A study of growth responses to nutrient inputs by modelling

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The potential of models in the pursuit of understanding and predicting animal responses to nutrient inputs was shown by Miller & Payne (1963). A model can be a combination of available experimental findings, corroborative circumstantial evidence, and assumption; as such it is no better than its components. Growth responses determined from an integrated model have little validity in their own right. The importance of demonstrating effective simulation is in the credibility that accrues thereby to the construction.

Given below are the source equations of a model which has been used at Edinburgh to simulate growth responses of pigs over the weight range 20–120 kg (Whittemore & Fawcett, 1974; 1975a,b; 1976; Whittemore, 1976; Whittemore & Elsley, 1976). These equations have been validated by comparison with results from controlled feeding trials, which confirm that pig growth is effectively simulated.

Growth responses by modelling are therefore best studied by an examination of the elements of the model, rather than by obtaining output from it. Output may, in any event, be regenerated from the source equations given.

A model for pig growth

The derivation of these equations is discussed by Whittemore & Fawcett (1976).

Input: DCP (digestible crude protein); DE (digestible energy); V (chemical score of protein); Pî (inherent limit to protein accretion); T (house temperature); N (score for insulation, draughts and bedding); LW (live weight at start); LWF (live weight at slaughter).

Programme

Pt (protein at start) $= 0.154 \, LW - 0.212$

Lt (lipid at start) $= 0.192 \, LW - 0.288$

At (ash at start) $= 0.032 \, LW - 0.073$ (Interpolated from Wood & Groves, 1965)

EBW (empty body weight) $= 0.952 \, LW$

MBW (metabolic body weight) $= LW^{0.75}$

F (feed intake) $= 7.5 - 8.267 e^{-0.010 LW}$ or $0.5 + 0.033 LW$ or $0.10 \, MBW$ or $1.0 + 0.025$ (days) or any other

Epf (protein free DE) $= DE - 23.6 \, DCP$

Pî (mature protein mass) $= 660 \, Pî - 35$

Pr/Px (protein accretion/protein synthesis) $= 0.23$ (Pf$-$Pt)/Pf

P (protein intake) $=$ (F) (DCP)

Pr $=$ (F) (DCP) (V)/[$0.94+(0.06/($Pr/Px$))$]

If Pr$>$Pf then Pr $=$ Pf

E (energy intake) $=$ (F) (DE)

Px $=$ Pr/(Pr/Px)

If Px<0.05 Pt then Px $= 0.05$ Pt

φPb (endogenous protein losses) $= 0.06$ (Px$-$Pr)

USP (protein not used) $=$ P$-$(Pr$+$φPb)

Pm (protein deaminated) $=$ USP$+$φPb

EU (energy in urine) $= 7.2$ Pm

ME (classical metabolizable energy) $=$ E$-$EU

Q̂ (available ME) $=$ (Epf) (F)$+11.5$ Pm$+23.6$ Pr

Em (energy cost of maintenance) $= 0.475$ MBW$-[7.3(0.05$ Pt)]

EPr (energy cost of protein accretion) $= 7.3$ Px$+23.6$ Pr

Lr (lipid accretion) $=$ [Q̂$-($Em$+$EPr$+$H^1)]/53.4 (H^1 $=$ energy cost of cold thermogenesis)

If Lr$<$Pr then Pr$=$Pr-10; loop

Ĥ (heat output) $=$ ME$-(23.6$ Pr$+39.3$ Lr) (Excluding cold thermogenesis)

T $=$ TN

Tc (critical temperature) $= 26.6-0.59$H

H^1 $= 0.016$ MBW (Tc$-$T); loop

Ĥ (heat output) $-$ H$+$H^1

Mg ('lean' gain) $=$ Pr $(5.1-0.009$W) ('lean' $=$ protein$+$protein associated water; interpolated from Kotarbinska (1969))

Fg ('fat' gain) $= 1.1$ Lr ('fat' $=$ fat$+$associated water)

Ag ('ash' gain) $= 0.215$ Pr

EBWG (empty body weight gain) $=$ Mg$+$Fg$+$Ag

LWG (live weight gain) $=$ EBWG$+0.05$ EBWG

EFC (efficiency of feed conversion) $=$ LWG/F

EEC (efficiency of retention of DE) $= (23.6$ Pr$+39.3$ Lr)/E

EPC (efficiency of retention of DCP) $=$ Pr/P

LW $=$ LW$+$LWG

Pt (total protein in empty body) $=$ ΣPr$+$Pt

Lt (total lipid in empty body) $=$ ΣLr$+$Lt

At (total ash in empty body) $=$ ΣAg$+$At

Md (dissected lean in carcass sides) $= 2.53$ Pt

Fd (dissected fat in carcass sides) $= 0.559$ Lt$+4.90$

Bd (dissected bones in carcass sides) $= 2.57$ At

C (backfat (mm) at C) $= 1.30$ Fd

P2 (backfat (mm) at P2) $= 0.80$C$+4.0$ (Dissection and backfat predictions calculated from data of R. Braude and J. S. P. Costa (private communication) and Okwuosa (1971) and A. J. Kempster (private communication))

Model components

Protein accretion. Protein accretion is sigmoidal with time: the daily rate (Pr) increasing in early life and decreasing as the asymptote of mature protein mass (Pf) is reached. From twenty investigations quoted by Thorbek (1975), the following quadratic function fits the data over the live weight range 5–170 kg: $Pr = 1.63\ LW - 0.0094\ LW^2 + 60$. For white breeds of pig, accretion diminishes at about 80–130 kg live weight (0.5 Pf) (Oslage, Fliegel, Farries & Richter, 1966; Kielanowski, 1969; Thorbek, 1975). It is also evident that even during active growth from 20–120 kg there must be some inherent limit to the daily rate of protein accretion (Pr̂); response to protein supply (P) being non-linear. The relationship: $Pr = 0.74P - 0.0072P^2$ may be interpolated from data of Rérat & Henry (1964). For the fowl, Velu & Baker (1974) expressed the response in terms of a broken line; linear ($Pr = 0.74P$) until the requirement for maximal protein retention was reached ($Pr = Pr̂$), when additional increments of protein effected no increment in retention.

Whether the limit to daily protein accretion (Pr̂) is constant or quadratic over the growth phase relevant to pig-meat production (20–120 kg) is contentious. Daily protein accretion has been shown to increase between 20 kg and 30–60 kg live weight (Wenk & Schürch, 1974; Cöp, 1974; Thorbek, 1975), but it is not clear whether this is expression of a gradually lifting boundary for Pr̂ or the result of an improving nutrient intake. The latter possibly leads to the view that Pr̂ is broadly constant during most of the growing phase; attained at 20 kg and maintained until 120 kg (Møllgaard, 1955; Oslage & Fliegel, 1965; Kielanowski, 1969; Rérat, 1972; Whittemore & Fawcett, 1976). Pr̂ clearly differs between sex and genotype. Purported limits for the three sexes are, 100 g for castrated males, 112 g for females and 130 g for entire boars (Piatkowski & Jung, 1966; Kielanowski, 1969). It is generally accepted that the lean tissue growth rate of entire boars is greater than that of females, as evidenced by faster growth and leaner carcasses. Genotypic limits of 80 g protein accretion daily for 'unimproved' pigs, 110 g for 'meat-type' pigs and 130 g for 'exceptionally fast growers' are suggested by Kielanowski (1969). Selection in Danish Progeny Test Stations was shown to have effected an improvement in Pr of 14 g, from 79 to 93 g, over a period of 30 years (Kielanowski, 1966a). In a comparison of ten strains of pigs (Meat and Livestock Commission, 1975), carcass lean growth rates ranged from 226 to 271 g daily. The relationship between dissected lean in carcass and protein in total body approximates to a factor of 2.53 (calculated from findings of R. Braude and J. S. P. Costa (private communication), and Okwuosa (1971)); it may thus be estimated that Pr ranged from 89 to 107 g.

Whittemore & Fawcett (1976) proposed Pr to be related to the rate of total protein synthesis (Px) by the equation: $Pr/Px = 0.23\ (Pf - Pt)/Pf$, where Pt is current protein mass and Pf mature protein mass. The expression Pr/Px decreases as maturity is approached. As the energy cost of protein accretion relates to Px rather than Pr, then the energetic efficiency of protein growth decreases with increasing maturity, but, at any given proportion of maturity, is not affected by the

value for Pr. Analysis of comparative slaughter trials (Kotarbińska, 1969; Kielanowski & Kotarbińska, 1970; Kielanowski, 1972; Müller & Kirchgessner, 1974; Houseman & McDonald, 1973; Burlacu, Băia, Ionilă, Moisa, Taşcenco, Vişan & Stoica, 1973) also suggests that younger pigs have lower energy costs for protein accretion; total energy cost/kg protein formed, inclusive of heat of combustion (MJ)=44·5+0·384 LW. Energetic efficiency will therefore only improve if Pf is increased relative to Pt at slaughter. Determinations of mature protein mass (Pf) for pigs are scarce, but there are some results (M. Kotarbińska, unpublished) which suggest values of 35–45 kg for sows and 50 kg for boars. Further, if different genotypes or sexes were to reach the same proportion of maturity at similar ages, it is axiomatic that an increase in Pr̂ will lead to a greater value for Pt̂. Assuming values of Pt̂ for castrated boars, females and entire boars to be about 30, 40 and 50 kg respectively, then Pt̂/Pr̂ would approximate to 300, 357, and 385; and the general equation, Pt̂=660 Pr̂−35. Although it seems unlikely that differences in age at maturity could be of sufficient magnitude to accommodate the range of values suggested in Pr̂ such that they could be attained at the same value of Pt̂, it is apparent that the relationship between Pt̂ and Pr̂ justifies further attention.

The relationship between Pr and total protein synthesis (Px) is crucial to energetic efficiency; Px demanding by far the higher proportion of the energy used for protein growth (Millward, Garlick, James, Sender & Waterlow, 1976; Buttery & Boorman, 1976). The energy cost of protein synthesis is probably within the range 5·6–9·1 MJ/kg (calculated from Armstrong, 1969). Millward *et al.* (1976) suggest 5·9 MJ/kg and Whittemore & Fawcett (1976) use an average value of 7·3 MJ/kg. The ratio Pr/Px has been suggested above to be a function of the proportion of mature protein mass attained, and for average pigs would be about 0·21 at 20 kg and 0·11 at 120 kg. It is implicit that a change in Pr effects a proportional change in Px (the proportion depending upon Pt, the protein mass); similar was argued by Kielanowski (1976). Again, Millward *et al.* (1976) demonstrated a relationship between protein intake and protein flux.

While the simple relationship for Pr/Px may be adequate over a normal range of active rates of growth, it is inadequate to explain the situation at or around maintenance when Pr=0, but Px has a significant value (suggested to be around 0·05 Pt). Further, the proposition that an increase in Pr will effect an increase in metabolic activity mediated through the rate of Px should not obviate the possibility that the maintenance level of protein synthesis may be sufficient to support protein accretion, with no concomitant increase in Px, when the value for Pr is small. Were this latter the case, then protein accretion may be energetically more efficient when metabolic rate is high and Pr is small in relation to Pr̂, i.e. in the immature animal.

Protein quality. The amount of dietary protein available for protein accretion depends upon the amino acid content of absorbed protein in relation to the requirements for new protein synthesis (Pn). Pn=Pr+φPb, where Pb is protein breakdown and φ the proportion of protein breakdown which is unavoidably lost

as a result of the inefficiencies of turnover. If Pr/Px=0·15 (see earlier) and φ=0·06, it may be calculated that if Pr=100 g then φPb=34 g. Thus, of the total amino acids required, about 0·33 are involved in protein maintenance and 0·66 in protein accretion.

Where the requirement for amino acids is expressed in terms of protein of a particular amino acid mix, then a biological value of unity represents the ideal amino acid balance. For purposes of protein accretion this might be expected to be similar to the amino acid profile to be found in the protein of the whole body of the pig. The critical role of methionine in protein re-synthesis (Lubaszewska, Pastuszewska & Kielanowski, 1973) suggests that a rather higher proportion of sulphur amino acids might be needed for maintenance than would be provided from labile body protein.

Maintenance. The confusing relationship between maintenance costs and energy used for protein synthesis is apparent when maintenance is determined by statistical apportionment; values usually varying inversely, while the estimate for the energy cost of fat deposition is much less variable (for example, see Houseman & McDonald, 1973, Burlacu *et al.* 1973; Thorbek, 1975). Neither is the position improved by determination of the basal metabolic rate, on account of the animal adjusting to the condition of fast (Holmes & Breirem, 1974; Millward *et al.* 1976). Close & Mount (1975) found that minimum fasting heat loss (0·380 MJ/kg LW$^{0.75}$) was only some 0·80 of maintenance energy requirement (0·475 MJ/kg LW$^{0.75}$).

Energy used for maintenance is not a linear function of live weight; tending to a decreasing proportion as weight increases. The appropriate exponent is still not resolved. Breirem (1939) favoured 0·57, while Kielanowski (1972) and Verstegen, Close, Start & Mount (1973), for example, used the Kleiber value of 0·75. It is possible that no single exponent adequately describes the data over the range 20–120 kg; neither may live weight be the appropriate variable.

Whichever exponent is used, the coefficient appears to decrease with age (Breirem, 1939; Thorbek, 1974; Gädeken, Oslage & Fliegel, 1974). Equally a different exponent might apply; unity being appropriate at 20 kg, falling to around 0·5 for pigs heavier than 60 kg (Mount & Holmes, 1969; Verstegen, 1971). Taken together, these estimates suggest the exponent (b), over the range 20–70 kg, to be related to live weight by the equation: b=1·24−0·011LW, which indicates an average for 60 kg of around 0·58. It is apparent, however, that if a relationship between the requisite exponent and live weight is to be derived, it is likely not to be linear.

A significant proportion of maintenance costs probably result from protein turnover; 0·24 at 20 kg and 0·36 at 120 kg have been suggested (Whittemore & Fawcett, 1976). Millward *et al.* (1976) also allude to the high proportion of basal energy expenditure which can be apportioned to protein turnover. A study of the basal metabolic rate in young sheep (Graham, Searle & Griffiths, 1974) led to the suggestion that an exponent of unity could be appropriate if the fat-free body mass, rather than live weight, were used. Unity was also suggested for the young pig. It is a characteristic of the pig that it contains little fat when young (about 1 fat: 1

protein at 20 kg), but accumulates fat with increasing rapidity as it grows (about 3 fat: 1 protein at 100 kg) and so it might be surmised that maintenance may be more properly a function of protein mass rather than live weight. In this respect, regression analysis of growth of protein mass between 20 and 120 kg, with dry matter mass (fat+protein+ash) as the independent variable indicates an exponent of 0·66.

There is limited evidence that maintenance requirement could differ between breeds. On the basis of performance and carcass results from comparative slaughter trials; Saddleback pigs appeared to use less energy for maintenance than white pigs (Okwuosa, 1971), Lacombe less than Yorkshire (Sharma, Young & Smith, 1971), and Duroc less than Landrace (Fuller, Yen & Lin, 1974). In each of these three cases the animals with the lower maintenance requirement were also fatter; it appears uncertain as to whether the increased fat resulted from the energy saving or was the cause of it.

Reported values for the energy cost of maintenance range from 0·40 MJ/kg $LW^{0.75}$ (Breirem, 1939) to 0·58 MJ/kg $LW^{0.75}$ (Sharma *et al.* 1971). The mean value of nine estimates (Breirem, 1939; Verstegen *et al.* 1973, Kotarbińska, 1969; Houseman & McDonald, 1973; Fuller & Boyne, 1972; Holmes & Breirem, 1974; Thorbek, 1975; Davies & Lucas, 1972; Sharma *et al.* 1971) is 0·458 MJ/kg $LW^{0.75}$. Verstegen *et al.* (1973) suggest a 'best estimate' of 0·475 and Kielanowski (1976) 0·418. The estimate used by Whittemore & Fawcett (1976) (corrected for the energy costs of protein maintenance) of 0·475 $LW^{0.75}$—0·365 Pt, by nature of the data from which it arose, remains equivocal.

Heat Production. Estimates for the efficiency of fat accretion range only from about 0·70 (Gädeken *et al.* 1974) to 0·78 (Burlacu *et al.* 1973); values from Thorbek (1975) and Kotarbińska (1969) being intermediate. An average of 0·74 gives a total (inclusive of heat of combustion of product) energy cost for fat accretion of 53·5 MJ/kg; 14·2 MJ being lost as heat. Protein synthesis generates approximately 35 MJ of heat/kg protein accreted at 20 kg and 56 MJ at 100 kg, assuming the relationship described above for Pr/Px. Deamination adds another 4·9 MJ/kg protein. Heat production (H) in a thermoneutral environment is therefore the sum of the heats of production from protein, fat and urea synthesis, together with the energetic costs of maintenance. Or, if calculated by difference, ME less the heats of combustion of protein and fat retained (23·6 MJ and 39·3 MJ/kg respectively).

At environmental temperatures (T) below the lower critical temperature (Tc), additional increments of energy will be diverted, from productive processes (usually fat production), into heat generation (H[1], cold thermogenesis). Foregoing 1 kg of fat accretion releases 39·3 MJ for heat production (not 53·5, as 14·2 MJ are foregone). Total heat production (Ĥ) is therefore the sum of H and H[1].

Critical temperature (Tc) depends upon the rate of heat production. For pigs accumulating constant amounts of fat and protein, maintenance determines variation in heat production, thus Tc is a function of live weight. Verstegen (1971) suggested Tc=20−0·1 LW. This relationship requires to be modified by the effects

of plane of nutrition; an increased level of feeding (and consequent rate of growth) causing a reduction in Tc (Verstegen *et al.* 1973; Holmes & Close, 1976). Tc could be derived directly from H: $Tc=26.6-0.59$ H, but for this derivation it was assumed that H was twice maintenance to enable transformation of a relationship based on live weight. Estimates of Tc by this equation are, however, in general agreement with those of Holmes & Close (1976) from more sophisticated calculations.

Energy needed for cold thermogenesis has been estimated for pigs in groups of four to be between 11 and 16 kJ per degree difference between T and Tc per kg $LW^{0.75}$ per day (Verstegen, 1971; Verstegen *et al.* 1973). Verstegen and van der Hel (1974) suggest 9 kJ for pigs in groups of nine. At any given T an unfavourable environment increases the demand for heat production (H). It can, therefore, be considered as equivalent to a reduction in T. Air speed (Bond, Heitman & Kelly, 1965) and floor insulation (Mount, 1968; Verstegen & van der Hel, 1974) are particularly relevant. These factors, together with group size, have been brought together by Mount (1975), who described the thermal environment in terms of the air temperatures required to give a standard temperature of 14°. The range is from 22° for an uninsulated, draughty environment, to 10° for an unimpaired environment, together with a good straw bed. Verstegen & van der Hel suggest that pigs lying on concrete slats require an extra 4° air temperature.

Not only is it apparent that T has a significant effect upon growth and efficiency, but also that T is an inadequate description of the environment for commercial pigs. Information on group size, air speed and floor insulation markedly improves the situation, but the total environment is more complex than can be described quantitatively by data presently available.

Ratio, fat:protein. Normal growth in the pig comprises a greater quantity of fat than protein. At 20 kg the whole empty body contains about 19% fat and 16% protein (Wood & Groves, 1965); regression coefficients on empty body weight of 0.13 for lipid and 0.15 for protein have been determined at Edinburgh for 42-day-old pigs weaned at 14 d. By 100 kg there is in the region of 30% fat and 13% protein. The water content of the body is inverse to that of fat; further, as the animal grows, the water associated with protein decreases. The relationship: Lean gain (Mg)=Pr $(5.1-0.009$ LW) has been derived from Kotarbińska (1969) and shows how fat accumulates at the expense of both the protein-containing tissues and the water content of these tissues.

A description of fat growth as a function of energy supply is adequate if fat is regarded as an energy reserve, but inadequate if fat has a physiological role. There is limited evidence that the pig aspires to maintain a minimum level of fat in its body that is broadly equivalent to a 1:1 ratio with protein. Pigs in energy deficit may not continue to maximize protein accretion (Pr) while retaining no fat; rather Pr is reduced pro rata to release energy for fat accretion (Lr). Wenk & Schürch (1974) indicate that below the energy threshold which allows expression of Pr, both Lr and Pr might be reduced; maintaining a ratio, Lr:Pr of 1.25:1. Pigs fed by Houseman & McDonald (1973) to be excessively lean had ratios, fat:protein

of about 0·8:1, and Kielanowski (1966b) suggested that even under severe feed limitation the ratio, Lr:Pr would be unlikely to be less than 1:1. Should such a rate apply to accretion, it clearly does not to depletion. In energy deficit, fat stores may be broken down with no loss of protein; indeed the pig may simultaneously exhibit a negative value for Lr and a positive value for Pr (Thorbek, 1975). It is possible that the minimum Lr:Pr may be related inversely to the ratio of total fat (Lt):total protein (Pt) in the body. The minimum 1:1 rule for Lr:Pr is likely to apply most rigorously when Lt:Pt is also unity. Under normal conditions, even for the production of lean pigs, the 1:1 ratio is exceeded. However, the young pig over the growth phase 20–40 kg is particularly susceptible; Lt:Pt will approximate unity and a limited appetite predisposes to an energy deficit. It is quite possible therefore that at live weights of below 40 kg, Pr̂ is not attained in consequence of a physiological requirement for Lr.

The minimum ratio for Lr:Pr may differ according to degree of maturity, sex and genotype. Minimum body fatness becomes a function of the prevailing minimum for Lr:Pr in conjunction with feed intake and Pr̂. Animals with a low appetite (or feed allowance) in relation to Pr̂ will follow the boundary dictated by the minimum value for the Lr:Pr ratio; that is, the animal will not fatten. As appetite increases with weight or energy density of diet, or the feed allowance is raised, or Pr̂ is reduced, then Lr>Pr̂ and fattening begins.

The parameter Pr̂ denies compensation for growth of protein. This is not to say that Pr might not be elevated on realimentation; where $\overline{Pr}<Pr̂$, then if $Pr<\overline{Pr}$ in one period, $Pr>\overline{Pr}$ may follow in apparent compensation. There is little evidence with which to ascertain the inviolate nature of Pr̂, despite the importance of this parameter to feeding strategy.

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