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A new mathematical model for combining growth and energy intake in animals: The case of the growing pig

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Abstract

A simultaneous model for analysis of net energy intake and growth curves is presented, viewing the animal's responses as a two-dimensional outcome. The model is derived from four assumptions: 1) the intake is a quadratic function of metabolic weight; 2) the rate of body energy accretion represents the difference between intake and maintenance; 3) the relationship between body weight and body energy is allometric and 4) animal intrinsic variability affects the outcomes so the intake and growth trajectories are realizations of a stochastic process. Data on cumulated net energy intake and body weight measurements registered from weaning to maturity were available for 13 pigs. The model was fitted separately to 13 datasets. Furthermore, slaughter data obtained from 170 littermates was available for validation of the model. The parameters of the model were estimated by maximum likelihood within a stochastic state space model framework where a transform-both-sides approach was adopted to obtain constant variance. A suitable autocorrelation structure was generated by the stochastic process formulation. The pigs' capacity for intake and growth were quantified by eight parameters: body weight at maximum rate of intake (149 - 281 kg); maximum rate of intake (25.7 – 35.7 MJ/day); metabolic body size exponent (fixed: 0.75); the daily maintenance requirement per kg metabolic body size ($0.232 - 0.303 \text{ MJ}/(\text{day} \times \text{kg}^{0.75})$); reciprocal scaled energy density ($0.192 - 0.641 \text{ kg}/\text{MJ}^{\theta_6}$); a dimensional exponent, θ_6 ($0.730 - 0.867$); coefficient for animal intrinsic variability in intake ($0.120 - 0.248 \text{ MJ}^{0.5}$) and coefficient for animal intrinsic variability in growth ($0.029 - 0.065 \text{ kg}^{0.5}$). Model parameter values for maintenance requirements and body energy gains were in good agreement with those obtained from slaughter data. In conclusion, the model provides biologically relevant parameter values, which cannot be derived by traditional analysis of growth and energy intake data.

Keywords: Growth, Energy intake, Pigs, Stochastic differential equations

1. Introduction

Growth in animals has been studied for centuries both from a biological and a mathematical view point and many growth functions are available (France and Thornley, 1984). These functions are especially valuable if growth and energy intake are studied for long periods of time where nonlinearities are visually detectable in data, i.e. sigmoid shapes and diminishing return behaviours. Analysis of intake and growth data is usual done separately by fitting nonlinear functions of time (Kanis and Koop, 1990; Lopez et al., 2000). Another approach for modelling growth and intake curves in animals is to describe the body weight (BW) as function of the cumulated intake (Andersen and Pedersen, 1996). This has an advantage because the efficiency of

utilizing nutrients for growth follows directly as the derivative with respect to intake (Andersen and Pedersen, 1996). Growth and intake processes are interrelated because it can be assumed that the animal grows as a consequence of the nutrients and energy consumed (push effect) or it eats to meet the demands of its growth potential (pull effect) (Emmans, 1997). Simultaneous modelling of growth and energy intake offers the possibility to formulate a mathematical model where the equations are linked so that more detailed information is extracted, e.g. maximum intake rate, maintenance requirements, body energy (*BE*) accretion. If complete records of growth and energy intake trajectories from individual animals are available, estimation of model parameters could be possible. In the following, we define dietary energy as net energy because net energy systems are currently the recommended energy evaluation system for formulating diets for growing mammals (Just, 1982; Noblet et al., 1994a; NRC, 2000).

Models in animal biology have usually been defined in terms of ordinary differential equations (ODEs) (France and Thornley, 1984). Another option is to use stochastic differential equations (SDEs). The main attraction of the SDEs and the primary difference to the corresponding ODEs is the inclusion of a diffusion term which accounts for model uncertainty. Model uncertainty is biological meaningful because there are many factors affecting intrinsic growth processes which cannot be explicitly modelled. Modelling growth and intake processes using SDE models provides the possibility of quantifying both the trend and variation in the processes. Furthermore, using SDE models instead of ODE models is a powerful approach to deal with serially correlated residuals that are likely to occur when analysing growth data (Sandland and McGilchrist, 1979; Garcia, 1983).

The objective of the present study is to develop a mathematical model for simultaneous analysis of serial net energy intake and BW measurements. From these easily obtainable data, the model should quantify the dynamics of growth and yield information on energy intake capacity, maintenance requirements and body energy gain.

2. Material and methods

2.1 *Animals and diets*

The data used in this analysis is part of a serial slaughter experiment set up to determine growth capacity, energy and nutrient utilization in growing pigs (Danfær and Fernandez, in preparation). A total of 183 pigs participated in the experiment. Data on intake and growth from 13 of these pigs were used in the present paper to estimate the parameters of the proposed model. The experiment was set up as a fully randomized block design with three blocks and six different treatment groups. Each experimental group referred to a combination of two factors, i.e. gender (male, female and castrate) and a genetic sub-index for feed efficiency (high and medium level). The experimental pigs used in this study were crosses of YL sows (Landrace and Yorkshire) and Duroc boars. The pigs were fed seven highly nutritious diets in the corresponding intervals: 4-7 weeks, 7 weeks-25 kg, 25-45 kg, 45-65 kg, 65-100 kg, 100-150 kg and 150 kg to maturity. The chemical composition of the seven diets is presented in Table 1. The pigs were housed individually under thermoneutral conditions and given ad libitum access to feed during the entire growth period to maximize growth. All pigs were weighed at birth, weaning, weekly until approximately 150 kg *BW* and then every second week until the time of slaughter. The cumulated feed intake was recorded twice weekly from feed dispensers and is summarized to the corresponding dates of *BW* measurement. The total net energy intake is calculated as the net energy content of the diets (Table 1) multiplied by the cumulated feed intake in the corresponding periods of use. For the present analysis, we assume that the methods for prediction of net energy contents of the seven diets (Just, 1982; Boisen and Fernandez, 1997) are valid in the entire growth period from 7 - 450 kg *BW*. This is somewhat simplistic, but is nevertheless supported by the findings of Noblet et al. (1994b). After slaughter, the chemical composition and energy content of the body was determined (Danfær and Fernandez, in preparation).

Insert Table 1.

2.2 *Mathematical derivation of the growth model*

In the following, we assume that animal growth and feed intake are driven by the state of the animal, which is described by the state variable BW (France and Thornley, 1984). Furthermore, it is assumed that allometry ($Y \propto X^a$) can describe the differential growth of BW and BE . Note that the augmented allometric function may for some traits or data sets provide a better description (Schinckel and de Lange, 1996); however, parameter identifiability is a key issue in statistical modelling and therefore the simpler allometric function is adopted. Suppose that rate of total net energy intake (NE) is a quadratic function of the metabolic body weight

$$\frac{dNE}{dt} = \theta_1 \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3} \quad (1)$$

where θ_1 , θ_2 , θ_3 are parameters. This functional relationship (1) has previously been used to describe protein accretion curves in boars of different breed (Tauson et al., 1998). The assumption that ingestion rate is a function of metabolic body size has also been used in dynamic energy budget models in animal ecology (Nisbet et al., 2000). Using the above function (1) implies that the rate of intake is symmetric in BW , but it does not imply that the rate of intake is symmetric in time because the growth rate is not constant over time. Using a quadratic function of metabolic size for modelling the rate of intake allows to parameterize the model in terms of the maximum rate of intake (θ_2^*) and the BW at which the maximum rate (θ_1^*) occurs. There are several advantages to reparameterize the model because the new parameters can be assigned biological meaning and reduce the intra-correlation between the two parameter estimates. The new parameters can be derived by differentiation of (1) with respect to BW

$$\frac{dNE/dt}{dBW} = \frac{\theta_1 BW^{\theta_3} \theta_3}{BW} - \frac{2\theta_2 BW^{2\theta_3} \theta_3}{BW} \quad (2)$$

and setting (2) equal to zero and solving (2) with respect to BW . This yields the BW at which intake is maximized and corresponding rate of intake, i.e.,

$$\begin{aligned} \theta_1^* &= \left(\frac{\theta_1}{2\theta_2} \right)^{1/\theta_3} \\ \theta_2^* &= \theta_1 \times \left(\frac{\theta_1}{2\theta_2} \right) - \theta_2 \times \left(\frac{\theta_1}{2\theta_2} \right)^2 = \frac{\theta_1^2}{4\theta_2} \end{aligned} \quad (3)$$

In order to reparameterize the model we need to express the parameters θ_1 and θ_2 as functions of θ_1^* and θ_2^* , i.e. to solve (3) with respect to θ_1 and θ_2 :

$$\begin{aligned}\theta_1 &= \frac{2\theta_2^*}{(\theta_1^*)^{\theta_3}} \\ \theta_2 &= \frac{\theta_2^*}{(\theta_1^*)^{2\theta_3}}\end{aligned}\tag{4}$$

which can be inserted into (1).

The increment in BE represents the difference between net energy intake and net energy for maintenance, and the rate of BE accretion can be written as follows:

$$\frac{dBE}{dt} = \frac{dNE}{dt} - \theta_4 \times BW^{\theta_3} = (\theta_1 - \theta_4) \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3}\tag{5}$$

where θ_4 is the maintenance energy requirement scaled to metabolic body size. The growth function derived here is without any assumption of an upper limit for the size of the animal. Since the mature size of an animal is an important biological growth parameter, the proposed growth model should accommodate calculation of such a trait. The basic idea built into the model is that the rate of intake approaches maintenance levels as the animal matures and thus the retention of BE should approach zero. Setting equation (5) equal to zero and solving with respect to BW yields the following equation, which can be used to calculate the mature BW of an animal based on the estimated parameters of the model

$$BW_{\max} = \exp\left(\log\left(\frac{\theta_1 - \theta_4}{\theta_2}\right) / \theta_3\right)\tag{6}$$

A link function is needed in order to convert the state variable BE into BW and by assuming that the allometric relationship between BW and BE is valid:

$$BW = \theta_5 \times BE^{\theta_6} \Leftrightarrow BE = \left(\frac{BW}{\theta_5}\right)^{1/\theta_6}\tag{7}$$

From this expression body energy density can be quantified throughout the entire growth period as $M_t = BE_t/BW_t$, which is an indirect measure of the fatness of the animal. Different animals at the

same BW can have different BE contents, which would reflect variation in the ratio of lean to adipose tissue mass.

We differentiate (7) with respect to BE

$$\frac{dBW}{dBE} = \theta_5 \times BE^{\theta_6-1} \times \theta_6 \quad (8)$$

and apply the chain rule to get

$$\frac{dBW}{dt} = \frac{dBW}{dBE} \times \frac{dBE}{dt} = (\theta_5 \times BE^{\theta_6-1} \times \theta_6) \times ((\theta_1 - \theta_4) \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3}) \quad (9)$$

However, BE is a latent state variable because the energy content of the animal was measured only once, i.e. after slaughter. Therefore further manipulations of (9) are needed for parameter estimation, which can be done by substituting (7) into (9). The manipulations produce two differential equations:

$$\begin{aligned} \frac{dNE}{dt} &= \theta_1 \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3}, \quad NE(0) = NE_0 \\ \frac{dBW}{dt} &= \theta_5 \times \left(\frac{BW}{\theta_5} \right)^{\frac{\theta_6-1}{\theta_6}} \times \theta_6 \times ((\theta_1 - \theta_4) \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3}), \quad BW(0) = BW_0 \end{aligned} \quad (10)$$

The parameter vector $\theta = (\theta_1^*, \theta_2^*, \theta_3, \theta_4, \theta_5, \theta_6)^T$ is to be estimated from data and the initial values $y_0 = (NE_0, BW_0)$ are obtained by using the measurements at $t = 0$ as starting values for the filtering and estimation procedures. We investigate if the parameter (θ_3) can be fixed at 0.75 because this is the traditional scaling factor applied in energy metabolism studies. This in turn makes it easier to compare the estimated maintenance requirement with published values. A complete list of all the parameters, their physical interpretation as well as dimensions is presented in Table 2.

Insert Table 2.

2.3 The stochastic growth model

Two sources of variation are considered in the model: 1) a dynamic noise term, which is part of the system (the animal) such that the value of the process at time t depends on this noise up to the time t , and 2) a measurement noise term, which does not affect the process itself, but only its observations. Separation of intra animal variation into two noise components requires additional

explanation. The system noise can be thought of as animal intrinsic variability due to the following; 1) animal growth is always embedded in a randomly varying environment (no matter how well the experimental conditions are controlled), 2) growth processes are subjected to external and internal influences that change over time (e.g. shifting diets, sub-clinical diseases, ambient temperatures, hormonal influences, emotional stress etc.) which may randomly affect the growth. Modelling all of these aspects that disturb the system would produce a very large and complicated model that renders model identifiability and parameter estimation given data. In the foregoing section, we derived an ODE model based on biological assumptions regarding intake and growth. It is now translated into a stochastic state space model. Thus, the equations governing the growth and intake processes can be written as the following continuous-discrete time state-space model where the two system equations are:

$$\begin{pmatrix} dNE \\ dBW \end{pmatrix} = \begin{pmatrix} \theta_1 \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3} \\ \theta_5 \times \left(\frac{BW}{\theta_5} \right)^{\frac{\theta_6-1}{\theta_6}} \times \theta_6 \times ((\theta_1 - \theta_4) \times BW^{\theta_3} - \theta_2 \times BW^{2 \times \theta_3}) \end{pmatrix} dt + \begin{pmatrix} \sigma_{NE} & 0 \\ 0 & \sigma_{BW} \end{pmatrix} dw_t \quad (11)$$

The first term on the right hand side of (11) is commonly called the drift term and the second is commonly called the diffusion term in which σ_{NE} and σ_{BW} are diffusion coefficients and w_t is a two dimensional Wiener process with independent increments. The two measurement equations can be written as:

$$\begin{pmatrix} y_{1,k} \\ y_{2,k} \end{pmatrix} = \begin{pmatrix} NE_{t_k} \\ BW_{t_k} \end{pmatrix} + \begin{pmatrix} e_{1,k} \\ e_{2,k} \end{pmatrix} \quad (12)$$

The observation equations describe what is actually measured at discrete time points

$t_k = (t_0 < t_1 < \dots < t_{N-1} < t_N)$ and $[y_{1,k}; y_{2,k}]^T$ are functions of the states $[NE_{t_k}; BW_{t_k}]^T$ contaminated with Gaussian white noise $[e_{1,k}; e_{2,k}]^T$ with variances S_{NE} and S_{BW} . The system w_t and observation noise e_k are assumed to be mutually independent.

Model diagnostics (residual and autocorrelation plots) are employed and visual inspection of the innovations plotted as a function of time is used to pinpoint if variance stabilization is required. It turned out that on the original scale variance was increasing with expected value and it was decided to work with transformed responses (square root or logarithmic) instead. For linear models it is possible to use the Box-Cox transformation approach, i.e. find the optimal (in a likelihood sense) transformation among the power and logarithmic transformations. A similar theory is not available for SDE models. Instead, we used a “transform both-sides” (TBS) approach, i.e. both responses and expected values in the model are transformed using the same transformation. The appealing feature about the TBS approach is that the parameter interpretations are unchanged. More specifically, the ODE system is transformed and then system noise is added to the transformed ODE system. Hence, system noise is assumed to have a constant intensity on the transformed scale. This approach can be generalized to accommodate any type of transformation. We may introduce $z_t = h(x_t)$ where x_t denotes the model states (NE and BW). If the original ODE (10) is written as $dx_t = f(x_t, t, \theta)dt$ then the ODE for the transformed response $h(x_t) = z_t$ is obtained by the chain rule:

$$dz_t = h'(h^{-1}(z_t)) \times f(h^{-1}(z_t), t, \theta)dt \quad (13)$$

where $h(x_t)$ is the transforming vector function, $h'(x_t)$ is the derivative with respect to the states x_t , $h^{-1}(z_t)$ is the inverse of $h(\cdot)$, and $f(\cdot)$ is the functional expression for the original ODE system (10). For instance, if $h(x_t) = (\sqrt{NE}, \sqrt{BW})$ then $h^{-1}(z_t) = (NE^2, BW^2)$ and $h'(x_t) = (1/2\sqrt{NE}, 1/2\sqrt{BW})$.

Using (13) and adding system noise yields the following SDE system

$$dz_t = \begin{pmatrix} \frac{1}{2NE} \times (\theta_1 \times BW^{2\theta_3} - \theta_2 \times BW^{4\theta_3}) \\ \frac{1}{2BW} \times \theta_5 \times \left(\frac{BW}{\theta_5}\right)^{\frac{2(\theta_6-1)}{\theta_6}} \times \theta_6 \times ((\theta_1 - \theta_4) \times BW^{2\theta_3} - \theta_2 \times BW^{4\theta_3}) \end{pmatrix} + \begin{pmatrix} \sigma_{NE} & 0 \\ 0 & \sigma_{BW} \end{pmatrix} dw_t \quad (14)$$

The transformed measurements are obtained as the square root of the original and then the additive measurement noise is added on the transformed scale. Visual inspection of the innovations plotted as function of time is used to choose between the two transformations (logarithmic or square root).

2.3 Parameter estimation

Given the model structure (11) and (12) approximate maximum likelihood (ML) estimates of the unknown parameters can be determined by finding the parameters θ that maximize the approximate likelihood function of a given sequence of measurements $Y_N = (y_0, y_1, \dots, y_{N-1}, y_N)$. The likelihood function can be expressed as the following by conditioning on the observations at time t_0 i.e., $y_0 = (y_{1,0}; y_{2,0})$,

$$L(\theta | Y_N) = p(Y_N | \theta) = \left(\prod_{k=1}^N p(y_k | Y_{k-1}, \theta) \right) \quad (15)$$

where p denotes the probability density function conditional on the parameters and the previous observations.

Since the SDE in (12) are driven by a Wiener process and since increments of a Wiener process are Gaussian, it is assumed that the conditional densities can be approximated by Gaussian densities, which means that a method based on the so-called extended Kalman filter (EKF) can be applied (Kristensen and Madsen, 2003). The EKF filter is a recursive algorithm. This means that only the estimated state from the previous time step and the current measurement are used to compute the estimate for the current state because the previous state contains all the information up to that time point. The EKF has two distinct phases: predict and update. The predict phase uses the state estimate from the previous time step to produce an estimate of the state at the current time step. In the update phase, measurement information at the current time step is used to refine this prediction to arrive at a new, more accurate state estimate, again for the current time step (see appendix for full details regarding the EKF algorithm).

Assuming a Gaussian density, which is completely characterized by its first and second order moments, the EKF is used because EKF describes the evolution of the first and second

order moments of the conditional probability densities in terms of ODEs and algebraic equations. In order to formally introduce the assumption of Gaussianity, the following notation is defined

$$\hat{y}_{k|k-1} = E\{y_k | Y_{k-1}, \theta\} \quad (16)$$

$$R_{k|k-1} = V\{y_k | Y_{k|k-1}, \theta\} \quad (17)$$

$$\hat{e}_k = y_k - \hat{y}_{k|k-1} \quad (18)$$

and the likelihood function is rewritten in the following way:

$$L(\theta | Y_N) = \left(\prod_{k=1}^N \frac{\exp\left(-\frac{1}{2} \hat{e}_k^T R_{k|k-1}^{-1} \hat{e}_k\right)}{\sqrt{2\pi \times \det(R_{k|k-1})}} \right) \quad (19)$$

The parameter estimates can now be determined by solving the following nonlinear optimisation problem:

$$\hat{\theta} = \arg \min_{\theta \in \Theta} \{-\log(L(\theta | Y_N))\} \quad (20)$$

where, for each value of θ in the optimization, \hat{e}_k and $R_{k|k-1}$, are computed recursively by the EKF.

The estimation scheme has been implemented in the parameter estimation software Continues Time Stochastic Modelling (CTSM). More details of the parameter estimation, filtering and smoothing are giving in the CTSM User and Mathematics guides (Kristensen and Madsen, 2003).

The growth and energy intake trajectories obtained from the 13 pigs are analysed separately. Population parameter estimates and their standard deviations are then calculated as the average and standard deviation of the 13 individual estimates. This procedure is called a two stage approach (Davidian and Giltinan, 1995).

3. Results and discussion

At a preliminary stage initial parameter estimates and their effect on convergence and final parameters estimates were monitored. In general, for all 13 animals in the data set the

convergence properties of the estimation procedure were good because all estimations converged in less than 150 object function evaluations. The two transforming functions were applied and diagnostic plots were inspected for all 13 animals, which showed that the best variance stabilizing function was the square root. Therefore, the parameter values and likelihood tests presented in the following is based on the square root transformation. The parameters were all estimated by maximizing the likelihood, and the improvement of fit when θ_3 was allowed to vary freely compared to being fixed at 0.75 was measured by the likelihood value at convergence. This is presented in Table 3. In ten of the thirteen analysed data sets, the value of θ_3 did not deviate significantly from 0.75 ($p > 0.05$). As a consequence, θ_3 was fixed at 0.75 for all animals in the subsequent analyses. Parameter values for each animal obtained by fitting the model to data is presented in Table 4 together with population averages and coefficient of variation (CV) for the drift part of the model.

Insert Table 3.

Population based methods (mixed models) have been more widely applied in analysis of pig growth (Criag and Schinckel, 2001; Kebreab et al., 2007). It is assumed that all animals follow the same functional form with parameters varying according to multivariate normal distribution. Thirteen animals as available in this data set are too few for application of a population based approach and thus the data from the 13 pigs were analysed separately. Population based methods are especially useful if the population values are of main interest. In the present study, the animal specific values are of primary interest (e.g. comparison with slaughter data), so the data was analysed pig by pig, but a population based analysis would be of interest, too. Such an approach would yield a complete description of the dynamics with animal-to-animal variation described by key structural parameters and the within-animal variation described by a stochastic process. An algorithm for non-linear mixed effects in combination with SDE-models has recently been developed (Mortensen et al., 2007; Mortensen and Klim, 2008), but needs further investigation. Moreover, note that the current model has a two-dimensional response. None of the standard

software packages, which are usually applied for nonlinear mixed modelling, will fit multivariate response models because these are developed for the univariate case (Pinheiro and Bates, 2000; Littell et al., 2006).

Measures made on the individual animal are likely to be more correlated than measures made on different individuals, and serial autocorrelation is present since measurements made closely in time tend to be highly correlated compared to measures made further distant in time (Sandland and McGilchrist, 1979). An autocorrelation structure is generated “automatically” due to the stochastic process formulation. Moreover, unequally spaced observations do not create a problem because the model is formulated in continuous time. This is an additional advantage compared to application of ARIMA models for modelling correlated residuals.

Insert Table 4.

3.1. Modelling growth and energy intake patterns

Growth curves and feed intake curves are often represented as a function of age because age can be recorded more easily and more precisely than for instance weight. The parameters θ_1^* (BW at maximum rate of intake) and θ_2^* (maximum rate of intake) are estimated in the range of 149 – 281 kg BW and 25.7 – 35.7 MJ NE/day. Our results indicate that the maximum intake was reached at a much later stage in life than usually reported in studies quantifying feed intake (Andersen and Pedersen, 1996; Lorenzo et al., 2003). This is probably caused by the fact that measurements were conducted outside the normal BW range (20-120 kg). According to the knowledge of the authors there is no information available on patterns of feed intake of pigs beyond 150 kg BW, which excludes the possibility for comparison. However, our results agree very well with the theory proposed by Emmans (1997), which suggests that intake is maximised at about half of the mature size. A prerequisite for the validity of model is of course that the framework is able to describe the observed patterns of intake and growth. Those are presented in Figure 1, for the drift part of the model and the one-step-ahead predictions generated by the EKF together with observed data from two representative pigs in the dataset. In Figure 1 we have plotted NE, BW, intake, and

growth rate against time to show that the model described data well. Taylor (1985) suggested that intake of animals with a large appetite might decline after having reached a maximum. Fowler (1980) found that the daily intake reached a peak at about 120 kg BW and then declined to very fluctuating values. The feed intake data presented by Thompson et al. (1996) suggested that the feed intake did not stabilize at 200 days of age. Moreover, large fluctuations in the feed intake during the course of time were observed as well, which corresponds well with the observations reported in this study. A feature of the model is that the rate of intake increases quickly in the early part of the growth period and then plateaus as the pig matures, which is a consequence of the energy being diverted towards maintenance. Moreover, it has the flexibility to identify that rate of intake has a peak and then decreases towards a plateau level, which corresponds to maintenance of body functions at maturity.

Insert Figure 1.

Modelling BW as a function of age requires a four parameter function like the Bridges, generalized Michalis-Menten or Richards functions for adequately describing the growth trajectory of pigs from birth to maturity (Kreab et al., 2007; Strathe et al., submitted). Lorenzo et al., (2003) presented an analysis of linear and nonlinear models and reported that a three parameter logistic function was appropriate for characterizing the pattern of feed intake in pigs. Thus, a total of seven structural parameters are needed when the responses are modelled separately. The proposed bi-variate model uses six parameters in its complete form. However, the dimensionless exponent θ_3 was fixed 0.75 during parameter estimation and thus restricting the number of free parameters to only five plus optional two initial state parameters. In terms of the number of structural parameters that has to be estimated the bi-variate approach is not much different than modelling the responses separately. However, the proposed framework offers other quantities (maintenance requirement, energy gain) to be derived compared to the traditional analysis of growth and intake, which are usually confined to estimate initial value, maximum value and inflexion points. The modelled

growth curves presented in Figure 1 have clear sigmoid shapes and their derivatives with respect to time increase in the early part of life towards a maximum and then decrease towards zero.

Figure 2 presents goodness of fit plots. The observed rates of energy intake and BW gain are plotted against the corresponding one-step-ahead predictions generated by the EKF for the 13 animals and the line $Y = X$ is also included. The model fits well to the observed data because the model dynamically tracks the fluctuations in the observations. A comprehensive review of Whittemore et al. (2001) concluded that prediction of short time fluctuations in feed intake was difficult, although the information is essential for the practical purposes of pig's day to day nutrition. Thus, application of SDE models may be a way to obtain precise predictions of short time fluctuations in intake and growth rates.

Insert Figure 2.

3.2 The biological implications of stochasticity

In Table 5 parameter estimates related to the stochastic part of the model, e.g. diffusion and measurement error terms are presented. First, it should be noted that the estimated system noise was significant at the 5% level (t-score around 10) for all modelled animals. The magnitude of difference between the system and measurement noise indicates that the measurement error is negligible compared to the system error for most of the pigs. Note however that it is very difficult to distinguish between the two sources of variation, in particular for equidistant observations. For the bodyweight, the total variance of the difference between two consecutive measurements $y_{1,1}$ and $y_{1,2}$ is approximately $\sigma_{BW}^2 \Delta t + 2S_{BW}$. If Δt is the same for all pairs of consecutive measurements, then only the sum, not the two distinct terms is identifiable. The irregular sampling scheme with weekly and bi-weekly sampling improves identification somewhat, but simulations have indicated that there are still problems for this sampling scheme. Still we can conclude that the animal intrinsic variability is more pronounced than the measurement noise, and fitting a model without measurement errors gives very similar results for the fixed effects. This

suggests that the incorporation of model uncertainty through a diffusion process is successful from both a biological and a statistical point of view.

Insert Table 5.

Previous attempts to model growth and intake processes are based on models, which are solutions to ODEs (France and Thornley, 1984; Lopez et al., 2000). SDE models provide a much more realistic representation of reality than their deterministic counterparts because system noise reflects that we do not have a full understanding of the complex processes, which regulate intake and growth. For this reason, the aim of the current model formulation has been focussed on modelling both the trend of the growth processes and the random fluctuations by means of SDEs. It further implies that an individual animal does not have a fixed growth curve from birth as growth is subjected to disturbances during life time. This can be demonstrated by a simulation study where the mean parameter values for the modelled growth and intake trajectories are used. The mean parameter vector is given as $\theta = (\theta_1^* = 221, \theta_2^* = 31.5, \theta_3 = 0.75, \theta_4 = 0.27, \theta_5 = 0.32, \theta_6 = 0.81, \sigma_{NE} = 0.17, \sigma_{BW} = 0.07)^T$. An Euler-Maruyama scheme was used with an integration step of 0.5 day (Kloeden and Platen, 1992). The results of the simulation analysis are shown in Figure 3. The figure is organized as follows: plots A and B show the simulated paths of the stochastic growth model along with the mean curves for the stochastic process; plots C and D show the derivatives with respect to time in order to display the hypothesis build into the model. In contrast to previously published deterministic approaches (e.g. Lopez et al., 2000) to model growth and intake, the trajectories are not smooth. In fact, a deterministic model assumes that: 1) the mathematical processes generating the observed intake and growth trajectories are smooth (continuous and continuously differentiable) within the considered time frame; 2) the variability of the actual measurements is due to observation error. The present approach results from the hypothesis that the underlying mathematical process is not smooth, but is subjected to random intrinsic perturbations. This system noise represents the complexed effect of many factors, each with a small individual effect, which are not explicitly represented in the deterministic part of the model (the drift term of

the model). Figure 3 also clearly illustrates the consequence of assuming that the system noise is additive on a square root scale (NE and BW) because once the simulated trajectories are transformed back to the original scale, it can be seen that the fluctuations in the intake process increase as the animal matures. This phenomenon has previously been described for intake (Fowler 1980; Thompson et al., 1996).

Insert Figure 3.

3.3 Estimation of maintenance requirement

Although the functional relationship might look complicated, the model was derived from basic biological ideas and thus biologically relevant results can be extracted from the analysis. A maintenance component is estimated and expressed on a net energy basis. The maintenance component θ_4 in the model was estimated to be in the range of 232 – 303 kJ/(day \times kg^{0.75}) with a mean of 268 kJ/(day \times kg^{0.75}) and a CV of 8.6%. In net energy systems the maintenance component is usually estimated by regressing the daily energy retention or heat production on daily ME intake, then the intercept represents the maintenance requirement (Just, 1982; Noblet et al., 1994). Schieman et al. (1972) estimated the maintenance requirement as 280 kJ/(day \times kg^{0.75}) for barrows at approximately 95-185 kg BW , whereas Just (1982) estimated 326 kJ/(day \times kg^{0.75}) for growing pigs weighing from 20 to 90 kg BW . The maintenance estimates produced by the present model are on average slightly underestimated compared to those values (Table 4). There are several explanations to this fact: 1) the maintenance requirement was represented by one parameter in the model and it is likely that this representation is too simplistic because the chemical composition of the body, organ size etc. changes during the course of growth (Tess et al., 1984); 2) fasting heat production measurements are usually conducted in the BW range of 20-110 kg and thus little information is available beyond this point; 3) the net energy contents of the seven diets used in the present study were calculated from dietary characteristics using the method proposed by Just (1982) and Boisen and Fernandez (1997). We will direct focus towards estimating a maintenance

requirement based on slaughter data because these can be used for validation. According to the definition of NE we may write the following equation:

$$NE = \Delta BE + NEM = \Delta BE + \int_0^t q \times BW^{0.75} dt \quad (21)$$

Where q represents the maintenance requirement and ΔBE is the measured increment BE from weaning (t_0) to the time of slaughter (t_I). The integral in (21) can be approximated by the trapezium rule, i.e.

$$NEM \approx \sum_{k=2}^N (t_k - t_{k-1}) \times q \times (BW_{k-1}^{0.75} + BW_k^{0.75}) / 2 \quad (22)$$

The relationship between NE and $\Delta BE + NEM$ is shown in Figure 4. When a q value of $326 \text{ kJ}/(\text{day} \times \text{kg}^{0.75})$ (Just, 1982) was used in the left plot, NE was overestimated in relation to measured NE intake. In the right plot, a q value was estimated from data by minimizing the weighted least sum of squares so that estimated NE would be in accordance with the measured NE intake. This procedure converged at $261 \text{ kJ}/(\text{day} \times \text{kg}^{0.75})$ and the results including the line $Y=X$ is shown in the right plot in Figure 4. The derived maintenance requirement can be regarded as a population requirement because each point in the graphs corresponds to one animal. This can be compared to the mean maintenance value of $268 \text{ kJ}/(\text{day} \times \text{kg}^{0.75})$ obtained with the model (Table 4), which indicates that the model predicted a realistic value. Rather than interpreting this as an absolute maintenance value (i.e. fasting heat production), the maintenance parameter should be considered as an apparent maintenance value because it depends upon the net energy system that has been used to calculate the dietary values.

Insert Figure 4.

3.4. Modelling relation between body energy retention and body weight

An allometric relationship was chosen to represent the relation between BE and BW due to its biological interpretation. The reciprocal scaled energy density θ_5 differed the most

between animals ($0.192 - 0.641 \text{ kg/MJ}^{\theta_6}$). All parameter estimates of θ_6 ($0.730 - 0.864$) in the model were less than unity, which means that the derivative with respect to BE is continuously decreasing. This corresponds to increasing energy density of the pig, which is an obvious consequence of the BE gain changing towards lipid accretion as the animal matures. The BE state variable is a latent variable in the model and is therefore eliminated from the differential equations due to the functional relationship between BE and BW . However, growth curves were modelled accurately, which means that the model should be able to predict energy retention at various stages of growth. We evaluated the proposed relationship (7) between BE and BW by comparing it with data from the 170 pigs in the serial slaughter experiment. The results are presented in Figure 5 on log-log scales where line ($\log(BW) = \log(\theta_5) + \theta_6 \log(BE)$) is added to the plot. The average of the 13 estimates of θ_5 and θ_6 is used to construct the population relation. In general, the line agrees well with the observed data, which indicates that the pattern of energy gain is reflected in the NE and BW measurements. However, close inspection of Figure 5 also reveals that BW is underestimated for low BE values and overestimated for high BE values. Furthermore, considering that the estimated maintenance level corresponds closely to the data obtained from serial slaughter experiments suggests that the rules for partitioning of net energy for maintenance and energy gain are adequate. Insert Figure 5.

Other functional relationships, like the augmented allometric, have been proposed for relating different body components, and for some datasets they may yield a better fit than the allometric (Schinckel and de Lange, 1996). The estimated standard errors for θ_5 were large relative to the estimates for many of the animals, and the correlation between the estimators of θ_5 and θ_6 was generally large, around 0.8. This indicates that the estimation procedure has difficulties in identifying and distinguishing these two parameters. An even more flexible function would enhance this problem. The statistical procedure presented here is suited for multi-response modelling (Kristensen and Madsen, 2003) and thus serial measurements of body composition, e.g. ultra sound or computed tomography scans can be directly integrated as well. Adopting multivariate response

modelling techniques provides the possibility to formulate structural equations that are fitted simultaneously to data. Analysis of energy balance data has also been approached by multivariate techniques and more information can be extracted from such data (van Milgen and Noblet, 1999).

4. Conclusion

The focus in the present investigation was to develop a mathematical model for energy intake, body energy accretion and body weight gain. The model is derived from simple biological assumptions and it can be used to study the interplay between net energy intake and body weight gain. The model is based on two coupled differential equations that describe the evolution in energy intake and body weight gain during the life time of animals. Animal intrinsic variability affects intake and growth and is build into the model through a stochastic differential equation approach. Experimental data obtained on growing pigs is used for parameter estimation and verification of the biological significance of the parameter values. We showed that eight parameters quantifies the time trend and variation in the two dimensional outcome, i.e. body weight at maximum rate of intake (149 - 281 kg); maximum rate of intake (25.7 – 35.7 MJ/day); metabolic body size exponent (fixed: 0.75); the daily maintenance requirement per kg metabolic body size ($0.232 - 0.303 \text{ MJ}/(\text{day} \times \text{kg}^{0.75})$); reciprocal scaled energy density ($0.192 - 0.641 \text{ kg/MJ}^{\theta_6}$); a dimensional exponent, θ_6 ($0.730 - 0.867$); coefficient for animal intrinsic variability in intake ($0.120 - 0.248 \text{ MJ}^{0.5}$) and coefficient for animal intrinsic variability in growth ($0.029 - 0.065 \text{ kg}^{0.5}$). In conclusion, the new mathematical model provides an important alternative to traditional analysis of energy intake and growth curves by treating the animal's response as two dimensional.

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Appendix - Extended Kalman Filtering

The approximate maximum likelihood (ML) estimation of parameters in SDEs involves the use of state filtering. Consider the general SDE model with the following system and measurement equation:

$$dx_t = f(x_t, t, \theta)dt + \sigma(t, \theta)dw_t \quad (\text{A.1})$$

$$y_k = h(x_k, t_k, \theta) + e_k, e_k \sim N(0, S) \quad (\text{A.2})$$

The extended kalman filter (EKF) is a set of equations that provides an efficient recursive approach to approximate the conditional distributions with Gaussian distributions of a sequence of measurements $Y_N = (y_0, y_1, \dots, y_{N-1}, y_N)$. The conditional densities are thus completely characterized by the one-step prediction error e_k and the associated one step prediction covariance matrix $R_{k|k-1}$ which are then used to construct the likelihood function.

Given the parameters θ , initial states $\hat{x}_{1|0} = E\{x_0\}$, and initial state covariance

$\hat{P}_{1|0} = V\{x_0\}$, the first step of the EKF involves the output predictions equation:

$$y_{k|k-1} = h(\hat{x}_{k|k-1}, t_k, \theta) \quad (\text{A.3})$$

$$R_{k|k-1} = CP_{k|k-1}C^T + S \quad (\text{A.4})$$

which predict the mean and covariance of the output at time t_k given all past information available at time t_{k-1} . Here S is the variance of the measurement error and C is the linearization of the measurement equation, i.e.

$$C = \left. \frac{\partial h}{\partial x} \right|_{x=\hat{x}_{k|k-1}} \quad (\text{A.5})$$

The second step of the recursions involves the innovation equation:

$$e_k = y_k - \hat{y}_{k|k-1} \quad (\text{A.6})$$

which determines the one-step-ahead prediction residual at time t_k . The third step of the recursions involves the Kalman gain equation:

$$K_k = P_{k|k-1}C^TR_{k|k-1}^{-1} \quad (\text{A.7})$$

This is basically a matrix of weights that determines the degree of updating in the fourth step because updating is based on a compromise between the observation and current model state. In a situation where the model is good, but the observations are dominated by measurement error, the state estimate should rely more on the model as opposed to fitting the observations. On other the hand, if the model is incomplete the states should rely more on the observations than the model. The updating equations are given by:

$$\hat{x}_{k|k} = \hat{x}_{k|k-1} + K_k e_k \quad (\text{A.8})$$

$$P_{k|k} = P_{k|k-1} - K_k R_{k|k-1} K_{k|k-1}^T \quad (\text{A.9})$$

where the predicted mean and covariance of the states at time t_k are updated based on the observed value via the innovation and the Kalman gain. The fifth and final step of the EKF algorithm involves the state prediction equations:

$$\frac{d\hat{x}_{t|k-1}}{dt} = f(\hat{x}_{t|k-1}, t, \theta) \quad (\text{A.10})$$

$$\frac{dP_{t|k-1}}{dt} = AP_{t|k-1} + P_{t|k-1}A^T + \sigma\sigma^T \quad (\text{A.11})$$

which are solved for $t \in [t_k, t_{k+1}]$ in order to predict the state $\hat{x}_{t|k}$ and the associated state covariance $P_{t|k}$. Since $f(\cdot)$ is a nonlinear function, a local first-order Taylor expansion of $f(\cdot)$ at each sampling time t_k is needed to approximate the matrix A i.e.

$$A = \left. \frac{\partial f}{\partial x} \right|_{x=\hat{x}_{t|k-1}} \quad (\text{A.12})$$

The new predicted mean and covariance of the states are then used to predict new values for the next observation and thus steps from A.3 to A.12 are repeated.

Figure legends

Fig. 1. The relationship between total net energy intake, body weight, net energy intake, growth rate and age of two representative pigs (top: 6206 and bottom: 5374) in the dataset. The circle symbols present the actual measurements where the observational rates were calculated as the mean rates within a given sub-period i.e. $(NE_2 - NE_1) / (t_2 - t_1)$ or $(BW_2 - BW_1) / (t_2 - t_1)$. The solid line represents the one-step-ahead prediction generated by the Extended Kalman Filter and the dotted line represents the solutions to the drift term of the model, respectively.

Fig. 2. Goodness of fit graphs for the 13 pigs. The rates of energy intake and BW gain are plotted against the corresponding one-step-ahead predictions generated by the extended Kalman filter. The solid line represents $Y = X$.

Fig. 3. Simulation results of the proposed model. Plots A and B presents three simulated paths and the mean curve for the total net energy intake and body weight for the selected parameters, respectively. Plots C and D present the derivative with respect to time for the process and drift term in the model.

Fig. 4. Plot of total net energy intake taken as the sum of body energy and integrated maintenance requirement against measured total net energy intake. The maintenance requirement (left) is 326 kJ/(day \times kg^{0.75}) and (right) 261 kJ/(day \times kg^{0.75}). The solid lines is $Y = X$ whereas the dotted (left) is the regression equation $Y = -310 + 1.18X$.

Fig. 5. Validation of the proposed relationship between body weight and body energy ($\log(BW) = \log(\theta_5) + \theta_6 \log(BE)$). Measurements of body weight are plotted as a function of body energy contents for 170 pigs with the mean estimated relationship (mean of the 13 parameter estimates).

Table 1.

Chemical composition of experimental diets.

Diet	1	2	3	4	5	6	7
Period of use	4-7 weeks	7 weeks-25 kg	25-45 kg	45-65 kg	65-100 kg	100-150 kg	150 kg-
Dry matter, g/kg diet	899	896	889	883	886	888	884
Net energy, MJ/kg diet ^a	9.57	9.26	8.96	8.41	8.26	8.11	7.80
Nutrients, g/kg DM:							
Crude protein	267	240	213	204	179	162	147
Crude fat	93.7	91.3	86.3	54.5	44.4	26.8	26.1
Sugars ^b	27.4	31.8	36.9	35.5	32.4	31.4	30.6
Starch	317	337	358	406	458	492	529
Dietary fibre ^c	157	172	176	171	178	157	159
Lysine	15.6	14.0	12.4	10.8	9.51	7.88	6.33
Methionine	5.49	4.69	3.80	3.34	3.02	2.68	2.25
Cystine	3.58	3.49	3.58	3.46	3.26	3.13	2.83
Threonine	10.4	9.48	8.48	7.31	6.74	5.75	4.52
Minerals, g/kg DM							
Ash	61.4	59.4	56.2	53.0	50.3	45.5	44.3
Calcium	10.2	9.4	8.7	8.2	7.9	7.7	7.3
Phosphorus	7.1	6.5	6.0	5.9	6.1	5.7	6.0

^aEstimated according to Just (1982) and Boisen and Fernandez (1997).^bGlucose, fructose, sucrose and fructans.^cNon-starch polysaccharides (NSP) + lignin.

Table 2.

Definitions of model parameters.

Parameters	Unit	Parameter interpretation
θ_1^*	kg	Body weight at maximum rate of intake
θ_2^*	MJ/day	Maximum rate of intake
θ_3		Metabolic body size exponent
θ_4	MJ/(day \times kg $^{\theta_3}$)	The daily maintenance requirement per kg metabolic body size
θ_5	kg/MJ $^{\theta_6}$	Reciprocal scaled energy density
θ_6		Dimensionless exponent
σ_{NE}	MJ	Diffusion coefficient related to animal intrinsic variability in intake
σ_{BW}	kg	Diffusion coefficient related to animal intrinsic variability in growth
S_{NE}	MJ 2	Measurement noise
S_{BW}	kg 2	Measurement noise

Table 3.

Fit statistics for models M_0 (varying θ_3) and M_1 (fixed θ_3).

Pig	$\text{Log}l_0^a$	$\text{Log}l_1^a$	LR^b	p-value ^c
5365	16.35	16.39	0.080	0.777
5374	28.77	29.16	0.780	0.377
5711	58.80	62.30	7.000	0.008
5713	53.79	54.28	0.980	0.322
5720	38.73	38.97	0.480	0.488
6053	45.80	51.80	12.00	0.001
6056	25.89	32.14	12.50	0.000
6205	10.69	11.97	2.560	0.110
6206	-7.178	-7.155	1.250	0.264
6211	20.60	20.83	0.460	0.498
6710	-0.270	0.815	2.170	0.141
6713	22.57	23.27	1.400	0.237
6716	18.86	19.76	1.800	0.180

^aLog-likelihood value at final convergence for the models.^bLikelihood ratio for comparison of the two models M_0 and M_1 .^cThe corresponding p-value in the chi-squared distribution with one degree of freedom.

Table 4. Parameter estimates with standard errors (SE) related to the drift part of the model and empirical mean and coefficient of variation (CV).

Pig id	θ_1^*	SE	θ_2^*	SE	θ_4	SE	θ_5	SE	θ_6	SE
5365	257	10.4	34.4	0.91	0.243	0.03	0.368	0.08	0.790	0.03
5374	236	10.9	27.0	0.66	0.236	0.02	0.641	0.11	0.730	0.03
5711	173	14.3	30.0	1.36	0.298	0.09	0.294	0.08	0.785	0.04
5713	268	17.3	35.1	1.38	0.291	0.04	0.199	0.08	0.867	0.05
5720	208	10.4	27.5	0.77	0.275	0.04	0.395	0.10	0.782	0.04
6053	240	17.7	34.9	1.56	0.241	0.06	0.291	0.12	0.808	0.05
6056	216	9.27	30.1	0.81	0.257	0.03	0.534	0.12	0.734	0.03
6205	281	10.8	34.8	0.78	0.291	0.03	0.256	0.08	0.842	0.04
6206	206	7.56	35.7	0.79	0.232	0.03	0.192	0.04	0.853	0.03
6211	149	10.7	25.7	1.00	0.303	0.06	0.328	0.16	0.813	0.07
6710	271	10.5	34.6	0.84	0.256	0.03	0.259	0.08	0.839	0.04
6713	184	8.84	29.3	0.93	0.271	0.04	0.242	0.07	0.838	0.04
6716	181	7.52	30.2	0.91	0.287	0.03	0.213	0.10	0.864	0.06
Mean	220.8		31.5		0.268		0.324		0.811	
CV (%)	19.0		11.3		9.4		41.3		5.6	

Table 5.

Parameter estimates related to the stochastic part of the model.

Pig	σ_{NE}	σ_{BW}	S_{NE}	S_{BW}
5365	0.152	0.048	0.000	0.000
5374	0.124	0.036	0.014	0.015
5711	0.248	0.060	0.098	0.000
5713	0.206	0.060	0.025	0.003
5720	0.157	0.053	0.000	0.008
6053	0.239	0.065	0.000	0.000
6056	0.143	0.035	0.003	0.016
6205	0.120	0.052	0.000	0.000
6206	0.132	0.029	0.023	0.001
6211	0.190	0.057	0.009	0.000
6710	0.131	0.041	0.000	0.001
6713	0.173	0.050	0.000	0.000
6716	0.165	0.054	0.000	0.000
Mean	0.168	0.049	0.013	0.003
CV (%)	25.1	22.4	205	170

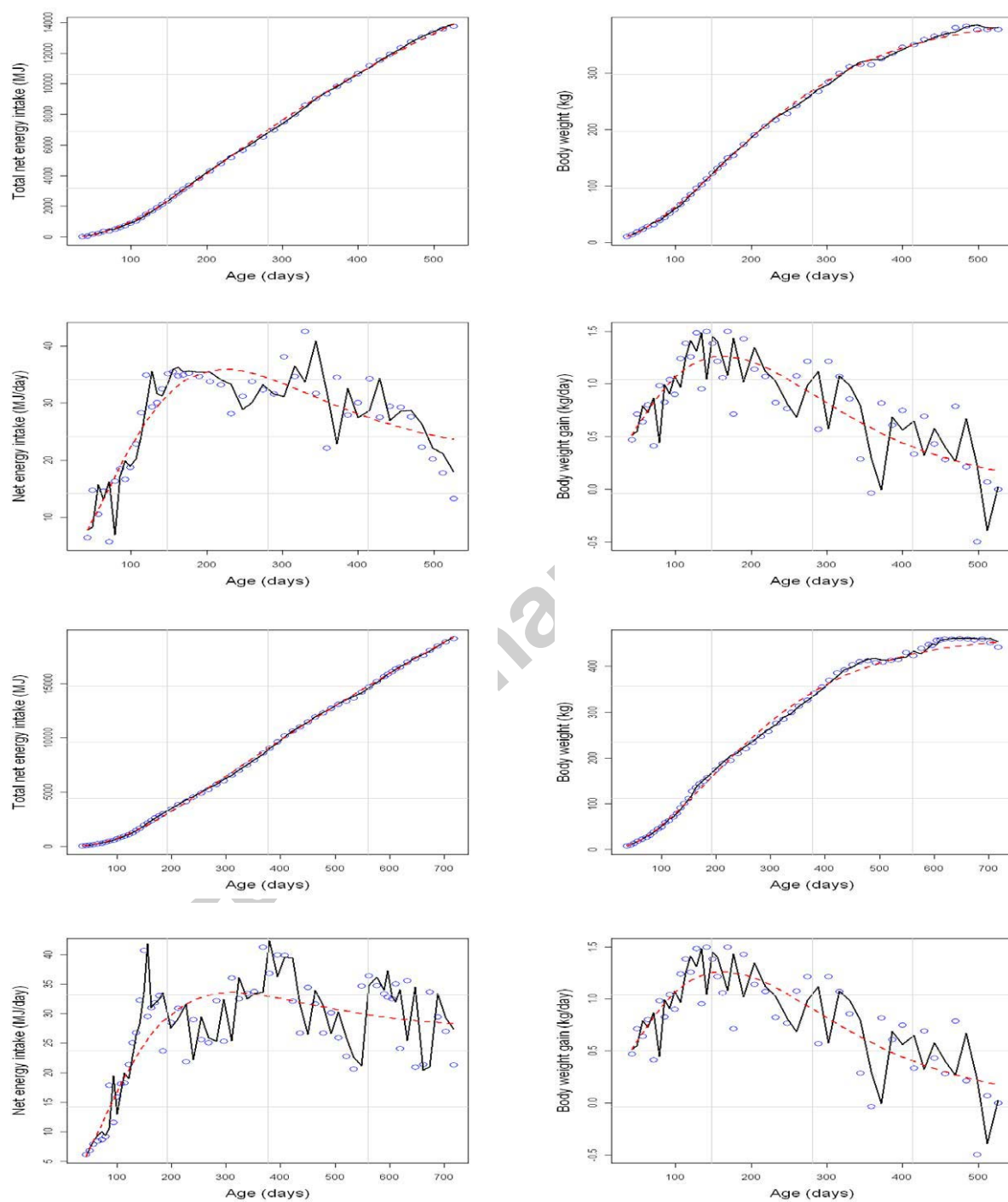


Figure 1.

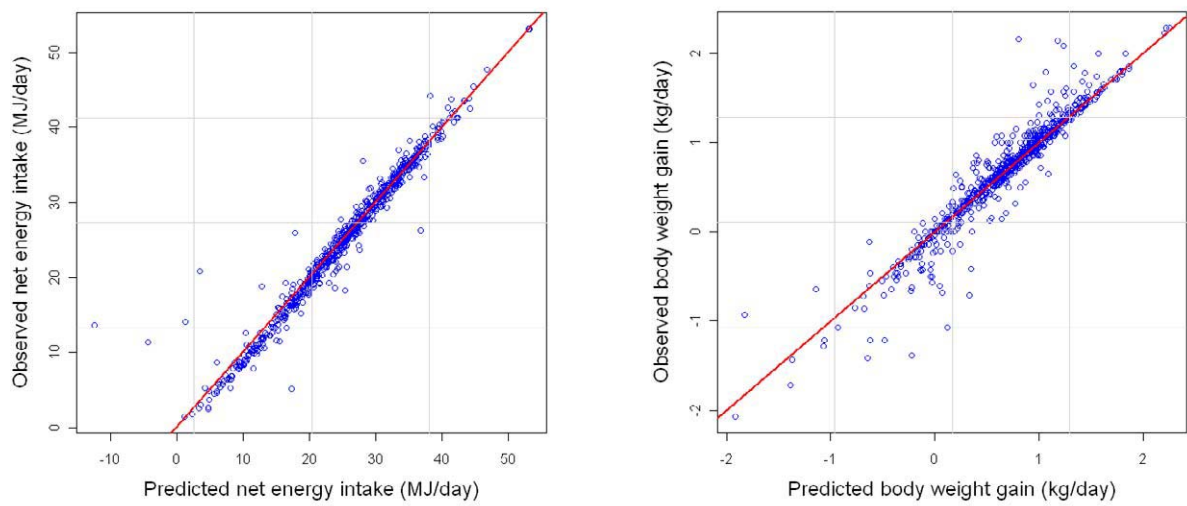


Figure 2.

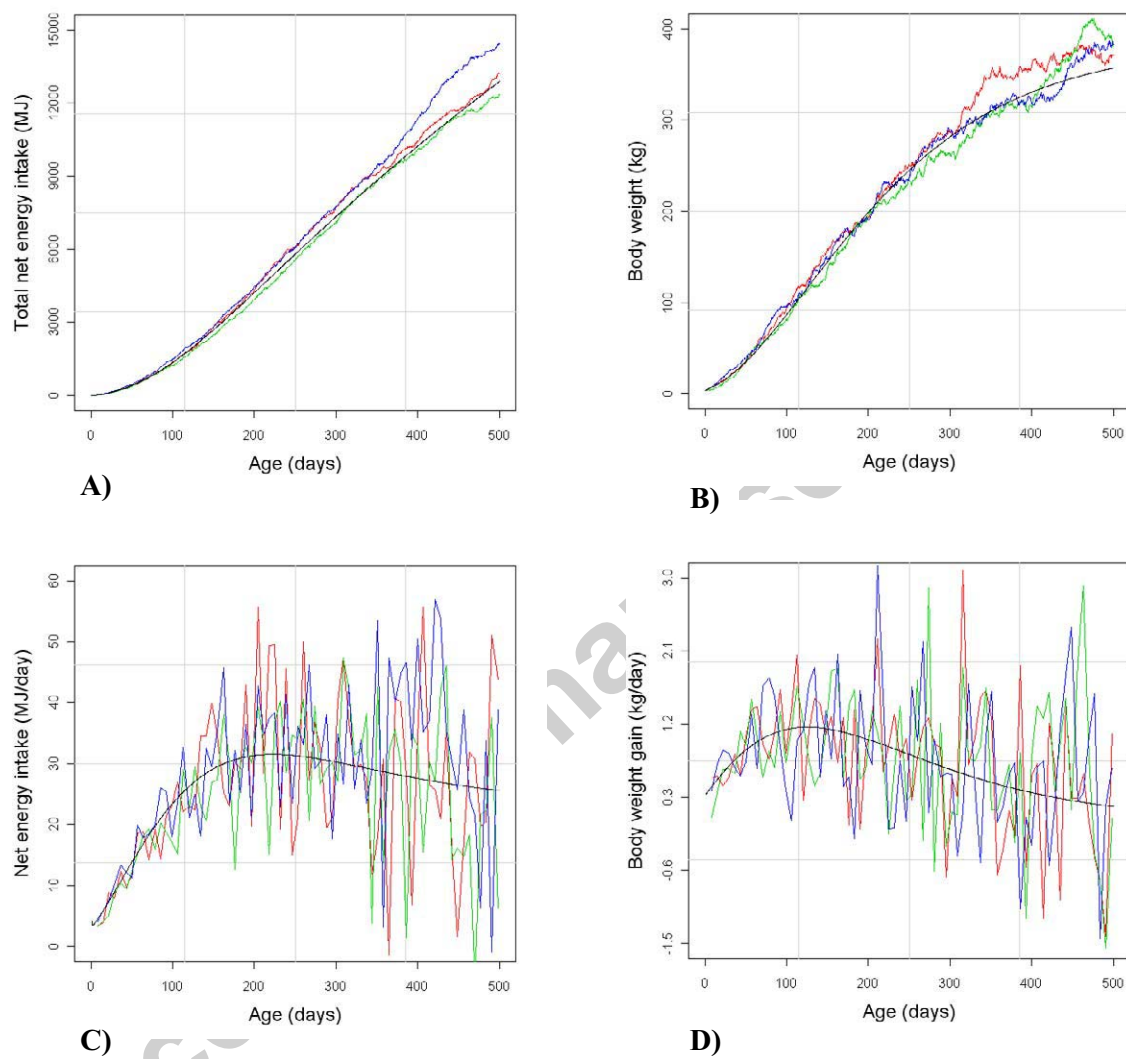


Figure 3.

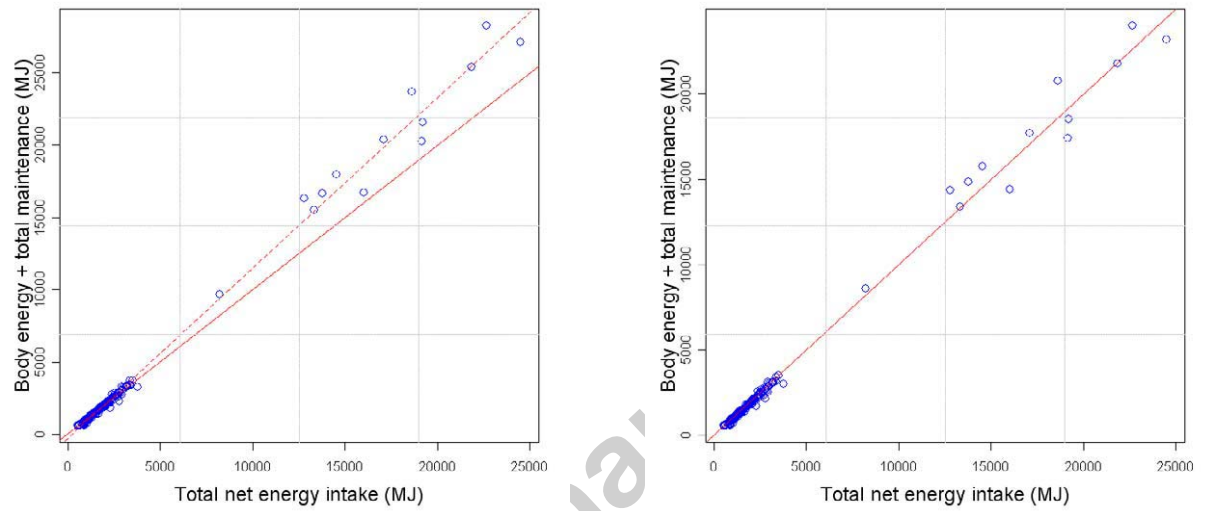


Figure 4.

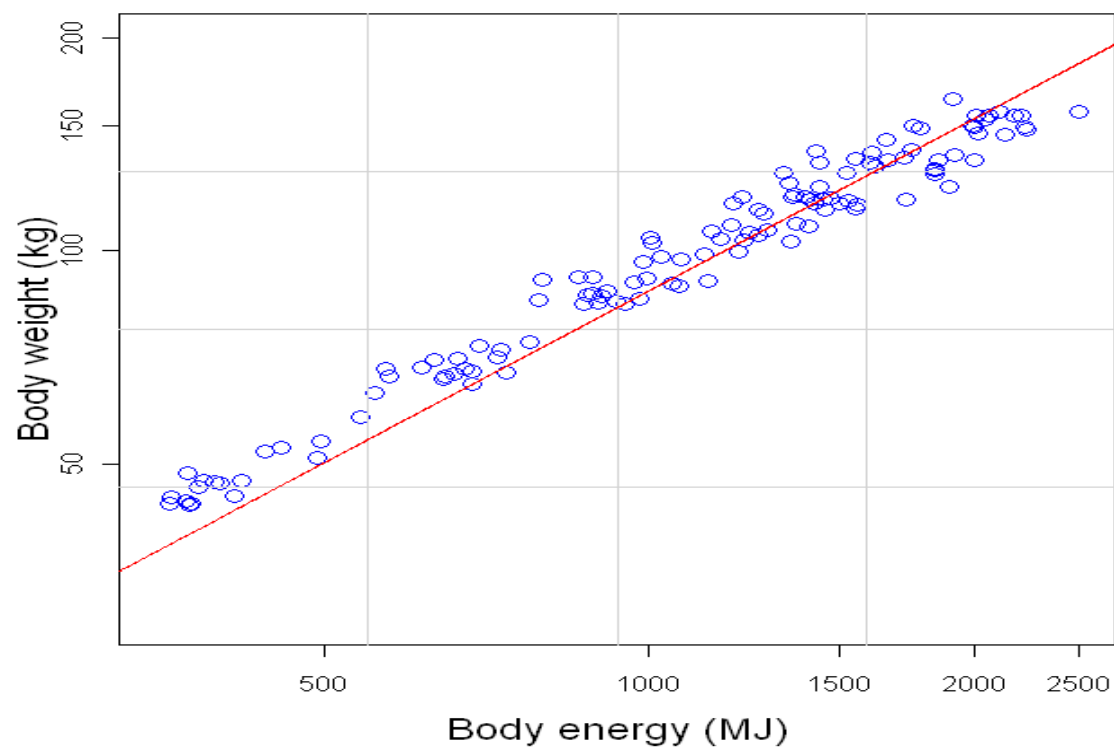


Figure 5.