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Calibration and sensitivity analysis of a model of the growing pig for weight gain and composition

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Abstract

The model concerned was a mechanistic model for pig growth and composition which was constructed using novel algorithms for the accumulation of protein and lipid. The model was parameterised using data collected from a serial slaughter trial of three different types of pigs and the sensitivity to parameters of biological importance was explored. The types ('Landrace' type, 'Pietrain' type and 'Meishan' type) were chosen to represent 'lean', 'meaty' and 'fatty' types.

After optimisation, fitted parameters were found to lie close to the values that would be expected given the assumptions made during the construction of the model, with a predicted maximum protein retention rate of 0.20 kg d^{-1} and an efficiency of recapture of amino acids during turnover of 0.94. Mean absolute percentage errors at slaughter point for modelled live weight were ca. 5%, compared with 8% for protein mass and 13% for lipid mass, suggesting that live weight gain is easier to predict than the partitioning of biomass into retained protein and lipid.

Keywords: Biological simulation models; Pig feeding systems; Model optimisation; Integrated management systems

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1. Introduction

The potential benefits of optimising pig response to nutrient supply by the targeting of specific production objectives, including that of environmental protection, rather than the satisfaction of generalised 'nutrient requirements' were recently reaffirmed by Jean dit Bailleul et al. (2000). Explicit in nutrition management is the means to accurately measure and control inputs, and to measure accurately and respond opportunely to outputs. The growth of the pig requires therefore to be managed toward the desired target throughout its growth course by an on-line Integrated Management System (IMS). IMS requires: an on-line measuring device for growth response (such as Visual Image Analysis (VIA), outlined below), a feeding system controlling the nutrient supply (such as electronic feeding stations), and a response prediction model to link the two, such as the mechanistic model presented here.

VIA uses video camera imaging to provide plan view images of a pig whenever it passes under the camera (Marchant et al., 1999; Whittemore and Schofield, 2000; Doeschl et al., 2003; White et al., 2003). These images are processed in real time by algorithms that provide biometric measurements to describe the shape and size of the animal. From such measurements, an estimate of the pig's weight may be made. Such measurements can be made frequently, without disturbance to the animal, and without the need of physical contact between it and the measuring equipment.

In the building of models to predict the growth response of pigs to nutrient supply, there are two extremes in the approaches used: models vary in type from purely data-based through to mechanistic forms. Mechanistic models have the advantage that in the absence of data (for example with a new batch of pigs of parameterised, but not previously modelled, genetic merit), predictions may be made with some safety using the biological algorithms encapsulated by the model. Conversely, data-based models are used unsafely when extrapolated beyond the range of the data, or the conditions of its collection, that were used to formulate the model, and usually the degree to which this extrapolation is unsafe is unknown.

Parameter sensitivity determines the relative importance of the parameters in the model. Only sensitive parameters can be profitably used in model calibration; and where the model is insensitive to a parameter, its accurate parameterisation is less vital. Additionally, during model parameterisation by fitting to collected data, where model output is similar across a wide range of parameter values, confidence in a parameter estimate will be low and biologically unreasonable parameter values may be obtained.

Green and Whittemore (2002, 2003) offered algorithms to construct a dynamic, mechanistic model for the growth of pigs in terms of the accumulation of lipid and protein mass. In this paper, a model is built using these algorithms and an internal validation of the model is carried out to examine whether, when calibrated by fitting this model to collected data, the parameters obtained carry biologically meaningful values. Meaningful values are to be expected where model algorithms and construction are realistic. Sensitivity determines which parameters can be used for successful model calibration under different nutritional and environmental circum-

stances. Model sensitivity over a range of conditions is therefore explored, to determine those model parameters to which model outputs are sensitive. Parameters suitable for calibration are required for the future development of IMS systems. These parameters must also carry biologically meaningful values, as the calibrated model would then be used for forward prediction of the individual pig response to nutrient supply, which is necessarily an extrapolation of the model beyond the data it is based upon.

2. Methods

2.1. Model overview

The IMS Pig model algorithms for the utilisation of dietary protein and energy have been described by Green and Whittemore (2002, 2003) using algorithms selected from the reviews of Whittemore et al. (2001a,b,c) and Whittemore and Green (2002). The key elements of the model architecture forwarded in these papers is outlined below, together with additional model algorithms required to make a complete, working model of the growing pig.

The algorithms primarily concern the accumulation of protein (Pt, kg) and lipid (Lt, kg) masses from digestible and fermentable dietary nutrients. The model maintains pools of absorbed amino acids, glucose, fatty acids, and volatile fatty acids. In the running model, but not in the description here, individual amino acids are modelled separately. A common core is concerned with the retention (Pr, kg d^{-1}) and mass of turnover (Px, kg d^{-1}) of protein. Protein retention is modelled according to a linear-plateau response, using a Gompertz function (Gompertz, 1825) with rate parameter B (d^{-1}) and mature protein mass Pt_{max} (kg). Turnover is additionally dependent upon a turnover parameter (z, dimensionless). This turnover includes maintenance protein usage (Px_m, kg d^{-1}):

$$Pr_{max} = Pt \times B \times \ln(Pt_{max}/Pt), \tag{1}$$

$$Px = Pr \times (1/z) \times Pt_{max}/(Pt_{max} - Pt), \tag{2}$$

$$Px_m = 0.05 \times Pt. \tag{3}$$

Additional amino acid losses account for endogenous losses in the gut and from the integument. The energy cost of that portion of protein turnover attributed to maintenance (Px_m) is already included within the larger general maintenance energy requirement, E_M, priced as moles of ATP (mol d^{-1}). This is a function of the size of the animal, in terms of body protein mass (Pt). A multiplier for activity level, also considered as an energy cost, is included ($F_{Activity}$)

$$E_M = (19.4 \times Pt^{0.78}) \times (1 + F_{Activity}). \tag{4}$$

Given set efficiencies of amino acid usage during turnover (ca. 0.06 of turned-over protein is deaminated), and the ATP cost of peptide bonding (4 mol ATP mol^{-1} peptide bonds), the energy and amino acid costs and efficiencies of maintenance and protein retention become outputs from the model.

All energy usage bar that for lipid retention is sourced via ATP. For both lipid synthesis and ATP synthesis, empirical estimates of usage efficiency of metabolised nutrients are combined with the corresponding theoretical, stoichiometric estimates. This enables the division of the energy use efficiencies into fractions corresponding to that of the efficiency loss during the processes concerned (k_s), and an efficiency loss between nutrient input and final end-use (k_t). In recombination, these provide an array of efficiencies (k) for each combination of nutrient input and nutrient use ($k = k_s \times k_t$).

In addition to Pr_{max}, protein retention is also determined by the target ratio for protein and lipid masses, $Lt{:}Pt_{pref}$ (Kyriazakis and Emmans, 1992). The same ratio is used to determine the target ratio of protein and lipid retained on a daily basis. Lipid levels above this target may be catabolised to provide energy for protein retention.

Further model algorithms calculate the effect of the thermal environment upon energy use, and the nitrogen balance of the pig.

2.2. New model algorithms

The above algorithms and their source papers deal with only the accumulation of protein (Pt, kg) and lipid (Lt, kg) mass, and the excretion of nitrogen. Further algorithms to fully describe the growth of the pig are needed to pursue the present work and are described here. The model algorithms were programmed, compiled and packaged as a dynamic link library (DLL) for further integration into graphical user interfaces, optimisation software, and batch programs.

Disease is assumed to have a variety of effects on model operation. Due to their relevance in real commercial life, disease effects are a necessary inclusion in growth models; but they are not yet fully quantifiable. Below, a range of values for the disease parameter $F_{Disease}$ are assumed to correspond to a range of health status, from perfect health (0), through a normal level of sub-clinical illness, at which empirically-derived model parameters are considered to be measured (3), to severe disease stress (10). Even under the best management conditions, there will always be a base-line level of sub-clinical illness present in the herd. Energy usage during disease of 30% above maintenance is assumed (Black et al., 1999); thus the range in $F_{Disease}$ of 0 to 10 can be considered to have a multiplicative effect upon E_M from 0.91 to 1.21. Over the same range, a fever of 2 K above normal core body temperature is tentatively forwarded here. It is reasonable to assume a protein cost to disease (Whittemore et al., 2001); the model here implements this *via* a correlation between $F_{Disease}$ and the rate of loss of amino acids during turnover, which has a default value of 0.94. Thus efficiencies of amino acid recapture during turnover of 1.0 down to 0.8 correspond to the range of values of $F_{Disease}$.

The outputs of the protein-energy algorithms are the computed daily values for the total protein and lipid mass of the modelled pig. From these the body of the pig and the weights of its component parts are constituted. For the growing pig, equations for whole-body water (Yt, kg) and ash (At, kg) are derived from the chemical analysis of the *Barrhill* data set (Fisher et al., 2003; Green et al., 2003; Whittemore et al., 2003), described below and in Appendix A. The pig is assumed to replace lipid mass lost from the maximum mass yet achieved (Lt_{high}) with water:

$$Yt = 4.01 \times Pt^{0.92} + (Lt_{high} - Lt), \tag{5}$$

$$At = 0.216 \times Pt^{0.94}. \tag{6}$$

Thus, empty body weight (EW, kg) is given by

$$EW = Pt + Lt + Yt + At. \tag{7}$$

Live weight (W, kg) is determined by gut fill, calculated according to Appendix B

$$W = EW + GutFill. \tag{8}$$

The surface area of the pig (A, m^2), as used by the thermoregulation algorithms, is given by the following equation (Bruce and Clark, 1979)

$$A = 0.09 \times W^{0.67}. \tag{9}$$

The initial conditions required by the model are live weight and an estimate of fatness, specified as the proportion of the live weight that is lipid (Lt/W). Using an initial estimate of gut fill of $0.135 \times EW^{0.67}$, Eqs. (5)–(8) are solved to determine Pt.

2.3. Calibration data set

A total of 104 pigs of three mixed genetic origins (here listed as 'Landrace', 'Pietrain', and 'Meishan' types) were serially slaughtered from 25 to 115 kg live weight, for the purpose of testing the IMS system (Green et al., 2003; Fisher et al., 2003; Whittemore et al., 2003). These pigs are subsequently referred to as the *Barrhill* trial pigs. They were fed ad libitum throughout, and individual daily feed intakes are known. The design of the serial slaughter trial is shown in Table 1.

Table 1
Number of pigs allocated to slaughter groups in the *Barrhill* data set, with days elapsed during trial period in brackets

	'Meishan' type	'Pietrain' type	'Landrace' type
Batch 1	10 (13) (5♂)	10 (17) (5♂)	10 (17) (5♂)
Batch 2	5 (34)	5 (37)	5 (31)
Batch 3	5 (48)	5 (58)	5 (52)
Batch 4	4 (69)	5 (79)	5 (73)
Batch 5	10 (104) (5♂)	10 (107) (5♂)	10 (101) (5♂)

All pigs were female except where listed.

The slaughtered pigs were dissected, chemically analysed and estimates of whole-body protein and lipid masses obtained (Fisher et al., 2003). Whole-body protein and lipid masses (Pt and Lt) were obtained by dissection (Fisher et al., 2003) and chemical analysis of the partially dissected carcase, as explained in Appendix A.

Dietary and environmental model parameters were set in accordance with the environment and diet described by Green et al. (2003). Environmental parameters were V (air speed) = 0.15 ms^{-1} (still air, Bruce and Clark, 1979); T_a (ambient temperature) = 18 °C; Rf_{45} (floor thermal resistance) = 0.08 $Km^2\ W^{-1}$ (concrete slats, Bruce and Clark, 1979); Y_a (air water content) = 2%, pig wet area = 10%; and a group size of 17 was assumed throughout. In brief, the diet had crude protein, lysine, and threonine contents of 194, 11.4, and 7.4 g kg^{-1}, and a calculated DE of 14.5 MJ kg^{-1}. For those nutrients where chemical analysis was not provided, it was interpolated using the Amipig (AmiPig, 2000), and Premier Atlas 2002 (Premier Nutrition Products Ltd., 2002) databases. All model runs assumed an activity score ($F_{Activity}$) of 0.1. Initial fatness (Lt/W) for each type was set at the average fatness of the type in the first slaughter batch of pigs: respectively, 0.114, 0.091, and 0.109 for 'Meishan', 'Pietrain', and 'Landrace' types.

2.4. Model calibration

The IMS Pig model provides a number of parameters that can be considered as 'controllers' suitable for optimisation in response to collected data, though initial estimates of these parameters can be proposed from the health status and genetic potential of the pigs in question. These include the efficiency parameters $F_{Disease}$ and z. The $F_{Disease}$ parameter has multiple effects on model algorithms, which have been described in detail. Higher values of z produce higher efficiencies for the use of amino acids and protein in protein retention. The Gompertz function used to calculate Pr_{max} is described by two parameters: the asymptotic protein mass, Pt_{max}, and a slope parameter, B. These parameters may be used as two further controllers, although they are not independent of each other. The preferred minimum ratio of lipid to protein (Lt:Pt_{pref}) is another descriptor of pig genetic potential suitable for optimisation.

Preliminary analysis of the *Barrhill* data set was carried out using a grid search algorithm to examine the shape of the model response surface and to determine best fit values for the parameters listed above, across a range of biologically feasible values for each parameter. Model output was generally smooth, and confidence that global, rather than local, optima were found was high. Therefore further analysis used the more efficient revised simplex algorithm (Nelder and Mead, 1965; Press et al., 1992). As the preliminary grid search showed the parameters Pt_{max} and B to be strongly correlated, only a single parameter, Pt_{max}, was fitted during the analyses described below. B was calculated from Pt_{max} using the scaling law employed by Emmans (1988), where the parameter B^* was assumed to be a constant and fixed at the value 0.035. Thus, with increasing Pt_{max}, the overall time taken to reach maturity increases also, though at a rate sufficiently slow that overall growth rate still increases

$$B^* = B \times \mathrm{Pt}_{\max}^{-0.27}. \tag{10}$$

Preliminary analysis showed that the model output was highly insensitive to $\mathrm{Lt{:}Pt}_{\mathrm{target}}$. Thus, this parameter was set at the low but biologically acceptable value of 0.4 for all types.

Parameter fitting was carried out using a revised simplex algorithm. Three parameters were fitted: $\mathrm{Pt}_{\max}$, F_{Disease}, and z. The sums of squares of model output ($\hat{\mathrm{Pt}}$, $\hat{\mathrm{Lt}}$) versus observation (Pt, Lt) for all slaughter dates for lipid and protein masses were minimised to yield a vector of parameters, $\hat{F}$

$$\hat{F} = \arg\min_{F} \sum_{\text{allpigs}} \left[\left(\mathrm{Pt} - \hat{\mathrm{Pt}}(F) \right)^2 + \left(\mathrm{Lt} - \hat{\mathrm{Lt}}(F) \right)^2 \right], \tag{11}$$

where the output from the arg min function is the value for $\hat{F}$ for which its argument is minimised. For such a non-linear model, a bootstrap procedure is an appropriate method to determine the standard error of model parameter estimates (Chernick, 1999). Where for model parameter i the estimate for bootstrap sample j is denoted by F_{ij}^* and the distribution of F_i^* is normal, then the mean of F_i^* should be close to the original estimate $\hat{F}$, whose standard error can be estimated by the standard error of the same bootstrap estimates. In this study, the number of bootstrap replicates was set to 100.

After calibration, the mean absolute percentage errors (MAPE) for W, Pt, and Lt were calculated as a measure of model goodness of fit, according to

$$\mathrm{MAPE} = \frac{1}{n} \sum_{i=1}^{n} \left[|Q - \hat{Q}| / Q \right], \tag{12}$$

where Q denotes a model output.

2.5. Model sensitivity

According to McCuen (1973) the general equation for the sensitivity of a model output Q to a change in a model parameter F_i could be given in terms of a differential as

$$S = \partial Q / \partial F_i. \tag{13}$$

However, for comparison of sensitivity values, the relative sensitivity, below, rather than the absolute sensitivity, above, is more appropriate

$$R = \frac{\partial Q}{\partial F_i} \cdot \frac{F_i}{Q}. \tag{14}$$

Throughout the results that follow, model outputs were measured with small perturbations in the model parameters and the partial differentials were estimated by finite differences. The dimensionless R values are presented. Sensitivities were calculated over a range of live weight from 20 to 120 kg, and from initial fatness proportions (Lt/W) of 0.05–0.15. Sensitivities were averaged across all initial fatness levels examined for each live weight.

Due to the incorporation of linear-plateau response algorithms in the model, model output sensitivity is necessarily dependent upon feeding level. Therefore, the model sensitivities shown in Fig. 2 were calculated at three feeding levels, low medium, and high (0.108, 0.120, and $0.132 \times W^{0.75}$ kg d^{-1}). Modelled protein retention (Pr) and lipid retention (Lr) over single day model runs were analysed. Live weight, W, is determined directly from Pt and Lt, and is especially closely correlated with Pt. Therefore sensitivity analysis was performed on Pr rather than dW/dt.

3. Results

Model calibration was performed as described above for the *Barrhill* data set. Fitted model parameters for each of the three pig types, and for all pigs, are shown in Table 2. Means and standard errors of the bootstrap parameter estimates are shown.

Fig. 1 shows live weight, W, and determined Pt and Lt figures for each of the 104 pigs (determined as shown in Appendix A) versus time. Using the model parameters described earlier and in Table 2, model estimates for each pig were calculated, and the deviations of these points from the observed data were also plotted. Each pig is modelled as an individual, with individual records of feed intake throughout the trials.

MAPE values indicate the goodness-of-fit of the calibrated models. For W, MAPE values were 4.8%, 5.1% and 6.4% for 'Meishan', 'Pietrain' and 'Landrace' types, respectively. For Pt, the corresponding figures were 7.8%, 7.3% and 8.4%, and for Lt 11.3%, 13.1% and 15.2%. Covariance between the model errors, $\mathrm{covar}(\mathrm{Pt} - \hat{\mathrm{Pt}}, \mathrm{Lt} - \hat{\mathrm{Lt}})$, was small.

Relative model sensitivity, R, at the best-fit parameters for all pigs is shown in Fig. 2. Sensitivity is shown for both protein (Pr) and lipid (Lr) retention rate at the three feeding levels described earlier. Parameter z has an effect on both Lr and Pr, as it controls the consumption of both energy and amino acids during turnover of protein mass. Pr is insensitive to z at high W, as at high W Pr is limited by the maximum rate of protein retention ($\mathrm{Pr}_{\max}$, determined directly by $\mathrm{Pt}_{\max}$ and B), rather than amino acid supply in the diet. Likewise, at high feed intake $\mathrm{Pr}_{\max}$ is the limiting factor controlling Pr, and Pr is relatively insensitive to z.

Table 2
Parameters obtained by fitting the model to the *Barrhill* data set

Parameter (F)	'Meishan' type	'Pietrain' type	'Landrace' type	All pigs
$\mathrm{Pt}_{\max}$	37.3 (9.3)	45.2 (7.4)	43.6 (10.1)	41.5 (7.4)
z	0.243 (0.072)	0.311 (0.083)	0.159 (0.036)	0.221 (0.041)
F_{Disease}	3.59 (0.94)	2.28 (1.37)	3.08 (0.63)	3.13 (0.83)

Standard errors are shown in brackets.

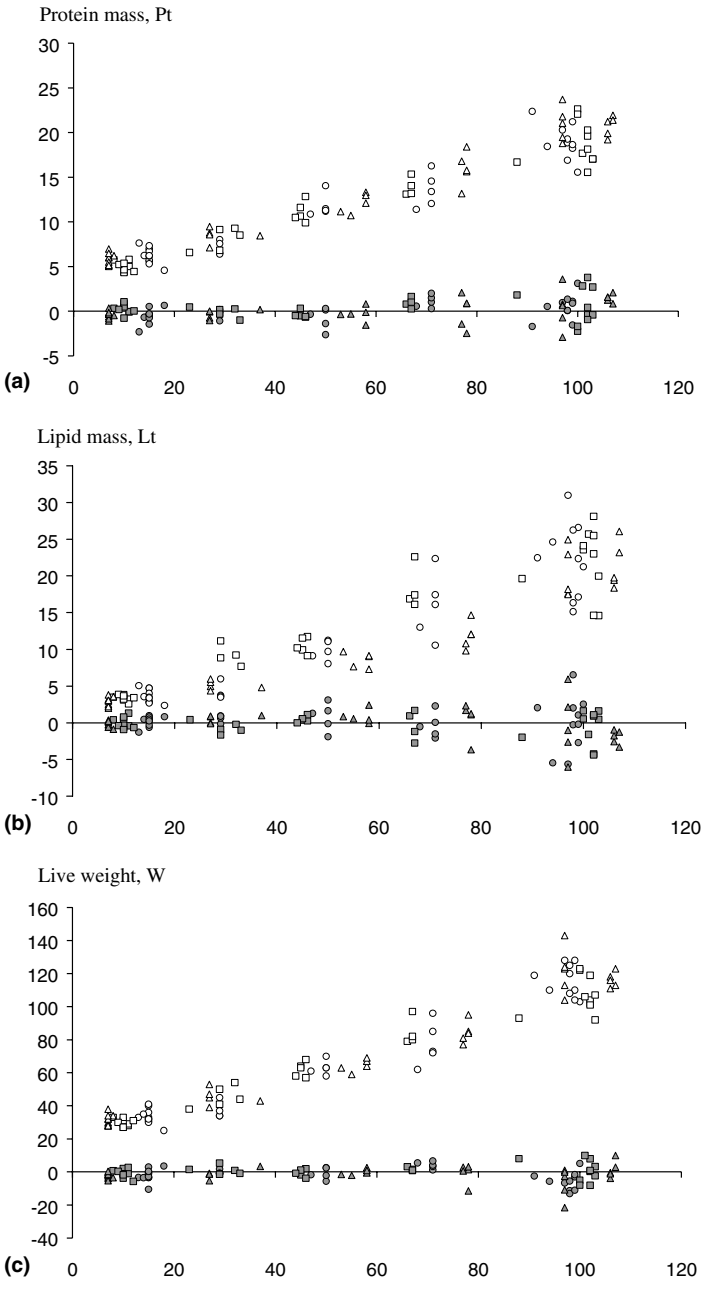
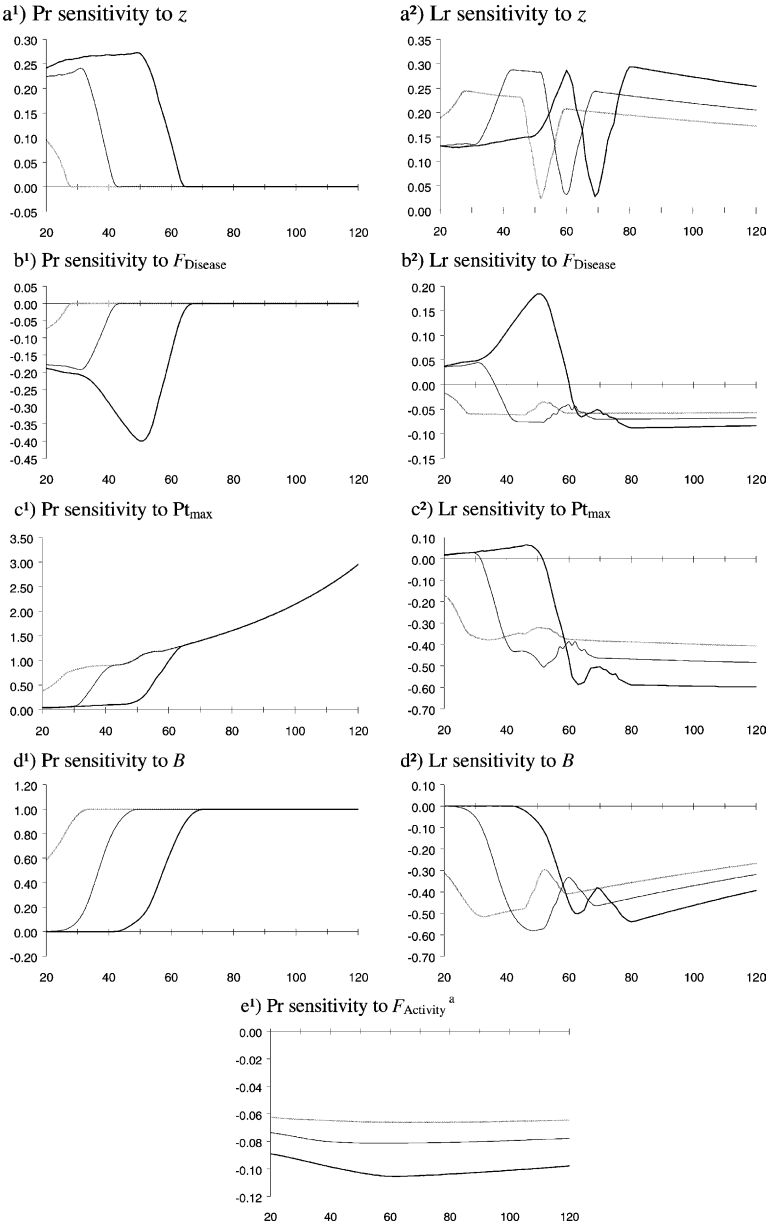


Fig. 1. Protein mass (Pt), lipid mass (Lt) and live weight (W) (y-axis) versus time (x-axis, days) since model initialisation for the three pig types: 'Meishan' type (□), 'Pietrain' type (Δ), and 'Landrace' type (○). Observed data (Q) are shown in open symbols, model deviations from the observed ($Q-\hat{Q}$) in solid symbols. Model parameters were as shown in Table 2 and the body text.



(a) Protein retention was insensitive to $F_{Activity}$

Fig. 2. Model sensitivity to variation in model parameters. Explanation is given in the body text. For each graph, the x-axis denotes live weight (W) and the y-axis relative sensitivity, R. Each pair of graphs shows sensitivity of model protein and lipid retention, Pr and Lr, at high ····, medium —, and low — levels of feed intake, 0.132, 0.120, and $0.108 \times W^{0.75}$. Other parameters are fixed at $Pt_{max} = 41.5$ kg, $B = 0.0128$ d^{-1} (derived from Eq. (10)), illness factor ($F_{Disease}$) = 3.13, $z = 0.221$, activity factor ($F_{Activity}$) = 0.1. The thermoregulation model was deactivated for sensitivity to activity factor.

Sensitivity of Lr has two components. First, amino acids not retained are channelled to lipid retention. Second, low turnover rate has a low cost of protein synthesis, with more energy remaining for lipid retention. Lr is sensitive to z through the full range of W examined, though more so where Pr is limited by Pr_{max} and extra available energy and amino acids are channelled purely to lipid retention. $F_{Disease}$ also controls the consumption by the model of energy and amino acids, and Figs. 2b[1] and b[2] share features with Figs. 2a[1] and a[2] (though are inverted, as higher $F_{Disease}$ indicates a less efficient state, but for z, lower values indicate a less efficient state).

For Pt_{max} and B, the reverse sensitivity for Pr is found. At high W and high FI, Pr is more sensitive to both parameters, as here Pr_{max} is the limiting factor in determining Pr, rather than amino acid supply. Lr sensitivity resembles the inverse of Pr sensitivity for these two parameters: where energy and amino acids are diverted away from Pr, Lr is increased, and vice versa. Pr is insensitive to $F_{Activity}$ as amino acid supply and use are unaffected by this parameter. The effect of $F_{Activity}$ upon Lr is near constant across the tested weight range, and the effect is relatively larger at low FI, where Lr itself is lower.

Sensitivity to the parameters controlling Pr_{max} was more deeply examined. Fig. 3 shows the ultimate modelled protein mass achieved for the final slaughter batch of pigs from the *Barrhill* data set (30 pigs, Table 1), using the parameters for all pigs from Table 2, but allowing B to vary. Ultimate protein mass can be seen to reach a plateau with high values of B, where protein intake, rather than the maximum daily protein retention Pr_{max}, becomes the limiting factor in determining protein retention rates. Fig. 3 demonstrates that the sensitivity of the model to parameters can be asymmetrical and have regions of parameter space where model output is insensitive to the parameter.

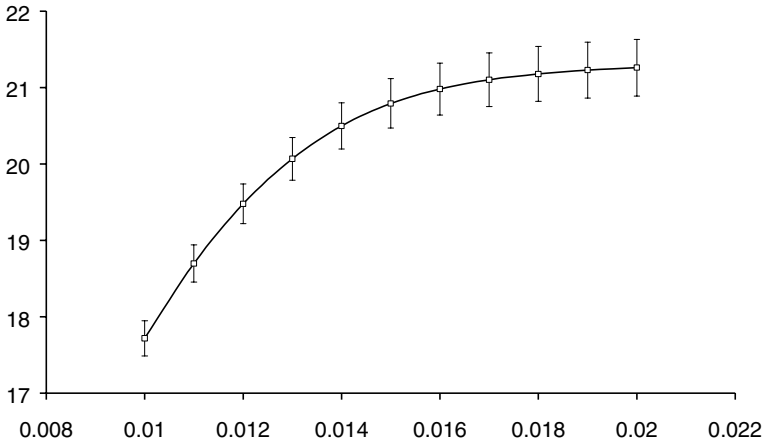


Fig. 3. Ultimate modelled protein mass (Pt) for the final slaughter batch (Table 1) of pigs for the *Barrhill* data set (y-axis, kg). Means and their standard errors are shown for different values of B (x-axis, d^{-1}). Other model parameters are set according to the all pigs column of Table 2.

4. Discussion

Fitted parameter values are mostly close to the values expected given the biological assumptions made when selecting model algorithms (Table 2). The average value of 0.22 for z is close to the default value of 0.23 (Whittemore and Fawcett, 1976). The 'Pietrain' type pigs were found to have a higher value for z. This would correspond to a lower proportional level of turnover as a function of protein mass than for the other two types. This may be because these pigs have a higher muscle mass (Fisher et al., 2003), and muscle protein is turned over less quickly than visceral protein. Nevertheless, the difference in the z values between types is not large.

The average value for F_{Disease} of 3.13 would correspond to an efficiency of recapture of amino acids during turnover of 0.937, or a loss of 0.0626, which is close to the value of 0.06 assumed by Whittemore and Fawcett (1976).

The maximum rate of protein retention, where protein retention is described by a Gompertz curve, is given by $\text{Pt}_{\max} \times B/\text{e}$ (Whittemore and Green, 2002). For the three types of the *Barrhill* data set, this expression evaluates to 0.18, 021, and 0.20 kg d^{-1} for 'Meishan', 'Pietrain' and 'Landrace' type pigs, respectively (using Eq. (10)). This similarity is not unexpected since previous studies failed to find a difference in growth rate between these three pig types (Green et al., 2003).

In the calibration of the growth model against experiment data, a conundrum is encountered. To operate the model, descriptions of the diet, feed intake, environment, and type of the pig are required. All these are obtainable, but rarely are the anabolic capabilities of the pig exercised by the experimental conditions to determine the upper bound of protein retention ($\text{Pr}_{\max}$) and the lower bound of target fatness. To use *achieved* levels of protein retention as the *potential* for a pig type will always result in a model under-prediction of protein retention where protein retention is modelled according to a linear-plateau response and feed intake varies on a short-term basis throughout the trial. The fitting of the model to collected data, either at run-time, or post hoc, alleviates this problem: where daily feed intake variation is modelled, the fitted curve for $\text{Pr}_{\max}$ necessarily lies higher than the achieved curve for protein retention. Nevertheless, it is not possible to say that these curves truly represent the upper limit for daily protein retention.

Model prediction errors (MAPE) for individual pigs were found rather similar for the three pig types, but greatest for Lt and least for W. MAPE values for W are closer to those of Pt than Lt. This results from Pt being the variable with the greatest contribution to live weight, followed by Lt and finally GutFill (Eqs. (5)–(8)). This would suggest that a major modelling difficulty is in predicting the partitioning of nutrients into lipid, though the overall efficiency and growth trajectory is more easily modelled.

Live weight and feeding level were shown to greatly affect the sensitivity of both protein retention (Pr) and lipid retention (Lr) to the model parameters (Fig. 2). Where nutrient supply is limiting protein retention, Pr is most sensitive to z and F_{Disease}, but relatively insensitive to $\text{Pt}_{\max}$ or B. The reverse situation is true where $\text{Pr}_{\max}$, not nutrient supply, limits Pr. Since nutrient intake must be partitioned between Pr and

Lr, and Lr is dealt with as a residual by the model after calculating Pr, model sensitivity to Lr closely follows that of Pr, generally with reversed signs.

Model sensitivity to parameters is not necessarily symmetrical (Fig. 3): increase in the B (or Pt_{max}) parameters will not cause the model to increase protein retention above the limit imposed by nutrient supply. Such plateaux in the model response to parameter changes may cause problems with function minimisation algorithms.

This sensitivity analysis implies that all the parameters investigated can be used to optimise the model in response to incoming data from individual pigs, but that optimisation may fail with certain combinations of parameters, dependent upon nutrient availability. A combination of parameters describing the genetic potential of the pig and its usage efficiencies for energy and amino acids may be necessary for optimisation.

The calibration and sensitivity analysis shown above has important corollaries where such a mechanistic model is incorporated into IMS systems for pig growth and nutrition. Through optimisation, the model can be fitted to collected data, yielding parameter estimates that are biologically meaningful, though since the importance of parameters varies according to circumstance, a combination of parameters may be needed. A combination of efficiency-controlling parameters and parameters determining partitioning of nutrients should enable fitting of the model to most data sets. Bounds must be set for parameter optimisation lest the optimisation process return biologically unreasonable parameter values. Here, z and $F_{Disease}$ have sensitivity values which are of the same sign for Lr and Pr across most conditions examined, hence these can be considered efficiency-controlling parameters. Conversely, sensitivity values for Pt_{max} and B have opposite signs, indicating that these are more suitable for controlling partitioning.

5. Conclusions

Internal validation of the model described above by calibration with collected data produced parameter values that were biologically reasonable, and in agreement with the values expected from the literature. Sensitivity analysis showed that not all model parameters have an effect upon model output across the full range of model inputs studied, affecting the choice of model parameters used for future model calibration. Additionally, in such a non-linear model, the effect of changing a parameter can be asymmetrical, with plateaux where the model is insensitive to parameter changes. These factors must be borne in mind during the development of future integrated management systems.

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Appendix A

For the *Barrhill* trial pigs, the experimental methodology used allowed the determination of the chemical composition of dissected lean and fat, and of the weights of all body components with the exception of blood and gut content. The residual information was therefore calculated by use of regression relationships calculated de novo from the data sets of Tullis (1982), who used similar techniques (Table 3).

The experimental methodology used determined the fully dissected composition of the half carcass of a substantial proportion of the total pigs. The pelvic limb of all pigs was dissected. All samples of dissected lean and fat were chemically analysed. The full dissections allowed relationships to be determined for the safe estimation of the chemical composition of those pigs for which only the pelvic limb was dissected. As shown below (Table 4), the relationships were not the same for the three pig types, but within each type, the error associated with the prediction parameters is small. The full dissection protocol is explained by Fisher et al. (2003).

Analysis for the protein, water, ash, and lipid composition of the wholly dissected pigs allows the derivation of body water (Yt, kg) and body ash (At, kg) content of pigs for which only the values of whole body protein and whole body lipid are known. Such is often the case in nutrient requirement models that simulate the retention of protein and lipid. Relationships were rather similar for the three pig types, and the equations detailed in the main text are forwarded as reasonable.

Table 3
Relationships calculated from Tullis (1982) and used for the determination of the chemical composition of non-carcass lean and fat components, according to the function $Y = a \times X^b$, where Y is the weight (kg) of chemical in the component and X is the weight (kg) of the component

Component	Y (kg)	a	b
Blood[a]	Protein (Pt)	0.207	1.003
	Lipid (Lt)	0.0013	1.080
Bone	Protein (Pt)	0.197	1.001
	Lipid (Lt)	0.0590	1.433
Skin	Protein (Pt)	0.421	1.001
	Lipid (Lt)	0.0227	0.895
Non-carcass[b]	Protein (Pt)	0.240	0.739
	Lipid (Lt)	0.0127	2.100
Head, feet, and tail	Protein (Pt)	0.200	0.921
	Lipid (Lt)	0.092	1.402

[a] Blood was estimated as $0.0179 \times W^{1.093}$.
[b] Gut fill was estimated as $0.176 \times W^{0.706}$.

Table 4
Relationships used for calculation of whole body protein and lipid mass (Y) from protein and lipid masses of the pelvic limb (X)

Model		a	b	RMSE (kg)
'Meishan' type	Pt	2.74	1.155	0.575
	Lt	4.60	1.028	0.619
'Pietrain' type	Pt	2.84	1.040	0.139
	Lt	4.23	0.974	0.688
'Landrace' type	Pt	3.07	0.958	0.382
	Lt	4.18	1.067	0.781

Functions of the form $Y = a \times X^b$ were used; coefficients for these functions along with the root mean squared error (RMSE) are shown.

Appendix B

Gut fill (GutFill, kg) is determined according to the following model. From the results of Le Goff et al. (2002), the overall mean and standard deviation of retention time can be given as 45.6 ± 12.7 h. It is assumed here that retention of digesta follows a gamma distribution over time, and thus the proportion, P, of retained digesta at t hours following a meal can be given by:

$$P(t) = 1 - \int_0^t (\beta^\alpha \Gamma(\alpha))^{-1} t^{\alpha-1} e^{-t/\beta} dt, \quad \text{(B.1)}$$

where α and β can be estimated from the corresponding normal distribution with mean μ and standard deviation s by $\beta = s^2/\mu$ and $\alpha = \mu/\beta$. Here, $\alpha = 13.0$ and $\beta = 3.5$. With these parameters, the proportion of digesta retained up to 0, 24, 48, and 72 h is, respectively, 1.00, 0.98, 0.39, and 0.03. Given recent daily feed intakes of $\mathbf{FI}_t$ and a proportion $\mathbf{I}$ of indigestible material in the diet, retained indigestible material can be given at day t by

$$R_t = \sum_{x=0}^{3} \mathbf{I}_{t-x} \mathbf{FI}_{t-x} P(24x), \quad \text{(B.2)}$$

where WHC is the water holding capacity of indigestible material, gut fill is given by

$$\text{GutFill}_t = \text{WHC} \times R_t. \quad \text{(B.3)}$$

Water holding capacity can vary widely, from below 2 to as high as 8.5. For calibration of the above equation, a value of 2.9 is forwarded here, based on an equation from Whittemore (1998, p. 570). No adjustment is made here for the effect of passage time through the gut, which will necessarily vary according to gut fill.

At the start of a model run, prior to collected feed intake data, feed intake is assumed to have previously followed the curve FI (kg d^{-1}) = $0.12 \times W^{0.75}$ (Whittemore, 1983), and gut fill is calculated on this basis.

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