet, 1999). Knap (2000) recounts evidence of maintenance estimates being positively associated with the rate of protein growth, (Pr). Knap (1996) suggested that for every 1% increase in the maximum rate of protein deposition (Pr_{max}) there will be a related increase of approximately 0.1% in E_M . Maintenance being a function of growth rate would be oxymoronic were it not for estimates of maintenance in growing pigs being required while they are indeed growing. Tess *et al.* (1984b) in a comprehensive review found k_{Pr} to vary from 0.36 to 0.57, and the value apportioned to be strongly related to (confounded with) E_M . The relationship between the energy cost of maintenance and the energy cost of protein retention will be discussed at greater length in the later section dealing with the energy requirement for protein retention. Van Milgen *et al.* (1998) asserted that fasting heat production is a function of the proportion of the body that is as viscera and van Milgen and Noblet (1999) found that it was the viscera (always a higher proportion of the body in the younger and more actively growing animal) and not the muscle which was the most significant contributor to maintenance heat production. Noblet *et al.* (1999) found that the viscera contributed three times more to E_M than the muscle mass.

A substantial component of maintenance must be the energy required for protein turn-over taking place

when $Pr = 0$. Knap and Schrama (1996) calculated that 0.35 of E_M was attributable to protein turn-over (at $Pr = 0$). When $Pr > 0$, protein turn-over is also the major component of k_{Pr} , in addition to E_M . Some 0.5 of E_M is devoted to activities relating to tissue turn-over and 0.5 to activities relating to the functioning of the organs (Milligan and Summers, 1986). The appropriate placement of the energy associated with tissue turn-over will presumably migrate from E_M to (E_{Pr}/k_{Pr}) as Pr increases. This reinforces the need to calculate both simultaneously from the same data, as demonstrated in the work of Noblet *et al.* (1999). The fearfulness of Whittemore and Fawcett (1976) of double-counting when utilizing estimates of E_M from data sets different from those estimating k_{Pr} and k_{Lr} was elaborated by Whittemore (1976). The former corrected E_M by the energy cost of protein synthesis associated with (minimal) maintenance turn-over (0.05Pt), which would in the growing pig be accommodated also in the estimate of k_{Pr} . Thus $E_M = 0.475.W^{0.75} - (7.3(0.05Pt))$. Black *et al.* (1986) cater for the same anomaly by first reducing the 1.85 coefficient of Whittemore (1983) to 1.67, and then adding an element that is a function of the rate of gain. Thus $E_M = 1.67 \cdot Pt^{0.78} + 2.8 \cdot LWG$, where LWG is the daily live-weight gain (kg). It is relevant that Black *et al.* chose a single fixed value for k_{Pr} , (that of ARC (1981); 0.54), whereas Whittemore (1983) chose a variable value for k_{Pr} , which increases with Pt, that is, as the pig grows. Knap and Schrama (1996) went on to argue that in view of the relationship between E_M and protein metabolism, E_M would necessarily vary both with protein mass (Pt), and with the proportion of Pt commanded by the various protein pools which differ widely in their rates of turn-over.

Van Milgen and Noblet (1999) exposed the data reported by Noblet *et al.* (1999) to an alternative and more rigorous multivariate analysis but came to generally similar conclusions that E_M ranged between 0.913 and $1.070.W^{0.60}$ when associated with k values above maintenance (thus avoiding double counting, but not avoiding confounding) of 0.60 and 0.82 for protein and fat respectively. Van Milgen and Noblet (1999), in common with others, express their dissatisfaction with the presentation of a 'maintenance requirement' for fast growing animals patently not seeking energy for purposes of maintaining themselves. Given the evidence of dependence of E_M on protein mass and metabolism, it might be suggested that there would be merit in not differentiating between E_M and (E_{Pr}/k_{Pr}). Van Milgen and Noblet (1999) however consider there to be no available alternative. An exposition of an energy expenditure system based around a framework of the thermic effect of feeding is given in van Milgen and Noblet (2000).

Argument as to the nature of 'maintenance' in an animal that is growing to a greater or lesser extent can be sterile (Moughan *et al.*, 1995; Knap, 2000). But what 'maintenance' in the growing animal cannot avoid being is a residual. For the animal in energetic balance, maintenance energy is all of its energetic input. For the animal that is growing it is that which is not accountable elsewhere. Maintenance is unavoidably that proportion of E that is left over after account is taken of energy usage for protein deposition, lipid deposition, cold thermogenesis, activity, disease, and all the rest. The rub is that it follows that reliable estimation of E_M requires knowledge not only of 'all the rest', but also of E, the dependent variable. These issues are further addressed by Emmans (1999). The Kielanowski (1965) regression approach to maintenance estimation, with $y = E$ and $x = E_R$, the energy retention, and the constant representing E_M , has the high predisposition to error common to all back-extrapolations of data sets distant from the origin. It is likely that E_M is not a constant function of W, regardless of choice of exponent, nor is sex and breed likely to be sufficient to account for variation in E_M , which appears inextricably bound up with both Pt and Pr. Even the sophisticated analysis of van Milgen and Noblet (1999), must presume that over the prevailing weight range k_{Pr} and k_{Lr} values are each constant. This is unrealizable. Values for k_{Pr} and k_{Lr} are necessarily a function at least of the nature of the energy supply (Whittemore, 1999). Further, there is little evidence to support constancy of the value for k_{Pr} over increasing values for Pt and for Pr, even when the same food is ingested, as discussed below. As apparent from the above, a variable value for k_{Pr} will inevitably lead to a variable value for k_M , and variation in E_M .

Milligan and Summers (1986) affirmed the probability that at food intakes above maintenance, a number of activities considered to be those of maintenance are elevated. For rapidly growing animals therefore the concept of an energy cost of maintenance is anachronistic. There might be benefit in not distinguishing between E_M and E_{Pr} , were it not for the important possibility that variation in the 'fixed costs' of growth are likely to have genetic, food and environmental components which would benefit from their separate identification (Knap, 2000).

In summary, it may be surmised that a general algorithm for the estimation of E_M will require at least to include elements of knowledge of concomitant protein mass and protein turn-over activity. Maintenance and production appear to be inextricably related when the pig is growing actively, while fasting metabolism may not make a proper

point of departure for a fully feeding animal. Linearity of E_M is unlikely if it is associated with a non-linear growth function. Fixed values for the coefficients and exponents have been shown to be unrealistic, and to try to identify such values may thus be futile. It is also likely that E_M may be a farm-specific characteristic.

Activity

Activity (E_A) is usually taken as a part of maintenance, although the assumption that the activity of fasted pigs, fed but hungry pigs and amply fed pigs is the same is clearly faulty. ARC (1981) and Noblet *et al.* (1993a and b) suggest E_A to be respectively about 0.20 and 0.15 of E_M . There is also the need to account for the cost of eating itself at some 0.1 MJ/kg of high-density diet (Noblet *et al.*, 1993b). Diets of lower density would accrue higher costs. Van Milgen *et al.* (1998) found E_A to be just less than 0.10 of fasting heat production in pigs in metabolism cages. From this it may be surmised that about half of the activity costs will be accommodated in the estimate for E_M , and a further 0.10 E_M should be added for active pigs in commercial groups. This is consistent with the energy costs of activity in pigs reviewed by NRC (1998). More recently van Milgen and Noblet (2000) have suggested a higher cost for E_A of some 0.25 E_M .

Gaseous losses

Energy eaten, but lost as gaseous escapes, are presumed trivial and rolled into E_M by default. E_{Gas} is presumed to be about 0.008 of the ME (ARC, 1981) but they may be substantially more than this if the food is fibrous. ARC (1981) accept that up to 0.08 of fibrous foodstuff energy may be lost as gas. Using diets of 120-280 g/kg NDF, Bakker (1996) measured methane losses of 0.007-0.024 of the ME. Being omnivores, the consumption of fibrous foods such as cereal by-products, grass and dried grass products, vegetables, roots and root by-products and whole-crop materials (such as maize silage), amongst many others, should be allowed for in any calculation of energy requirement. The calculation of gaseous loss as a function of the fibre content of the diet would appear reasonable. NRC (1998) list neutral-detergent fibre (NDF) compositions of pig foods from 487 g/kg (brewers' grain) to 20 g/kg (bakery waste), and Whittemore (1998) from 450 g/kg (wheat bran) to 80 g/kg (cassava). Values for maize and soya meal are about 90 and 140 g/kg respectively. The proportion of ME lost as gas may thus increase by about 0.0001 (Bakker) to 0.0003 (ARC) for each gram of NDF above that of 0.008 appropriate for 'normal' diets of 100-150 g NDF per kg. Even approximate estimation of gaseous loss is fraught, and the position further confused by the inadequacy of NDF

as a means of defining diets with regard to hind gut disappearance. Jorgensen *et al.* (1996) have suggested that the disappearance of NSP may be as high as 0.6 to 0.8 and this value is highly specific to ingredient and to fibre level.

Disease

Disease may reduce values for k_{pr} through elevation of nitrogen loss (Arman, 1971; Whittemore and Hastie, 1977) and reduced protein retention concomitant with no reduction in protein turn-over, or it may increase E_M , or there may be a frank requirement for energy in support of the immune system (Bray *et al.*, 1993), E_D . Knap (2000), flirting with the topic in a review of the work of various authors appears to suggest that disease may increase heat loss (presumably E_M) proportionately by some 0.15 due to elevated body temperature, and by a further 0.15 due to the costs of an active immune system. Similar magnitude of E_D may be inferred from Bray *et al.* (1993). It may be proposed that disease both increases the rate of protein turn-over while decreasing the rate of retention. The subject has been recently and authoritatively reviewed by Black *et al.* (1999), and the substantial increase in maintenance requirement confirmed. Black *et al.* (1999) report that AUSPIG responds to chronic disease by 'increasing maintenance energy requirements by up to 1.3 times the normal predicted value, decreasing the rate of protein deposition by 0.9 times normal and decreasing food intake down to zero depending upon the severity and duration of the disease'.

Thermoregulation

The ambient air temperature (T_a , °C) range over which the pig identifies that it is neither uncomfortably cold nor uncomfortably hot and for which there is no energetic penalty (the 'thermoneutral zone') is probably rather small. The ability of the pig to compensate by behavioural adjustments is limited in housed production systems. Values for ambient temperature less than comfort (or critical) temperature (T_c , °C) will therefore incur energy costs expended solely in the interests of increasing heat output from the body to alter T_c until it approaches the prevailing temperature. The prevailing temperature as perceived by the pig (T_e , °C, the effective temperature) may be equal to, or different from, T_a . Some housing conditions would allow T_e to exceed T_a , while in other housing T_e will fall short of T_a .

Empirical approach

NRC (1998) relate T_c to W ,

$$T_c = 26 - 0.061W.$$

Verstegen (1971) suggested the slope to be steeper at around 0.15. Both the slope and the constant are found to vary with W , indicating W to be a rather inadequate independent variable. Evidently, comfort temperature, T_c , is a function of the heat output from the body of the pig (H).

$$H = E - E_{\text{Retention}} - E_{\text{gas}}$$

or,

$$H = E_M + ((E_{pr}/k_{pr}) - E_{pr}) + ((E_{Lr}/k_{Lr}) - E_{Lr}) + E_A.$$

Exactly which function is however rather difficult to determine. Whittemore and Fawcett (1976) derived

$$T_c = 26.6 - 0.59H$$

mainly with an assumption that the heat output will be about twice maintenance for actively growing pigs at a given W , and using an approximation of Verstegen's (1971) slope. Verstegen *et al.* (1995) were unable to provide an all-embracing quantitative principle, and presented a table of values for T_c as a function of W and feeding level (one, two, and three times maintenance). Bruce and Clark (1979) deduced T_c from thermodynamic principles. These values are shown in Table 1, together with those that would result from Whittemore and Fawcett (1976). Given the presence of the subsequently determined data, the approach of Whittemore and Fawcett may be revisited, and the following best fit relationship determined if k_{growth} is assumed to be 0.50, and H as $E - E_R$.

$$T_c = 35.5 (\pm 2.43) - 7.02 (\pm 0.911) \cdot \ln H \quad (r^2 = 0.64).$$

The degree of cold felt by the pig is the difference between T_c and the effective ambient temperature (T_e). The effective temperature (T_e) is derived as a modification of the air temperature surrounding the pig (T_a). Behaviour, especially huddling, will

Table 1 Values for T_c (°C) in relation to live weight (W) and feeding level (MJ metabolizable energy) at 1X, 2X, and 3X maintenance (values in brackets () are those that would result from Whittemore and Fawcett (1976) if the energy above maintenance was used with 50% efficiency for energy retention and values in brackets [] are those from the model of Bruce and Clark (1979))

W (kg)	Feeding level		
	0.420 $W^{0.75}$	0.840 $W^{0.75}$	1.260 $W^{0.75}$
20	24 (24) [26]	19 (23) [21]	15 (22) [16]
60	23 (22) [22]	18 (19) [16]	13 (16) [11]
100	22 (19) [20]	17 (15) [14]	12 (11) [9]
140	21 (17)	15 (12)	10 (7)

increase T_e when $T_a < T_c$. This has conventionally been accounted in the determination of T_c , but may equally logically be accounted in T_e . ARC (1981) identify the following moderating influences on T_a : rate of air movement, temperature of house surfaces, relative humidity, bedding and floor type. Factors with which to multiply H in the estimation of T_c (note; not in an estimation of T_e) are given according to housing characteristics as: insulation/no draughts - 1.00; insulation/draughts - 0.89; no insulation/no draughts - 0.97; no insulation/draughts - 0.84; good straw bed - 1.10. Whittemore (1998) presents a more elaborate set of factors for the purposes of multiplying T_a in the estimation of T_e . Thus,

$$T_e (\text{°C}) = T_a \cdot (Ve \cdot VI).$$

Values for Ve are given as: insulated/not draughty (a draught is presumed when air speed > 0.2 m/s) - 1.0; not insulated/not draughty - 0.9; insulated/slightly draughty - 0.8; insulated/draughty - 0.7; not insulated/draughty - 0.6. Values for VI are given as: deep straw bed - 1.4; no bedding on solid insulated floor - 1.0; slatted floor with no draughts - 1.0; no bedding on solid uninsulated floor - 0.9; slatted floor with draughts under - 0.8; no bedding on wet, solid, uninsulated floor - 0.7. Taken separately these factors are compatible with the factors offered by Versteegen *et al.* (1995) but their being multiplied together is largely unsupported. The determination of T_e would appear inappropriately pragmatic.

The energy cost of cold thermogenesis (E_T , MJ ME) forwarded by NRC (1998) was that earlier estimated by ARC (1981) as increase in heat output in response to cold (H_T); there is potential for confusion here between the metabolizable and the net requirement.

$$H_T = (0.00131 \cdot W + 0.0953) \cdot (T_c - T_e).$$

The ARC (1981) review showed the reducing effect upon live-weight gain of temperatures below T_c to be consistent with measurements of increase in heat output. There is an explicit presumption that E_T increases linearly with difference between T_c and T_e . The choice of W to the power one, and the rôle of the constant term are not elaborated. The source data for the ARC calculation suggested that the increase in heat output for pigs kept individually was about twice that of pigs kept in groups, and that for groups preferred estimates were 0.011 and 0.007 MJ \cdot W^{0.75} for pigs of 20-50 and 50-100 kg live weights respectively. It is presumed that the differences between individuals and groups reflect the greater possibilities for the latter to make behavioral

adaptations. There is therefore confounding with the determination of T_e , and perhaps the values for individual pigs may be the more appropriate for the factorial determination of energy requirement, even for pigs kept in groups. The presentation of separate values for the two weight classes of pigs makes illogical the choice of the 0.75 exponent, and may justify $W^{1.0}$.

Noblet *et al.* (1985) are quoted by NRC (1998) in presenting the increase in heat production in response to cold as

$$H_T = 0.0155 - 0.0189W^{0.75}(T_c - T_e).$$

ARC (1981) found the efficiency of conversion of ME to heat output for purposes of cold thermogenesis to be similar to that for maintenance, thus

$$E_T = H_T / 0.80.$$

This estimate for E_T is comfortably in accord with the comprehensive review of Close (1987) from which it may be inferred that E_M is increased by about 0.020 MJ W^{0.75} per degree temperature drop.

The earlier work quoted by ARC, showing that a degree of cold would reduce gain by some 0.017 kg, is consistent with the Versteegen *et al.* (1982) estimate that a 60-kg pig would require to eat 0.039 kg of extra food to compensate for each degree of cold. The estimate for E_T given above translates to about 0.035 kg of food. It would appear that the AUSPIG model (Black *et al.*, 1999) uses a coefficient of around 0.026, rather to the upper end of the scale but not importantly different. The model of Whittemore and Fawcett (1976) was rather more conservative, using 0.016.

Deductive approach

Bruce and Clark (1979) began with the principles of thermodynamics in order to determine heat output from the pig (H), critical temperature (T_c), and the determination of the increase in heat production per °C change in T_a (H_T).

$$H = E_M + (1 - k) \cdot (E - E_M)$$

where k is the efficiency of use of E for energy retention (E_R). E is the energy intake, and E_M was valued as $0.440 \cdot W^{0.75}$. Elsewhere, power is measured in Watts. The thermoneutral heat production (H , Watts) is declared as Q_n . The total heat loss from the pig below T_c (Q) is the sum of the heat loss from skin to air (Q_a), the heat loss by evaporation from the pig's surface (Q_e), and the heat loss from skin to floor

(Qf). Q_e is given as $0.09(8.0 + 0.07W).W^{0.67}$. Q is a function of the area of skin exposed to air (A_a), to floor (A_f), and to other pigs (A_c), together with the differences between air temperature (T_a), skin temperature (T_s) and deep body temperature (T_b , 39°C), and the relevant thermal resistances to heat transfer (R , °C.m² per Watt). Heat is transferred by radiation (Q_r) and convection (Q_c).

$$Q_r = 5.3.A_a.(T_s - T_a)$$

$$Q_c = H_c.A_a.(T_s - T_a)$$

$$Q_a = Q_r + Q_c$$

where H_c is the convective heat transfer coefficient, which is a function of surface area (A) and air velocity (V). In turn, A is a function of W ($A = 0.09W^{0.67}$). The velocity of still air is set at 0.15 m/s.

The thermal resistance of skin exposed to air (R_a) is

$$R_a = 1/(5.3 + (15.7.(V^{0.6}/W^{0.13})))$$

and the thermal resistance skin exposed to floor (R_f) is approached intuitively and also scaled to empirical values determined for 45 kg pigs on solid flooring;

$$R_f = R_{f_{45}} . (W/45)^{0.33} . (A_f/(0.2 . A)).N^{0.5}$$

where N is the number of pigs in the group that can contact each other. Bruce and Clark chose example $R_{f_{45}}$ values of $R_f = R_a$ for open mesh, 0.07 for concrete slats, and 0.5 for a straw bed. The thermal resistance of tissue between deep body and skin (R_t) is taken as

$$R_t = 0.02.W^{0.33}.$$

The proportion of skin in contact with the floor (A_f/A) is taken to be 0.2 if the pigs are not cold ($R_f > = R_a$), or 0.1 if they are ($R_f < R_a$). The proportion of skin in contact with other pigs, when cold, (A_c/A) is taken as

$$A_c/A = (2(N - 1)/N). 0.075$$

$2(N - 1)$ being the total number of shielded surfaces when pigs lie in a row together. Hot pigs are modelled as standing apart.

The heat loss (Q , Watts) is determined as

$$Q = (A(1 + ((A_f/A)((R_a - R_f)/(R_t + R_f))) - (A_c/A))(T_b - T_a) + (Q_e.R_a)/(R_a + R_t)$$

The derivative of total heat production with respect to air temperature below the critical temperature is determined as

$$dQ/dT_a = -(A(1 + ((A_f/A)((R_a - R_f)/(R_t + R_f))) - (A_c/A)))/(R_a + R_t)$$

and critical temperature (T_c) is determined as

$$T_c = T_b - (((Q_n(R_a + R_t)) - (Q_e.R_a))/(A(1 + ((A_f/A)((R_a - R_f)/(R_t + R_f))) - (A_c/A)))).$$

Values determined by the Bruce and Clark (1979) model for T_c in still air are given in Table 1. The model performed creditably in its calculation of heat loss, although it has to be said that heat loss was typically 0.5 of the energy input, which was spread over a large range ($\times 3$). The elements of the model dealing with the housing environment were not exercised. The coarse value for k used by Bruce and Clark is an unwarranted simplification where k_{pr} and k_{lr} values are separately available, as would normally be the case. The notion of deducing heat output and critical temperature from first principles, rather than by empirical measurement remains seductive. It was to be noticed however that the acknowledged experts in the field did not yield when recently tempted in their preparation of a review of the subject (Verstegen *et al.*, 1995).

Black *et al.* (1986) used the Bruce and Clark model as the basis of their AUSPIG estimations for the influences of environment upon energy requirement and upon food intake. They extended the model to account for the consequences of temperatures above T_c . The seminal contribution of the Black *et al.* (1986) model was to include the possibility of cooling by evaporation of water from the skin surface, thus accommodating wallowing and spray cooling. The additional heat fluxes modelled comprise absorption of heat from a radiant heater (Q_h), and evaporative heat losses from the lungs (Q_l) and skin (Q_s). These evaporative losses are adjusted according to the humidity of the atmosphere. For the estimation of Q the term $(Q_e.R_a)$, in the Bruce and Clark (1979) equation above, is replaced by $((Q_s.R_a) - (Q_h.R_a))$, and the term Q_l is added at the end of the expression. For the estimation of T_c the term $((Q_n.(R_a + R_t)) - (Q_e.R_a))$ is replaced by $(Q_n - (Q_l.(R_a + R_t)) - (Q_s.R_a) + (Q_h.R_a))$. A minimum rate of evaporative heat losses from the lungs and skin (in the proportion 1 : 1) is set as

$$Q_l + Q_s = A.(8.0 + 0.07W)$$

and a maximum rate (2 : 1 lungs : skin) for dry pigs is set as

$$Q_l + Q_s = A \cdot (18 + 91/W^{0.33}) \cdot (1.36 - W_a/35.9)$$

the term W_a being the water content of air (g/kg), calculated from the relative humidity. If the pig is wet then

$$Q_s = (A - A_f) \cdot ((45.4 \cdot V^{0.6})/W^{0.13} \cdot (46.1 - W_a)).$$

Amongst the possible contributions of the Black *et al.* (1986) enhancements to the Bruce and Clark (1979) model is the means to determine the necessary reduction in E to equate heat loss with heat production and thus to calculate food intake reduction when pigs are hot. Model predictions accorded well with the findings of Sugahara *et al.* (1970) for food intake reduction. The paper of Black *et al.* assumes, but does not vouch for, the veracity of the Bruce and Clark model. Although the concept of a unified model to give a continuum over the range from when T_c is below T_a to when it is above T_a is compelling, the evaluation of the benefit of the Bruce and Clark approach is not elementary.

The Bruce and Clark (1979) model has also been developed by Turnpenny (1997), particularly with respect to losses from the skin surface under conditions of various degrees of wetness and rate of ventilation (V). This work is commented upon by Knap (1999) in a recent synthesis of the deductive approach to thermoregulation in the growing pig.

The Knap (2000) model builds upon Bruce and Clark (1979) and Black *et al.* (1986) and therefore includes various elements of both while offering no independent verification for them. Knap was not directly interested in critical temperatures, but in heat flux from the pig under given conditions. Therefore, the main functions are different in appearance from those of Bruce and Clark (1979) and Black *et al.* (1986). But many of the model's building blocks relate to the two earlier models. Knap takes his equation for the thermal resistance of skin exposed to air (R_a) from Black *et al.* A term from the equation of Bruce and Clark (1979) supplies an effective surface area for the pig, taking into consideration the contact between the focal pig and both the floor and other pigs. Using the nomenclature of Bruce and Clark, effective surface area is given by:

$$A_{\text{eff}} = A \cdot (1 + (A_f/A) \cdot [(R_a - R_f)/(R_t + R_f)] - (A_c/A))$$

where A , A_f , A_c , R_a and R_f are as described above. R_t , however, is novel. An empirical approach was used to determine the insulation effects of the body tissues, derived from experimental data detailed by

Knap (2000). For hot pigs, R_t is set at 0.038 Km^2 per Watt, whereas for cold pigs it is given by

$$R_t = 0.05 - 0.002 \cdot \text{BF}$$

where BF is body fat depth (mm).

Knap (2000), when considering evaporative heat loss, uses equations from Bruce and Clark (1979) for the cold pig, and from Black *et al.* (1986) for the hot pig. The equation for evaporative heat loss from a wet pig (Q_{wet}) is taken direct from Black *et al.* (1986), which is the Q_s equation for a wet pig, above. The situation of a cold, wet pig is not modelled, and in this case Q_{wet} is taken as zero.

$$Q_{S_{\text{hot}}} = A \cdot (12.2 + 110.8 \cdot \text{BW}^{-0.33})$$

$$Q_{S_{\text{cold}}} = A \cdot (7.4 + 0.089 \cdot \text{BW})$$

Heat loss is now given by:

$$Q = Q_s + Q_{\text{wet}} - (T_a - T_b) \cdot A_{\text{eff}} / (R_a + R_t)$$

If the actual power output of the pig, Q , is known, then the equation above can be solved to find T_a , the critical temperature.

The algorithms of Bruce and Clark (1979), Black *et al.* (1986), Turnpenny *et al.* (2000) and Knap (2000) have been translated *de novo* by one of the present authors (DMG), and the performances of the models compared. Lower critical temperature was defined as that ambient temperature at which the heat output of the pig, (H), is equal to the modelled heat loss, where the form of the model is chosen such that heat loss from the pig is minimized. Below this ambient temperature, heat loss from the pig exceeds heat production, and the pig is cold. Likewise, upper critical temperature is defined as that ambient temperature at which the heat output of the pig is equal to the heat loss, where the form of the model is chosen to maximize heat loss. Above this ambient temperature, heat production exceeds heat loss, and the pig is hot. Modelled pigs can moderate the degree to which surface blood vessels are dilated, their posture, and the degree of evaporative cooling. Body core temperature is fixed at whatever default value is specified by the particular model, and is not allowed to rise to store heat. It is assumed that the pig will not allow its core temperature to rise while within the comfort zone. Table 2 shows critical temperatures compiled for different example points in environmental parameter space. In general, it is seen that the Black *et al.*, Knap, and Bruce and Clark models predict similar values for the lower critical temperatures, but the Turnpenny model consistently

Table 2 Estimates of critical temperature (T_c , °C) from deductive approaches

Case†		Bruce and Clark (1979)	Black <i>et al.</i> (1986)	Turnpenny <i>et al.</i> (2000)	Knap approach (2000)	Empirical approach ‡
Case 1	Tc (lower)	24	22	20	22	24
	Tc (upper)		31	26	32	
Case 2	Tc (lower)	12	11	6	16	14
	Tc (upper)		21	17	23	
Case 3	Tc (lower)	15	15	8	19	19
	Tc (upper)		31	18	40	

† Case 1. W = 20 kg, H = 5 MJ metabolizable energy (ME) per day, group size = 10, floor = slatted, skin = dry, wind speed = 0.15 m/s. Case 2. W = 120 kg, H = 20 MJ ME per day, group size = 10, floor = slatted, skin = dry, wind speed = 0.15 m/s. Case 3. W = 120 kg, H = 20 MJ ME per day, group size = 10, floor = slatted, skin = 20% wet, wind speed = 0.50 m/s.

‡ From $T_c = 35.5 - 7.02 \ln H$; together with estimates of V_e/V_l .

returns lower values. In the case of the upper critical temperatures, the predicted temperatures are more variable. In particular, the Knap model predicts higher temperatures than the Black *et al.* model, due to the larger effect of evaporative cooling in this model. The magnitude of evaporative cooling is similar in the Knap and Black *et al.* models. Though parameterization of the equations varies, evaporative cooling is dominated by the heat loss from wet skin, for which the same equation is used in both models. The two models then treat this number differently. In the Knap model, it is simply added into the heat loss equation, while in the Black model it is multiplied by a factor $Ra/(Ra + Rt)$. Since this is less than one, the evaporative cooling effect in the Black model is less than that of the Knap model. When evaporative cooling is reduced to a minimum, the Knap and Black *et al.* models return similar upper critical temperatures. Comfort zones are of variable width, but are particularly wide in the Knap model, with its large evaporative cooling effect. As would be expected, reducing the potential for heat loss from the pig by reducing wet area, reducing wind speed, changing to a more highly insulating bedding material, or increasing the pig density within the housing all reduce the values of both upper and lower critical temperatures. Also, according to all models, critical temperatures decrease with increasing pig size. This results from the lower surface area to volume ratio of larger pigs. All the models show a high sensitivity to heat production. The slopes of the heat production versus critical temperature lines are generally quite shallow. Therefore a small difference in heat production can

shift the critical temperatures a considerable distance. On the other hand, a small difference in ambient temperature has a modest effect on the heat production required to maintain in heat balance.

Lipid retention

The energy content of lipid may be given as 39.6 MJ/kg. A total of 0.8 of body lipid is recovered as fatty acids in the approximate proportions of 0.35–0.50 18 : 1, 0.20–0.30 16 : 0, 0.12–0.18 18 : 0, 0.10–0.20 18 : 2, being highly dependent upon dietary source (Lizardo *et al.*, 2000). The fatty acids of body lipid arise from recycling of existing deposits, direct incorporation of dietary fatty acids and *de novo* synthesis. A high proportion (0.5 to 1.0) of ileal digested fatty acids are selected for incorporation into body tissue lipid; Lizardo *et al.* (2000) assume 0.85. In the presence of ample dietary supply of fatty acids, the efficiency of conversion of diet lipid energy to body lipid energy will be high. Estimates of k_{Lr} , the efficiency of use of ME for purposes of depositing lipid, fall within the general range 0.6 to 1.0. Tess *et al.* (1984b) reported a range of 0.81 to 0.57. ARC (1981) selected 0.74. This or other 'best estimates' are often presented as constants. The energy cost of lipid deposition will however vary with (amongst other things) the composition of the lipid deposited, the rate of turn-over of tissue containing lipid and the nutrient sources metabolized. The value of 0.74 is presumptive upon lipid being synthesized from dietary carbohydrate but, in the interest of simplicity, ARC largely put this aside in their text. Whilst accepting that k_{Lr} is bound to be a function of the efficiencies with which absorbed nutrients are utilized for lipid deposition, Black *et al.* (1986) nonetheless also placed a single value (that of 0.74) in the AUSPIG model (although some adjustment to ME was made for lipid and fibre content of the diet).

To do so is, however, unnecessarily simplistic. Body lipid may be re-synthesized from endogenous lipid moieties, when k_{Lr} values close to 1 might be realistic. Lipid from exogenous sources may also be incorporated into body fatty tissue with little change, and therefore little energy expenditure. This would be especially the case for lipids added to diets in the form of supplementary-food fats and oils where a k_{Lr} of 0.9 is possible (Stranks *et al.*, 1988). Frappe (1986) referring to the horse, gives k_{Lr} values of 0.85, 0.77, 0.60 and 0.32 for ME from dietary lipids, barley, proteins and hay respectively. The efficiency of use of VFA by pigs is often taken to be some 0.5 of that for glucose (Noblet and Henry, 1991); ARC (1981) gave 0.43 to 0.67. Armstrong (1969) gives k_{Lr} values of 1.0, 0.85, and 0.70 when the materials metabolized are fat, starch and protein respectively. These coefficients do not, however, include the work of eating and

digesting, and are therefore some 0.1 too high (Whittemore, 1997). Noblet and Henry (1991) offer k_{Lr} values of 0.98, 0.73 and 0.52 for digested fat, starch and protein respectively.

Protein retention

The classical empirical work of the INRA group over the past decade relating to the protein (and lipid) growth response to energy supply is summarized by Quiniou *et al.* (1999). Protein retention increases with energy supply according to a linear/plateau response. The same group have also presented a curvilinear model, but with the same elements of increasing and asymptotic phases when energy intake is expressed in multiples of maintenance (van Milgen *et al.*, 2000). The slope of the response appears dependent upon pig type and the stage of growth (pig weight) (Black *et al.*, 1986), and will relate, amongst other things to the proportion of energy supply flowing to maintenance and to the retention of lipid. Whilst widely accepted, and whilst alternatives are not apparent, the 'linear/plateau model' is open to wide interpretation with regard to the quantified definition of both its slope and its asymptote; and with regard to the underlying causes of these. The adaptation of the propositions of Black *et al.* (1986) by NRC (1998) is not especially helpful, as has been commented upon by Whittemore (2000).

The protein in the body of the pig has an energy content of some 23.8 MJ/kg. The efficiency with which this is deposited (k_{Pr}) varies at least between 0.36 and 0.57 (Tess *et al.*, 1984b). ARC (1981) had earlier also presented a range of values, but criticized the lower ones in the range and settled for a single preferred value of 0.54. Black *et al.* (1986) in their design of AUSPIG use the ARC value, whilst accepting its illogicality. Whittemore (1976) and Whittemore and Fawcett (1976) presented evidence to support the argument that there appeared to be an age effect, in that efficiencies measured with younger (lighter) pigs were usually higher than those measured in older (heavier) pigs. Notably, Fowler (1979) concluded 0.40 to be the appropriate k_{Pr} value for growing pigs, and Kielanowski (1972) determined by slaughter the value of 0.36. Whittemore (1997) proposed 0.44. Emmans (1999) taking a slightly different approach calculates 0.40. Emmans (1999) attempts, by allocating heat production elsewhere, to seek a particular value for k_{Pr} , whereas the approach developed here will presume that the source of energy substrate and the mass of body protein (amongst others) will have a substantial influence upon k_{Pr} . Because the attributions of energy to the various functions must sum to unity, it is axiomatic that the value for k_{Pr} will depend on the methodology used (calorimetry, serial

slaughter) and the extent of the attribution of energy flows elsewhere.

The confounding of the energy costs of maintenance and the energy costs of protein retention is vexed. Thus, the recent value for k_{Pr} from van Milgen and Noblet (1999) of 0.58 was associated with an E_M estimate of $0.913\text{-}1.070W^{0.60}$, which is higher than $0.440W^{0.75}$. It is evident that the values for k_M and for k_{Pr} should not be presented independently. For Large White pigs, Quiniou *et al.* (1996) found $k_{Pr} = 0.49$, when measured together with $k_{Lr} = 0.81$ and $E_M = 0.860W^{0.60}$ MJ ME daily. Tess *et al.* (1984b) determined by regression compatible values of $E_M = 2.19Pt^{0.79}$, $E_{Pr} = 48.2$ ($k_{Pr} = 0.49$) and $E_{Lr} = 63.7$ ($k_{Lr} = 0.62$). The efficiency of use of ME for lipid deposition was strikingly lower than other estimates, suggesting that the efficiency of use of ME for protein deposition may have been estimated high. But perhaps the more significant aspect of the report of Tess and co-workers was that in common with many others, they found great variability to be associated with the estimate of k_{Pr} . Notwithstanding the notorious error associated with its estimation, k_{Pr} will be a function of at least: (a) the absorbed substrate being metabolized for the synthesis of body protein, both with respect to the sources of energy and the sources of amino acid moieties, (b) the rate of total protein tissue turn-over associated with the retention of newly accreted protein (Pr) and not accounted in that part of the estimate of maintenance which accommodates protein turn-over at maintenance, and (c) the mass of protein tissue involved in turn-over. With respect to the latter two, Knap (2000) also proposes a genetic component.

With regard to the effects of diet substrate upon k_{Pr} , Whittemore (1997), reviewed the work of Noblet *et al.* (1993a and 1994a, b and c). This group reported the combined ($k_{Pr} + k_{Lr}$) value to average around 0.74. Efficiencies for ME/NE ($k_{Pr} + k_{Lr}$) according to substrate used were 0.90 to 1.00 for energy from lipid, 0.80 to 0.85 for energy from starch and sugar, 0.60 to 0.70 for energy from digested protein, and 0.55 to 0.60 for energy from digested fibre. These are a little higher than those given earlier by the same group for lipid alone.

Milligan and Summers (1986) and Moughan (1989) present evidence from a number of sources that total protein synthesis is positively related to the rate of protein retention. Thus as Pr increases then so will the total body protein turn-over, and thereby the energy cost attributed to protein retention (E_{Pr}). Values presented by Riis (1983) may be taken to suggest that increasing Pr from 0.1 to 0.2 kg daily will increase total protein synthesized from 0.8 to

1.2 kg. Knap (1995) presents a simulation which suggests that the energy cost of protein turn-over is a function of both pig mass and the rate of protein deposition.

Armstrong (1969) suggested that 8-12 moles of ATP are required to synthesize 1 mole of peptide bonds. A mole of ATP has a value of about 50 kJ, formed with an efficiency of about 0.6. Whittemore and Fawcett (1976) argue that a mole of ATP thus requires 83.7 kJ ME, and with the average molecular weight of pig protein amino acids being 110 to 120, then the energy used to form together a kg of pig protein would be 5.6 to 9.1 MJ (average 7.3). Van Es (1980) points out that the energy requirement per mole ATP depends upon the substrate, being 74, 78, and 93 kJ ME for glucose, fatty acids and VFA respectively. Van Es (1980) further suggests 5 moles ATP will arrange 1 mole of peptide bonds, so the energy cost of forming the bonds in 1 kg of arranged protein would be 3.92 MJ ME (Knap and Schrama, 1996). Five is the 'popular' number for moles of ATP for the incorporation of an amino acid into a peptide chain (Milligan and Summers, 1986), this including the 1 ATP for transport across membranes. These latter authors however were keen to emphasize the tentative nature of this value. From Reeds *et al.* (1980), and others, it appears that each mole of ATP used in a unit of protein retention brings with it a further 2.5 moles or so of further expenditure. This may be interpreted (not necessarily correctly) as the cost of additional turn-over associated with the retention of each additional unit of protein. This multiplier would give a k_{pr} value of some 0.63, which is at the higher (more efficient) end of the values discussed here. This may however be reflective only of differences in energy costs determined in laboratory pigs as compared to costs found in practical production systems with a significant disease presence.

It is apparent that protein turn-over issues are central to the matter of the determination of energy requirement. However, quantification is complex, and dependent upon methodologies that may be open to misinterpretation. The factorial (deductive) estimation of energy requirement is thus necessarily founded on an insecure base. Resolution might be assisted by the construction and testing of pragmatic models. Whittemore and Fawcett (1976), using derivations from the protein turn-over studies of Millward *et al.* (1974), proposed that protein turn-over (P_x) could be estimated from the rate of protein retention and the degree of maturity;

$$P_x = Pr / (0.23(Pt_{max} - Pt) / Pt_{max})$$

where P_t is the present protein mass, and $P_{t_{max}}$ the mature protein mass. If the energy used for protein formation is taken as 7.3 MJ/kg, as the average value suggested above, then the energy cost of protein deposition is now,

$$E_{pr} = 7.3P_x + 23.6Pr$$

Thus, if the mature protein mass were taken as 50 kg, the k_{pr} value for a 20-kg pig retaining 100 g protein daily would calculate to 0.41 and that for a 120-kg pig retaining 200 g to 0.32. These values must be considered in relation to the correction of $0.365P_t$ MJ ME made to E_M to allow for protein turn-over being also counted in the estimate of maintenance. This latter value assumes the rate of protein turn-over is 0.05 of total body protein at maintenance (when $Pr \sim 0$). Such a correction is evidently right in principle, and well supported by others as described above. In execution however, it is only logical when the correction employs the same exponent as the estimate for maintenance; otherwise the adjustment as a proportion of maintenance will change with body mass. The correction in the form of $0.365P_t$ MJ ME calculates to 1.2 MJ at 20 kg and 6.6 MJ at 120 kg. Knap and Schrama (1996) suggested that 0.35 of E_M was attributable to protein turn-over (1.7 MJ and 6.3 MJ respectively). But Reeds *et al.* (1980) propose the proportion of maintenance energy attributable to protein synthesis to be 0.15, only half of the previous values. Further, it would appear to be more generally understood (Fuller, 1980; Buttery and D'Mello, 1994) that at maintenance the daily turn-over of protein is some 16 g per $W^{0.75}$. This calculates to 0.6 MJ ME at 20 kg and 2.32 MJ ME at 120 kg.

For practical purposes, some 0.5 of body protein is in muscle, about 0.25 in connective tissue, and about 0.25 in viscera and blood, accounting respectively for 0.35, 0.10, and 0.55 of total body turn-over (Riis, 1983). Thus the rate of protein turn-over in the viscera is much greater than in the muscle mass (van Milgen, 1998; Knap, 2000). The proportion of the protein mass that is viscera will be less in the more mature animal. This will result in the overall rate of total body synthesis diminishing both (a) as the pig grows, and (b) for genotypes with a lower proportion of their body mass as viscera.

From the value of 16 g protein per $W^{0.75}$, daily whole body protein turn-over rates at maintenance are around 0.05 of the total body protein at 20 kg and 0.03 at 120 kg. Moughan (1989), reviewing the work of Reeds and co-workers at the Rowett Research Institute, generated a value of 0.04 for the daily fraction of total body protein turned over when $Pr = 0$. For growing animals, whole body protein

turn-over rates of various species, measured in various ways, appear to be around 0.10 (or above) of the total protein mass daily (see Riis, 1983). Johnson *et al.* (2000) draw attention to the difficulties of obtaining accurate estimates of protein synthesis rates, while suggesting rates of around 0.15 for (non-growing) muscle and 1.17 for liver. For 50 kg growing pigs, Riis (1983) proposes from a survey of relevant work an overall value for the daily fraction of total body protein turned over of 0.14. Of this, Knap (2000) has calculated that some 0.10 is associated with the turn-over of the existing protein mass and 0.04 with the deposition of new protein. With a total body protein content of 7.3 kg, the value of 0.14 gives a daily turn-over of 1.05 kg. If Pr is 0.150 kg daily, then the total turn-over associated with a kg of protein retained is 7.0 kg. At a cost of 3.92 MJ ME per kg, this is 27.4 MJ ME, indicating $k_{Pr} = 0.46$. If the value of 0.14 pertains over the active growth period, then at 20 kg, k_{Pr} calculates to 0.59 if Pr = 100 g; and at 120 kg, k_{Pr} calculates to 0.33 if Pr = 200 g. The likelihood that k_{Pr} decreases with increasing pig weight is also forwarded by Danfaer (2000). However, a single value for the fractional rate of turn-over may not be safe, as increase in animal size and degree of maturity are associated with decreasing turn-over rate (Riis, 1983), down to an adult maintenance value of about 0.05. Danfaer (2000) derives from a number of sources the expression

$$6.72 + 19.8 \cdot \exp(-0.799 \cdot Pt)$$

to estimate the percentage of the total protein pool turned over daily. This suggests that at zero retention (mature size) turn-over will be about 0.07 of the protein mass, whilst the upper limit in pigs of small size but rapid retention would be about 0.25. The equation operates effectively for small pigs but appears to reach its constant value at around 50 kg W. The formula of Danfaer (2000) does not itself constitute experimental evidence of a direct relationship between turn-over rate and body protein mass. The statement that protein turn-over changes with body weight may simply reflect the change in distribution of whole body protein mass over the various pools with their respective (differing) turn-over rates (Knap and Schrama, 1996).

Empirical determination of energy costs (as exemplified by those quoted in the ARC (1981) and NRC (1998) reviews, and the INRA group of Noblet and co-workers) requires k_{Pr} as a seminal driver. When energy costs are deduced from protein turn-over characteristics k_{Pr} is not a driver, but an out-turn; a product, not a part of the process. It is apparent that the deductive determination of k_{Pr}

should take account of, at least: (a) the energy requirement of forming bonds between amino acids and any other costs directly accruing to formation of body proteins from endogenous and exogenous amino acid moieties; (b) the masses of protein turning over and their relative turnover rates; (c) the rate of synthesis of new protein (together with the replacement of endogenously lost protein), and any influence that may have upon the rate of turn-over of the tissue into which it is incorporated; (d) the degree of maturity attained, and any influence that may have upon the rate of turn-over of total body protein; (e) the extent to which the energy costs of protein turn-over are likely to be 'double counted' into the estimate of maintenance requirement, not least when Pr is small. As the rate of synthesis of new protein will decrease with increasing maturity it is possible that the decrease in turn-over rate as a function of decreasing protein retention rate, and the decrease in turn-over rate as a function of pig weight are one and the same.

Broadly, empirical and deductive approaches taken together would suggest k_{Pr} for the 20- to 120-kg growing pig to average about 0.40 to 0.50. Higher values will pertain for the early part of the growth period, and lower values for the later part. At any weight, higher rates of retention will be associated with an increase in marginal efficiency, but at lower rates of retention the 'fixed costs' of protein turn-over associated with maintenance will reduce the overall efficiency of the energy economy of the pig.

Conclusion

Central to the determination of energy requirement of the actively growing lean pig is the understanding of variability in the energy costs of maintenance and protein retention, and the relationship between these. Amongst the propositions forwarded in this review has been the rôle played by protein turn-over in both retention and maintenance costs. It may therefore be salutary to attempt a preliminary, but quantitative synthesis, and to make comparison of the values deduced with empirical determinations.

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. 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. This minimum rate of protein turn-over can be described by the equation

$$Px_{\min} = 0.05Pt$$

where Px indicates protein turn-over, and Pt is the current protein mass of the pig. If 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;

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

For purposes of the present exercise, the maximum protein retention rate of a pig (Pr_{\max}) can be described by the Gompertz equation:

$$Pr_{\max} = Pt \cdot B \cdot \ln(Pt_{\max}/Pt)$$

where Pt_{\max} is the mature protein mass of the pig, which the pig approaches asymptotically. These may

now be combined to determine protein turn-over rate where nutrient supply is not limiting.

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

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

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

The energy cost of the turn-over of existing tissue and the retention of new, is taken to be 3.92 MJ ME per kg protein synthesized. Maintenance costs can be expressed as a function of protein mass (Pt) and the equation $1.85Pt^{0.78}$ MJ ME per day is forwarded here. This value includes that portion of the energy costs

Table 3 Metabolizable energy (ME) costs 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
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_p) ⁵	0.55	0.53	0.49	0.45	0.41
Maintenance element (MJ ME per day) ⁶	0.784	0.157	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/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 $Pr_{\max} = Pt \cdot B \cdot \ln(Pt_{\max}/Pt)$; B = 0.012, A = 40.

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

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

⁴ (Px. 3.92).

⁵ (Pr. 23.6)/((Px. 3.92) + (Pr. 23.6)).

⁶ (0.05. Pt). 3.92.

⁷ Energy cost of maintenance calculated independently of turn-over from $E_M = 1.85 \cdot Pt^{0.78}$.

⁸ Proportion of maintenance energy that can be attributed to protein turn-over when Pr = 0.

⁹ Total energy expended in protein retention (Px X 3.92) + (Pr X 23.6).

¹⁰ $E_M^{(7)}$ - maintenance element (⁶).

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

¹² $k_p = 0.49$ (Quiniou *et al.*, 1996).

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

¹⁴ Sum of energy cost of maintenance and energy cost of protein retention.

¹⁵ $k_p = 0.45$ (NRC, 1998).

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

¹⁷ Sum of energy cost of maintenance and energy cost of protein retention.

of maintenance which arise from protein turn-over occurring at maintenance, suggested as 0.05Pt. Table 3 gives the energy costs that may be deduced from the characterization of protein turn-over, together with equivalent values that would be determined using coefficients and costs determined empirically by others. All the derivations are given in the form of footnotes to the Table. It is concluded that there may be consistency and value in the protein turn-over paradigm to account for (at least some of) the variation in energy requirement.

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