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Bayesian analysis of energy balance data from growing cattle using parametric and non-parametric modelling

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Abstract. Linear and non-linear models have been extensively utilised for the estimation of net and metabolisable energy requirements and for the estimation of the efficiencies of utilising dietary energy for maintenance and tissue gain. In growing animals, biological principles imply that energy retention rate is non-linearly related to the energy intake level because successive increments in energy intake above maintenance result in diminishing returns for tissue energy accretion. Heat production in growing cattle has been traditionally described by logarithmic regression and exponential models. The objective of the present study was to develop Bayesian models of energy retention and heat production in growing cattle using parametric and non-parametric techniques. Parametric models were used to represent models traditionally employed to describe energy use in growing steers and heifers whereas the non-parametric approach was introduced to describe energy utilisation while accounting for non-linearities without specifying a particular functional form. The Bayesian framework was used to incorporate prior knowledge of bioenergetics on tissue retention and heat production and to estimate net and metabolisable energy requirements (NE_M and ME_M, respectively), and the partial efficiencies of utilising dietary metabolisable energy for maintenance (k_m) and tissue energy gain (k_g). The database used for the study consisted of 719 records of indirect calorimetry on steers and non-pregnant, non-lactating heifers. The NE_M was substantially larger in energy retention models (ranged from 0.40 to 0.50 MJ/kg $BW^{0.75}$.day) than were NE_M estimates from heat-production models (ranged from 0.29 to 0.49 MJ/kg $BW^{0.75}$.day). Similarly, k_m was also larger in energy retention models than in heat production models. These differences are explained by the nature of *y*-intercepts (NE_M) in these two models. Energy retention models estimate fasting catabolism as the *y*-intercept, while heat production models estimate fasting heat production. Conversely, ME_M was virtually identical in all models and approximately equal to 0.53 MJ/kg $BW^{0.75}$.day in this database.

Additional keywords: energy retention, heat production, maintenance.

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Introduction

Nutrient requirement recommendations for livestock are based on estimates of the efficiency of dietary energy utilisation for maintenance and production functions in most feeding systems. The determination of the animal energy requirement is also necessary when formulating diets and examining the environmental impacts of livestock production (Moraes *et al.* 2012). Body energy retention rate is expected to be non-linearly related to the energy intake level in growing animals because successive increments in energy intake above maintenance result in diminishing returns for tissue energy accretion (Blaxter 1980; Garrett and Johnson 1983). Likewise, the efficiencies of utilising

dietary metabolisable energy (ME) for maintenance and tissue energy deposition may be different under various feeding situations. Piecewise and non-linear models have been frequently used to examine energy deposition in growing animals and investigate dietary and animal characteristics associated with efficiencies of utilising dietary energy for growth (Blaxter and Boyne 1978; France *et al.* 1989; NRC 2000). For instance, the piecewise linear model uses two linear functions that intersect at the zero energy retention point to model energy retention as a function of ME intake (NRC 2000). Alternatively, Blaxter and Boyne (1978) suggested the use of the Mitscherlich equation for modelling energy retention as a

function of feed intake in sheep and cattle. This framework was later used as the basis for the ME system in the United Kingdom (ARC 1980). However, France *et al.* (1989) suggested that the relationship between retained energy (RE) and ME intake may not behave according to the law of diminishing returns over all levels of intake. As a consequence, response functions with diminishing returns may not properly describe energy retention in various feeding situations and additional non-linear response functions should also be considered (France *et al.* 1989). The choice of model to describe energy deposition as a function of energy intake seems therefore to depend on the independent variable chosen to describe energy intake and on the range of intake level.

Net energy and ME requirements for maintenance (NE_M and ME_M, respectively), in growing cattle have been customarily determined through the measurement or estimation of heat production (HP, e.g. Lofgreen and Garrett 1968; Tedeschi *et al.* 2002; Marcondes *et al.* 2013). For instance, a linear regression model relating logarithmic transformed HP and ME intake was used by Lofgreen and Garrett (1968) to estimate NE_M as the antilog of the model intercept. The logarithmic transformation was justified by the authors as a more realistic extrapolation to zero ME intake. Tedeschi *et al.* (2002) and Marcondes *et al.* (2013) chose exponential functions instead to model HP as a function of ME intake and estimate NE_M and ME_M. Non-linear functions have been extensively utilised for modelling energy utilisation in food production animals (e.g. France *et al.* 1989; Kebreab *et al.* 2003; Strathe *et al.* 2010). These models are usually selected through the underlying biological mechanisms and model parameters often have a biological interpretation. However, energy balance data is often stratified by clusters, for example, repeated-measures designs, and meta-analytic studies are frequently adopted and a mixed model approach is therefore utilised. In the non-linear mixed-effects model, the marginal likelihood function of the data, obtained by integrating out the random effects from the joint density of the data and random effects, usually does not have a closed form expression (Pinheiro and Bates 2000). Accordingly, parameters are often estimated by algorithms with an approximate likelihood function and the choice of the response function and initial values for the algorithm initialisation are crucial. Lack of algorithm routine convergence is common when modelling energy utilisation in cattle with non-linear mixed models (Kebreab *et al.* 2003). In contexts such as this one, simpler non-linear models are preferred and often the choice of the response function is based on its ability of providing a good fit to the data rather than the underlying biological principles. Alternatively, the use of non-parametric techniques when modelling animal-related responses has increased considerably over the past two decades. For instance, penalised and B-splines models have been used in zero-inflated Poisson models in animal abundance studies (Chiogna and Gaetan 2007), animal models in genetics (Cantet *et al.* 2005), longitudinal non-parametric ANOVA models (Crainiceanu *et al.* 2005) and random regression models in genetic analyses of cattle growth (Meyer 2005). Further, support vector regression was used by Faridi *et al.* (2013) to predict the ME content of corn for ducks and neural network models were used by Faridi *et al.* (2012) to evaluate egg production in response to dietary nutrient intake

by hens. Non-parametric models often suffer from the lack of biological interpretation on parameters directly determining the shape of the response curve. However, the estimation of a non-parametric response function allows biological information to be extracted from the curve itself because its shape is largely determined by the data. For example, the non-parametric curve can be used to determine the overall shape of the relationship between two variables and to investigate the presence of thresholds and change points in the data. Further, the non-parametric framework naturally accommodates non-linearities in the data and does not rely on the specification of a particular functional form describing the relationship between dependent and independent variables.

In this context, the objective of this study was to develop Bayesian parametric and non-parametric models for the investigation of differences in energetic parameters from energy retention and HP models under varying biological assumptions. The Bayesian framework naturally accommodates the hierarchical structure of the data and standard errors of functions of parameters are directly estimated by the Markov chain Monte Carlo (MCMC) sampling. The parametric and non-parametric frameworks can be seen as complementary in the sense that the non-parametric framework will identify any biological signal present in the data without imposing any functional form and suggest the use of a reduced parametric model. Further, the Bayesian implementation is presented with two distinct data analysis strategies. The first strategy utilises minimal prior knowledge in the analysis and the inference is mostly influenced by the database. The second strategy combines the data at hand with prior knowledge on bioenergetics through the use of a Bayesian model with informative prior distributions. Therefore, for each energy response (RE or HP), parametric and non-parametric models are fitted with both informative and non-informative prior distributions.

Materials and methods

As an initial step of the data analysis, the adequacy of non-linear models proposed by France *et al.* (1989) and Kebreab *et al.* (2003) in describing RE as a function of ME intake in this database was investigated. Models were implemented in a hierarchical Bayesian framework using the steps described in the following sections. A variety of prior distributions were examined, ranging from non-informative flat priors to informative priors (Gelman *et al.* 2004). Further, robust modelling techniques were examined with the use of Student's *t*- and double exponential likelihoods as well as several re-parameterisations of the non-linear response functions. In all cases, poor chain mixing or lack of convergence of the MCMC algorithm was observed. The visual inspection of Fig. 1 suggests that the relationship between RE and ME intake is not governed by diminishing returns or sigmoidal laws, therefore, the lack of convergence with non-linear response functions may be a result of the use of an inappropriate functional form for this dataset. Further, it is interesting to notice the relationship between HP and ME intake (Fig. 1) appears to be roughly linear, suggesting that a linear model may be a good function to describe these data.

Moreover, bioenergetics research over the past six decades has substantially increased the knowledge on energy utilisation
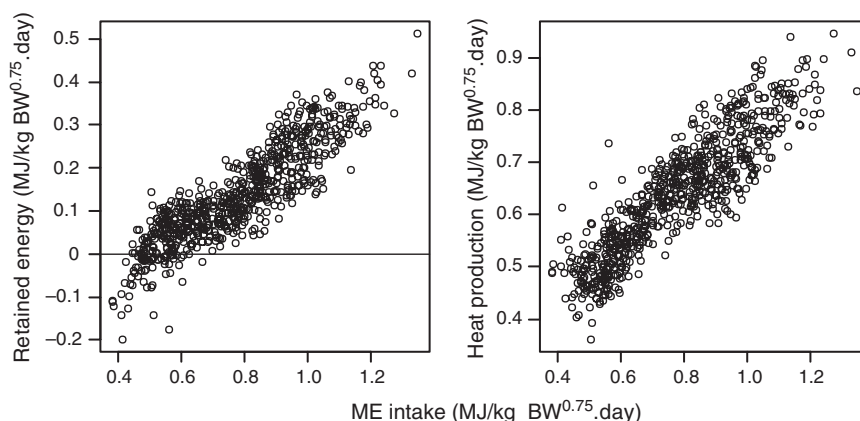
Fig. 1. Retained energy plotted against metabolisable energy (ME) intake (left) and heat production plotted against ME intake (right). All variables are scaled to kg BW$^{0.75}$.

by farm animals. In particular, maintenance requirements and energetic partial efficiencies have been extensively examined (e.g. Lofgreen and Garrett 1968; Moe *et al.* 1972; France *et al.* 1989; Baldwin 1995; Strathe *et al.* 2010) and several biological principles governing energy utilisation by farm animals have been established (Baldwin 1995). In this context, a statistically valid framework, which combines the prior knowledge on energy utilisation with new data is attractive. In particular, Strathe *et al.* (2011) proposed the use of Bayesian inference for updating the prior knowledge on the state of nature of energy utilisation by lactating cows with the data at hand. In the Bayesian setting, the inference is based on the posterior density, which combines information from the prior densities and the density of the observed data. Specifically, the Bayes rule gives that the posterior density is $p(\boldsymbol{\theta}|\mathbf{y}) = \frac{p(\mathbf{y}|\boldsymbol{\theta})p(\boldsymbol{\theta})}{p(\mathbf{y})}$, where $\mathbf{y}$ represents the observed data, $\boldsymbol{\theta}$ the vector of parameters, $p(\mathbf{y}|\boldsymbol{\theta})$ is the density of the data, $p(\boldsymbol{\theta})$ is the prior density and $p(\mathbf{y}) = \int p(\boldsymbol{\theta})p(\mathbf{y}|\boldsymbol{\theta})d\boldsymbol{\theta}$ is the marginal density of the data, which is a constant once the data has been observed. Therefore, the posterior density is proportional to the product of the density of the data and the prior, i.e. $p(\boldsymbol{\theta}|\mathbf{y}) \propto p(\mathbf{y}|\boldsymbol{\theta})p(\boldsymbol{\theta})$. Therefore, the inference is by definition dependent on prior information available before the data is observed. The following three main types of prior distributions were described by Gelman *et al.* (2004): (1) informative priors for which a full generative model for the data is specified and the prior brings substantial information for the inference, (2) weakly informative priors, which deliberately utilise less information than usually available and some prior information constrains the inference, and (3) non-informative priors for which the posterior distribution is dominated by the new data. In this study, prior distributions for the energetic parameters were specified using both non-informative and informative types of prior distribution. In the first part of the analysis, models were fitted with non-informative priors for the energetic parameters so the observed data had a major role in the inference. In the second part of the analysis, informative priors on energetic parameters were used to combine prior knowledge of bioenergetics on growing cattle with the data. In this second approach, estimates of energetic parameters represented a compromise between information provided by

this dataset and prior knowledge of bioenergetics on growing cattle.

The database

A database containing 719 energy balance records from heifers and steers was assembled from 15 studies conducted at the former USDA Energy Metabolism Unit at Beltsville, Maryland. Records represent at least four consecutive days of indirect calorimetry and originated from Holstein, Angus, Hereford and Angus-Hereford cross steers and non-pregnant, non-lactating heifers. Animals ranged from 6 to 22 months of age and records with hormone supplementation or ruminal infusions were removed from the database. A complete list of references of individual studies is available in Moraes *et al.* (2014) and summary statistics of the database are in Table 1. A comprehensive description of the experimental procedures has been reported by Flatt *et al.* (1958) and Moe *et al.* (1972). The data containing RE, ME intake and HP is presented in Fig. 1. It is important to notice that the data has a hierarchical structure, such that there are multiple observations on the same animal although animals are not fully nested within studies since those were used in multiple studies. The fact that records from this database are grouped into studies, conducted under different experimental procedures and biological hypotheses, poses a major challenge for drawing causality conclusions. A meta-analytic approach was employed for which study-based differences in model parameters were estimated through a mixed model approach. However, studies designed for different breeds and among heifers and steers were substantially different and associated differences or similarities on energy utilisation may therefore be a consequence of experimental treatments rather than breed and gender-based differences. Additionally, gender- and breed-based differences on energy utilisation have been extensively studied over the past decades (e.g. Frisch and Vercoe 1977; AFRC 1993; NRC 2000; Tedeschi *et al.* 2002; CSIRO 2007; Marcondes *et al.* 2013). Therefore, data were pooled from the various breeds and two genders and breed and gender effects on model parameters were not estimated. However, it is important to note that

Table 1. Descriptive statistics of the database

BW, the bodyweight; CH_4, the daily methane emissions; CP, the dietary crude protein; DEI, the daily digestible energy intake; DMI, the daily dry matter intake; EE, the dietary ether extract; GEI, the daily gross-energy intake; Max, the maximum value; ME, the dietary metabolisable energy content; MEI, the daily metabolisable energy intake; Min, the minimum value; NDF, the dietary neutral detergent fibre; 1st Qt. and 3rd Qt., the first and third sample quantiles; RE, the retained energy; s.d., the sample standard deviation

Item	Min	1st Qt.	Median	Mean	3rd Qt.	Max	s.d.
NDF (% of DM)	13.15	26.76	35.63	39.42	52.17	78.29	16.02
ME (MJ/kg DM)	7.71	10.66	11.33	11.31	12.05	14.28	1.14
CP (% of DM)	10.39	13.34	15.19	15.89	18.13	25.35	3.43
EE (% of DM)	0.89	2.68	3.21	3.48	4.12	7.55	1.22
Age (months)	6	11	13	13.18	15.25	22	3.49
DMI (kg/day)	2.09	4.01	5.01	5.25	6.47	11.12	1.61
BW (kg)	168.20	264.75	314.60	326.95	372.85	630.70	82.19
GEI (MJ/day)	39.47	77.92	98.63	102.80	127.50	210.00	32.02
DEI (MJ/day)	27.74	52.97	65.70	69.60	85.30	151.20	21.25
MEI (MJ/day)	22.06	44.57	55.51	59.17	72.74	133.40	18.67
CH_4 (MJ/day)	2.59	4.96	6.11	6.41	7.57	13.60	1.97
RE (MJ/day)	−12.06	4.23	8.82	10.60	16.65	42.71	11.29

treatment and group differences can be easily accommodated by the parametric and non-parametric models utilised in this study (Crainiceanu *et al.* 2005).

Modelling energy retention

Energy retention was described, as a function of ME intake, by two modelling approaches. The first approach utilises a piecewise linear model for which two lines, which intersect at ME_M, represent the energy mobilisation and deposition below and above maintenance. The second approach utilises of a non-parametric model, which describes energy retention by a smooth non-parametric curve. In this framework, NE_M represents the fasting catabolism (FCAT), which is defined as the total body energy loss of an animal previously fed at maintenance (Baldwin 1995). Further, by definition $ME_M = FCAT/k_m$ where k_m is the efficiency of utilising dietary ME for maintenance, i.e. $\Delta RE/\Delta ME$ intake from FCAT to ME_M. Using the notation from Baldwin (1995) the FCAT is equal to $H_eE + F_eE + U_eE + H_wE$ where H_eE is heat loss due to fasting metabolism, F_eE is the endogenous fecal energy, U_eE is the endogenous urinary energy and H_wE HP due to waste synthesis. Further, the efficiency of utilising dietary ME for tissue energy gain (k_g) is the $\Delta RE/\Delta ME$ intake above ME_M. When using informative prior distributions for energetic parameters, results from Baldwin (1995) were used to construct an informative prior distribution for the NE_M. In particular, Baldwin (1995) suggested that FCAT should be approximately 0.34 MJ/kg $BW^{0.75}$.day and typical k_m and ME_M values are within an interval of [0.80, 0.95] and [0.36, 0.46] MJ/kg $BW^{0.75}$.day, respectively. In this context, an informative prior distribution for the NE_M was constructed by assuming that our prior belief before observing this data dictated that NE_M was 0.34 MJ/kg $BW^{0.75}$.day with 95% confidence interval of [0.27, 0.42] MJ/kg $BW^{0.75}$.day.

Piecewise linear model

A piecewise linear function with an unknown breakpoint (Toms and Lesperance 2003) was used to estimate

maintenance requirements and energetic efficiencies through the following hierarchical model:

$$y_{ijl} = \beta_{0,ij} + \beta_{1,ij}\, x_{ijl} + \beta_{2,ij}\, (x_{ijl} - \kappa)_+ + \varepsilon_{ijl}, \qquad (1)$$

where y_{ijl} denote the lth record ($l = 1, \ldots, n_{ij}$) of RE (MJ/kg $BW^{0.75}$.day) on animal i ($i = 1, \ldots, A$) and study j ($j = 1, \ldots, B$), x_{ijl} is the corresponding ME intake (MJ/kg $BW^{0.75}$.day), $\beta_{0,ij}$ denotes the intercept, $\beta_{1,ij}$ is the slope before the breakpoint and $\beta_{2,ij}$ is the change in the slope after the breakpoint for the ith animal and jth study. Further, κ is the unknown breakpoint, $(x_{ijk} - \kappa)_+ = \max(0,\ x_{ijk} - \kappa)$ and ε_{ijl} is the error. Energetic parameters are directly represented by this piecewise linear model, for instance NE_M is represented by the intercept $\beta_{0,ij}$, ME_M is represented by the breakpoint κ, k_m is represented by $\beta_{1,ij}$ and k_g is represented by $\beta_{1,ij} + \beta_{2,ij}$ as described in Baldwin (1995).

The Bayesian implementation of the model requires the specification of a probabilistic model for the data and prior distributions for the unknowns. The implementation is described in three hierarchical stages for which the first stage represents a model for the data given the model parameters:

$$y_{ijl} \mid \beta_{0,ij},\ \beta_{1,ij},\ \beta_{2,ij},\ \kappa,\ \sigma^2 \sim$$
$$N\left(\beta_{0,ij} + \beta_{1,ij} x_{ijl} + \beta_{2,ij} (x_{ijl} - \kappa)_+, \sigma^2\right), \qquad (2)$$

where $\beta_{0,ij}$, $\beta_{1,ij}$ and $\beta_{2,ij}$ are animal- and study-specific regression coefficients and σ^2 is the variance. Regression parameters are represented by $\boldsymbol{\theta}_{ij} = (\beta_{0,ij},\ \beta_{1,ij},\ \beta_{2,ij})^T$ and further decomposed into $\boldsymbol{\theta}_{ij} = \boldsymbol{\theta}_\mu + \boldsymbol{\alpha}_i + \boldsymbol{\gamma}_j$, where $\boldsymbol{\theta}_\mu$ is the vector of population parameters, $\boldsymbol{\alpha}_i$ is the vector of random effects associated with animal i and $\boldsymbol{\gamma}_j$ is the vector of random effects associated with study j. In the second stage, prior distributions for the random effects given their variance components were specified. Random effects were assumed to be mutually independent and distributed as:

$$\begin{cases} \boldsymbol{\alpha}_i \mid \boldsymbol{\Sigma}_\alpha \sim N(\mathbf{0}, \boldsymbol{\Sigma}_\alpha), & i = 1, \ldots, A \\ \boldsymbol{\gamma}_j \mid \boldsymbol{\Sigma}_\gamma \sim N(\mathbf{0}, \boldsymbol{\Sigma}_\gamma), & j = 1, \ldots, B \end{cases}, \qquad (3)$$

where $\boldsymbol{\Sigma}_\alpha$ and $\boldsymbol{\Sigma}_\gamma$ are covariance matrices of the vectors of random effects associated with animals and studies, respectively. In the third stage, prior distributions for the model parameters were specified. Let $\boldsymbol{\Sigma}_\alpha = diag\{\sigma^2_{\alpha_0}, \sigma^2_{\alpha_1}, \sigma^2_{\alpha_2}\}$, $\boldsymbol{\Sigma}_\gamma = diag\{\sigma^2_{\gamma_0}, \sigma^2_{\gamma_1}, \sigma^2_{\gamma_2}\}$, $\boldsymbol{\theta}_\mu = (\beta_{\mu0}, \beta_{\mu1}, \beta_{\mu2})^T$ and the prior distributions as follows:

$$\begin{cases} \sigma^{-2}, \sigma^{-2}_{\alpha_0}, \sigma^{-2}_{\alpha_1}, \sigma^{-2}_{\alpha_2}, \sigma^{-2}_{\gamma_0}, \sigma^{-2}_{\gamma_1}, \sigma^{-2}_{\gamma_2} \sim \text{Gam}(10^{-3}, 10^{-3}) \\ \beta_{\mu0} \sim N(0, 10^6) \quad \text{or} \quad \beta_{\mu0} \sim N(-0.34, 0.0016) \\ \beta_{\mu1}, \beta_{\mu2} \sim N(0, 10^6) \\ \kappa \sim \text{Unif}(0.51, 0.63) \end{cases}, \tag{4}$$

where $\text{Gam}(a, b)$ is the Gamma density with mean $= a/b$ and variance $= a/b^2$, $\beta_{\mu0} \sim N(0, 10^6)$ when a non-informative prior was used for the NE_M and $\beta_{\mu0} \sim N(-0.34, 0.0016)$ when an informative prior for the NE_M was used. Further, $\text{Unif}(a, b)$ is the Uniform density with parameters a and b, which were set as the lower and upper limits of a 95% credible interval for the ME_M from a previous analysis of this database using animals in positive energy balance.

Non-parametric approach

A non-parametric model was utilised for modelling energy retention, as a function of ME intake, by representing the response function with a smooth curve, which directly accommodates changes in the relationship between RE and ME intake under various feeding levels. The model is generally described as follows:

$$y = m(x) + \varepsilon, \tag{5}$$

where y (MJ/kg $BW^{0.75}$.day) is the RE, x is the ME intake (MJ/kg $BW^{0.75}$.day), m is a smooth function describing the conditional mean of y and ε is the error. We estimate $m(x)$ by spline functions, which are described using the notation from Ruppert (2002):

$$m(x, \boldsymbol{\theta}) = \beta_0 + \beta_1 x + \ldots + \beta_p x^p + \sum_{k=1}^K b_k (x - \kappa_k)_+^p, \tag{6}$$

where $\boldsymbol{\theta} = (\beta_0, \ldots \beta_p, b_1, \ldots, b_k)^T$, $\beta_0, \ldots, \beta_P$ are the regression coefficients, $b_1, \ldots, b_K$ are the coefficients associated with the spline bases $(x - \kappa_k)_+^p = [\max(0, x - \kappa_k)]^p$, and $p \geq 1$ and $\kappa_1 < \ldots < \kappa_k$ are the knots or 'breakpoints'. Equation 6 describes a sequence of pth degree polynomials tied at the knots to form a continuous curve with $p - 1$ continuous derivatives. Additionally, we propose the use of penalised splines for which a relatively large number of knots is specified but parameters $b_1, \ldots, b_K$ are penalised by shrinking them towards zero (Gurrin *et al.* 2005). In this context, specification of knots plays a minor role because smoothing is governed by the penalty parameter (Wand 2003; Gurrin *et al.* 2005). Strategies for knot placement and selection have been extensively examined by Ruppert (2002). In this study, we use the empirical result from Wand (2003) that the number of knots $K = \min(\frac{n}{4}, 35)$ works well as a good default rule (*n* here denotes the number of observations). The knots are then set at $\kappa_k = (\frac{k+1}{K+2})$th sample quantile of x ($1 \leq k \leq K$). The number of observations in the database is 719, therefore, K was set to 35.

The non-parametric regression model is extended to accommodate the hierarchical structure of the data by letting y_{ijl} denote the *l*th record ($l = 1, \ldots, n_{ij}$) of RE on animal i ($i = 1, \ldots, A$) and study j ($j = 1, \ldots, B$) and x_{ijl} be the corresponding ME intake. The model for the data is then defined as:

$$y_{ijl} = f(x_{ijl}) + f_i(x_{ijl}) + f_j(x_{ijl}) + \varepsilon_{ijl}, \tag{7}$$

where $f(\cdot)$ is the overall curve, $f_i(\cdot)$ are the deviations from the overall curve for the *i*th animal, $f_j(\cdot)$ are the deviations from the overall curve for the *j*th study and ε_{ijl} is the error. Using a first-order basis, the three functions are defined as follows:

$$\begin{cases} f(x_{ijl}) = \beta_0 + \beta_1 x_{ijl} + \sum_{k=1}^K b_k (x_{ijl} - \kappa_k)_+ \\ f_i(x_{ijl}) = \alpha_{0,i} + \alpha_{1,i} x_{ijl} + \sum_{k=1}^K a_{ik} (x_{ijl} - \kappa_k)_+, \\ f_j(x_{ijl}) = \gamma_{0,j} + \gamma_{1,j} x_{ijl} + \sum_{k=1}^K s_{jk} (x_{ijl} - \kappa_k)_+ \end{cases} \tag{8}$$

where β_0 and β_1 are regression coefficients associated with the overall curve, $\alpha_{0,i}$ and $\alpha_{1,i}$ are random effects associated with the *i*th animal, $\gamma_{0,j}$ and $\gamma_{1,j}$ are random effects associated with the *j*th study, b_k are parameters associated with the spline basis $(x_{ijl} - \kappa_k)_+$ in the overall curve, a_{ik} are parameter associated with the spline basis $(x_{ijl} - \kappa_k)_+$ in the animal-specific curves and and s_{jk} are parameters associated with spline basis $(x_{ijl} - \kappa_k)_+$ in the study-specific curves and other terms are defined as before. The mixed model representation of penalised splines was used and b_k, a_{ik} and s_{jk} were treated as random effects, which may be determined by their best linear unbiased predictions (Wand 2003; Crainiceanu *et al.* 2005). The Bayesian model implementation is described in three hierarchical stages for which the first hierarchy specifies a model for the data given the model parameters:

$$y_{ijl}|\boldsymbol{\theta}, \sigma^2 \sim N\big(f(x_{ijl}) + f_i(x_{ijl}) + f_j(x_{ijl}), \ \sigma^2\big), \tag{9}$$

where $\boldsymbol{\theta} = (\beta_0, \beta_1, \alpha_{0,i}, \alpha_{1,i}, \gamma_{0,j}, \gamma_{1,j}, \{b_k\}_{k=1}^K, \{a_{ik}\}_{k=1}^K, \{s_{jk}\}_{k=1}^K)^T$, σ^2 denotes the variance and the other terms are defined as before. The second hierarchy stage specifies prior distributions for the random effects given their variance components. It is assumed that random effects are mutually independent and distributed as follows:

$$\begin{cases} b_k|\sigma^2_b \sim N(0, \sigma^2_b), \ k = 1, \ldots, K \\ \alpha_{0,i}|\sigma^2_{\alpha_0} \sim N(0, \sigma^2_{\alpha_0}), \ i = 1, \ldots, A \\ \alpha_{1,i}|\sigma^2_{\alpha_1} \sim N(0, \sigma^2_{\alpha_1}), \ i = 1, \ldots, A \\ \gamma_{0,j}|\sigma^2_{\gamma_0} \sim N(0, \sigma^2_{\gamma_0}), \ j = 1, \ldots, B \\ \gamma_{1,j}|\sigma^2_{\gamma_1} \sim N(0, \sigma^2_{\gamma_1}), \ j = 1, \ldots, B \\ a_{ik}|\sigma^2_a \sim N(0, \sigma^2_a), \ i = 1, \ldots, A, \ k = 1, \ldots, K \\ s_{jk}|\sigma^2_s \sim N(0, \sigma^2_s), \ j = 1, \ldots, B, \ k = 1, \ldots, K \end{cases} \tag{10}$$

The third-stage hierarchy specifies prior distributions for the regression coefficients and variance components as follows:

$$\begin{cases} \beta_{\mu 0} \sim N(0, 10^6) \quad \text{or} \quad \beta_{\mu 0} \sim N(-0.34, 0.0016) \\ \beta_1 \sim N(0, 10^6) \\ \sigma^{-2}, \sigma_b^{-2}, \sigma_{\alpha_0}^{-2}, \sigma_{\alpha_1}^{-2}, \sigma_{\gamma_0}^{-2}, \sigma_{\gamma_1}^{-2}, \sigma_a^{-2}, \sigma_s^{-2} \sim \text{Gam}(10^{-3}, 10^{-3}) \end{cases} \tag{11}$$

Energetic parameters can be naturally represented through the overall curve, for instance NE_M is defined by the intercept β_0. To estimate the ME_M, the ME intake at zero energy retention or the point at which the overall curve intersects the x-axis needs to be identified. The use of a bisection method is proposed, which identifies the x interval at which y becomes positive. The ME_M is then defined as the ME intake for the first positive energy retention up to the third decimal digit of precision. The efficiencies k_m and k_g were estimated according to France *et al.* (1989), which defines the average efficiencies as follows:

$$\bar{k}_m = \frac{\int_{-NE_M}^{0} dy}{ME_M} = \frac{NE_M}{ME_M} \quad \text{and} \quad \bar{k}_g = \frac{\int_{0}^{f(x=\delta ME_M)} dy}{(\delta-1)ME_M} = \frac{f(x=\delta ME_M)}{(\delta-1)ME_M},$$
$$\tag{12}$$

where $f(x = \delta ME_M)$ is the value of the overall curve at level $(\delta > 1)$ of feeding above ME_M.

Modelling heat production

The NE_M in growing cattle has been traditionally determined through the estimation or measurement of fasting heat production (FHP) (NRC 2000). For instance, Lofgreen and Garrett (1968) regressed the logarithm of HP on the corresponding ME intake and estimated the NE_M as the antilog of the linear regression intercept. In this study, three approaches are utilised for the estimation of FHP: the Lofgreen and Garrett (1968) model, a linear model and a non-parametric approach. In this framework, NE_M represents FHP, which is essentially equal to H_eE (Baldwin 1995). By definition NE_M from HP models is smaller than the NE_M from energy retention models, which is based on FCAT (Baldwin 1995). The ME_M in the HP models is traditionally determined as the value at which HP equals the ME intake (Tedeschi *et al.* 2002; Marcondes *et al.* 2013) and the efficiency by definition $k_m = NE_M/ME_M$. Results from Lofgreen and Garrett (1968) were used to construct an informative prior distribution for NE_M. In their original study, Lofgreen and Garrett (1968) stated '... the heat production of fasting beef cattle probably lies between 72 and 82 kcal per $W^{0.75}$ kg with mean value being 77 kcal ...' Therefore, an informative prior distribution for the NE_M (measuring FHP) was constructed by assuming that our prior belief before observing this data dictated that NE_M has a 95% confidence interval of [0.30, 0.34] MJ/kg $BW^{0.75}$.day centred at 0.32 MJ/kg $BW^{0.75}$.day. The Bayesian implementation of all four HP models described below is virtually the same as the implementation of the energy retention models.

Lofgreen and Garrett (1968) approach

The relationship between the logarithm of HP and ME intake is described by following hierarchical model:

$$\log_{10}(y_{ijl}) = \beta_{0,ij} + \beta_{1,ij} x_{ijl} + \varepsilon_{ijl}, \tag{13}$$

where y_{ijl} is the lth record ($l = 1, \ldots, n_{ij}$) of HP (MJ/kg $BW^{0.75}$.day) on animal i ($i = 1, \ldots, A$) and study j ($j = 1, \ldots, B$) and x_{ijl} the corresponding ME intake (MJ/kg $BW^{0.75}$.day), $\beta_{0,ij}$ and $\beta_{1,ij}$ are the parameters describing the relationship between the logarithm of HP and ME intake and ε_{ijl} is the error. In this framework, $10^{\beta_{0,ij}}$ represents the NE_M for the ith animal and jth study. Further, a modified version of the Lofgreen and Garrett (1968) model is fitted, by using y_{ijl} as the dependent variable rather than its logarithm. This modified version of the model has the advantage that it can be compared with the other two models through a model selection criterion. Specifically, the modified hierarchical model is

$$y_{ijl} = 10^{\beta_{0,ij} + \beta_{1,ij} x_{ijl}} + \varepsilon_{ijl}, \tag{14}$$

where y_{ijl} is the lth record ($l = 1, \ldots, n_{ij}$) of HP (MJ/kg $BW^{0.75}$.day) on animal i ($i = 1, \ldots, A$) and study j ($j = 1, \ldots, B$) and x_{ijl} the corresponding ME intake (MJ/kg $BW^{0.75}$.day), $\beta_{0,ij}$ and $\beta_{1,ij}$ are the parameters describing the relationship between HP and ME intake and ε_{ijl} is the error. The NE_M, for the ith animal and jth study, is given by $10^{\beta_{0,ij}}$.

Linear model approach

The visual inspection of Fig. 1 suggests that the relationship between HP and ME intake may be linear. Therefore, a linear model for modelling HP as a function of ME intake was proposed with the following structure:

$$y_{ijl} = \beta_{0,ij} + \beta_{1,ij} x_{ijl} + \varepsilon_{ijl}, \tag{15}$$

where y_{ijl} is the lth record ($l = 1, \ldots, n_{ij}$) of HP (MJ/kg $BW^{0.75}$.day) on animal i ($i = 1, \ldots, A$) and study j ($j = 1, \ldots, B$) and x_{ijl} the corresponding ME intake (MJ/kg $BW^{0.75}$.day), $\beta_{0,ij}$ and $\beta_{1,ij}$ are the parameters describing the linear relationship between HP and ME intake and ε_{ijl} is the error. The NE_M in this model, for the ith animal and jth study, is given by $\beta_{0,ij}$.

Non-parametric approach

In the last part of the analysis, HP is modelled non-parametrically with the estimation of a smooth HP curve, which does not rely on the specification of any parametric form. Specifically, the hierarchical model is described in Eqn 7 where y_{ijl} is the lth record ($l = 1, \ldots, n_{ij}$) of HP (MJ/kg $BW^{0.75}$.day) on animal i ($i = 1, \ldots, A$) and study j ($j = 1, \ldots, B$) and x_{ijl} the corresponding ME intake (MJ/kg $BW^{0.75}$.day). Further, $f(\cdot)$ represents the overall curve, $f_i(\cdot)$ represents the deviations from the overall curve for the ith animal and $f_j(\cdot)$ are the deviations from the overall curve for the jth study. The curves were defined by spline functions with first-order bases in Eqn 8 where β_0 and β_1 are regression coefficients associated with the overall curve, $\alpha_{0,i}$ and $\alpha_{1,i}$ are random effects associated with the ith animal, $\gamma_{0,j}$ and $\gamma_{1,j}$ are random effects associated with the jth study, b_k are parameters associated with the spline basis $(x_{ijl} - \kappa_k)_+$ in the overall curve, a_{ik} are parameter associated with the spline basis $(x_{ijl} - \kappa_k)_+$ in the animal-specific curves and and s_{jk} are parameters associated with spline basis $(x_{ijl} - \kappa_k)_+$ in the study-specific curves. In this approach NE_M is defined by the intercept β_0. The penalised

splines approach was used to estimate the curves as described in the previous sections.

Model implementation and comparison

Posterior densities were simulated by MCMC methods in the statistical software WinBUGS (Lunn *et al.* 2000). Two chains with over-dispersed initial values were specified for each parameter and chain mixing, auto-correlation, posterior densities and the Gelman–Rubin diagnostics (Gelman and Rubin 1992) were used to visually assess chain convergence and determine the required burn-in period. The tests of the convergence diagnostic and output analysis package (Best *et al.* 1995) were used to formally assess chains' convergence. Model comparison was performed using deviance information criteria (DIC) as described by Spiegelhalter *et al.* (2002). The DIC is a model comparison tool, which assesses the trade-off between goodness of fit and model complexity and is approximately equal to the Akaike's information criteria in Gaussian models (Ntzoufras 2009). Formally, the DIC is given by $DIC = \overline{D} + p_D$, where $\overline{D} = E_{\theta|\mathbf{y}}[-2\log p(\mathbf{y}|\boldsymbol{\theta})]$ (i.e. the expected minus twice the log-likelihood) and p_D is the penalty for the number of effective parameters. In practice, reductions of 5 and 10 DIC units often represent a tendency and a substantive improvement of fit to data, respectively (Spiegelhalter *et al.* 2002).

As a final step of model evaluation, posterior predictive distributions were used to check the adequacy of models' predictions. The posterior predictive distribution is often used to check if the model is consistent with the data (Gelman *et al.* 2004) and is given by $p(\mathbf{y}^{\mathbf{rep}}|\mathbf{y}) = \int p(\mathbf{y}^{\mathbf{rep}}|\boldsymbol{\theta})p(\boldsymbol{\theta}|\mathbf{y})d\boldsymbol{\theta}$, where $\mathbf{y}^{\mathbf{rep}}$ is defined as the replicated data. The replicated data represent data which could have been observed or may be observed if the study is replicated under the same model and parameter vector $\boldsymbol{\theta}$, which

generated $\mathbf{y}$ (Gelman *et al.* 2004). The posterior predictions can therefore be interpreted as an average of the conditional predictions over the posterior distribution of $\boldsymbol{\theta}$. A closed form expression is usually not available for the integral, but an approximation is provided by the MCMC sampling.

Results and discussion

Energy retention models

Analysis with non-informative priors

Maintenance requirements and energetic efficiencies for both energy retention models were estimated using a Bayesian framework with non-informative prior distributions for the energetic parameters. The prior distributions, therefore, play a minor role in the inference and the posterior densities are mostly dominated by the observed data. Estimated maintenance requirements and energetic efficiencies are in Table 2. Estimated NE_M and ME_M values were close in the piecewise linear and non-parametric models. Specifically, NE_M estimates (FCAT) were 0.50 MJ/kg $BW^{0.75}$.day in the piecewise linear model and 0.49 MJ/kg $BW^{0.75}$.day in the non-parametric regression model. Furthermore, ME_M was 0.52 MJ/kg $BW^{0.75}$.day in the piecewise linear model and 0.53 MJ/kg $BW^{0.75}$.day in the non-parametric model. The efficiencies were also similar between the piecewise linear and non-parametric regression models. Specifically, k_m was 0.94 and 0.92 in the piecewise linear and non-parametric models, respectively. Additionally, k_g was 0.54 and 0.61 in the piecewise linear and non-parametric models respectively. The similarity of the energetic parameters from both models suggests that the piecewise linear model is a good representation of the data and the use of a single breakpoint at the zero energy retention point may be enough to describe energy retention in this database. These results are consistent with Lofgreen and Garrett (1968) who suggested

Table 2. Parameter posterior means and standard deviations in parentheses for the piecewise linear and non-parametric energy retention models, correlation between observed and predicted values and deviance information criteria (DIC)

[A]Non-informative represents models fitted using non-informative prior distributions for the energetic parameters and informative represents models fitted using informative prior distributions for the NE_M according to Baldwin (1995). NE_M, the daily net energy requirement for maintenance (MJ/kg $BW^{0.75}$.day); ME_M, the daily metabolisable energy requirement for maintenance (MJ/kg $BW^{0.75}$.day); k_m and k_g are the efficiencies of utilising dietary ME for maintenance and tissue gain; and σ^2, the error's variance. Note that ME_M is a parameter only in the piecewise linear model. In the non-parametric model it is determined through the bisection method. The average k_g for the non-parametric model was calculated at 2.45 times ME_M level of feeding, which was the maximum feeding level above maintenance in the database. Further, $r(\mathbf{y}^{\mathbf{rep}}, \mathbf{y})$ is the correlation between observed values and posterior predictive distributions medians. DIC is a model comparison tool which trades-off between a measure of goodness of fit and model complexity. Models with smaller DIC represent a better fit to the data and reductions of 5 and 10 DIC units often represent a tendency and a substantive improvement of fit to data (Spiegelhalter *et al.* 2002)

Parameter	Piecewise linear		Non-parametric	
	Non-informative	Informative	Non-informative	Informative
NE_M	0.50 (0.04)	0.40 (0.03)	0.49 (0.05)	0.40 (0.03)
ME_M	0.52 (0.01)	0.53 (0.01)	0.53	0.52
k_m	0.94 (0.09)	0.77 (0.06)	0.92 (0.09)	0.77 (0.06)
k_g	0.54 (0.02)	0.54 (0.03)	0.61 (0.06)	0.60 (0.06)
σ^2	0.00081 (0.00005)	0.00082 (0.00005)	0.00074 (0.00005)	0.00076 (0.00005)
$r(\mathbf{y}^{\mathbf{rep}}, \mathbf{y})$	0.89	0.89	0.90	0.89
DIC	−2935.76	−2929.90	−2964.66	−2956.00

that the partial efficiencies k_m and k_g are roughly constant below and above maintenance, respectively.

Nevertheless, when comparing both models using an information criterion, the non-parametric model is preferred over the piecewise linear model as suggested by the smaller DIC (Table 2). The DIC is a model assessment tool, which favours models that provide a good fit to the data while penalising for model complexity (Spiegelhalter *et al.* 2002). In particular, the DIC for the non-parametric model was reduced by 29 units from the piecewise linear model suggesting that the non-parametric model has a greater ability in describing the RE data (as expected, due to the greater flexibility of the non-parametric approach). It is also important to notice that the non-parametric model provided estimates of NE_M and k_m slightly smaller than the linear piecewise model but estimates from both models were substantially larger than the NE_M of 0.32 MJ/kg $BW^{0.75}$.day proposed by the Lofgreen and Garrett (1968) and the typical k_m values [0.6, 0.8] for ruminants (France *et al.* 1989). This database therefore suggests that NE_M requirements, estimated through energy retention models, are greater than current NE_M estimates from the literature. Further, it also suggests that dietary ME is used more efficiently for maintenance purposes than previously reported. Consequently,

estimates of ME_M from both models (0.52 and 0.53 MJ/kg $BW^{0.75}$.day) were within the range of typical maintenance requirements from growing cattle [0.46, 0.68] MJ/kg $BW^{0.75}$. day (Jenkins and Ferrell 1983; Ferrell and Jenkins 1985; Old and Garrett 1985; Marcondes *et al.* 2013).

The fact that NE_M and k_m in these models were substantially larger than previously reported deserves special consideration. Two main reasons for NE_M and k_m larger than previously reported are characteristics associated with animals in negative energy balance and the biological interpretation of the *y*-intercept. The majority of the records on negative tissue energy balance (i.e. RE <0) seem to be from younger animals. Specifically, for the records for which the age of the animals is available, the sample quantiles of age (in months) for animals where RE < 0 is $(x_{0.10} = 8, x_{0.25} = 10, x_{0.50} = 11, x_{0.75} = 13.75, x_{0.90} = 16)$, where in this notation $\Pr(\text{Age} \leq x_p) = p$. The idea that maintenance energy requirement per unit of bodyweight changes as the animal ages is well established (NRC 2000). For instance, Carstens *et al.* (1989) reported a 6% decrease in FHP between cattle of 9 and 20 months. Moreover, an important distinction between NE_M from these models and the ones from the literature is that the latter are often based on HP models. In energy retention, NE_M represents FCAT while in HP models it
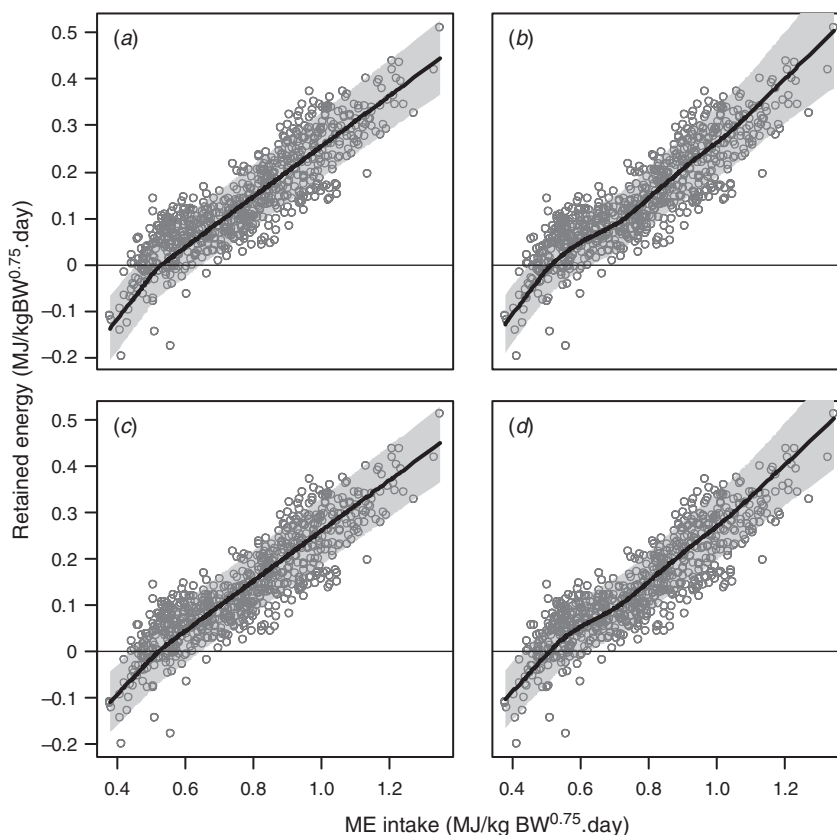

Fig. 2. Posterior predictive distributions of the piecewise linear (left) and the non-parametric (right) energy retention models plotted against the metabolisable (ME) intake. All variables are scaled to kg $BW^{0.75}$. The line represents the posterior predictions medians and the grey-shaded area is the 95% credible interval for the predictions. The graph shows (*a*) the piecewise linear model with non-informative prior, (*b*) the non-parametric model with non-informative prior, (*c*) the piecewise linear model with informative prior and (*d*) the non-parametric model with informative prior.

represents FHP (e.g. Lofgreen and Garrett 1968; Tedeschi *et al.* 2002; Marcondes *et al.* 2013). FCAT is equal to $H_eE + F_eE + U_eE + H_wE$ whereas FHP is essentially H_eE (Baldwin 1995), therefore, FCAT > FHP and NE_M from energy retention models are greater than those estimated by HP models. Furthermore, by definition $k_m = NE_M/ME_M$, and this partial efficiency for a given ME_M is larger in energy retention models compared with HP models. In particular, Baldwin (1995) reported that k_m is mostly influenced by animal and diet characteristics and ranges from 0.80 to 0.95 in energy retention models. These values were in good agreement with k_m estimates from the piecewise linear and non-parametric energy retention models in this study (Table 2).

The estimates of the efficiency of utilising ME for gain (Table 2) from both models (0.54 and 0.61) were similar to typical k_g values from the literature [0.2, 0.8] (France *et al.* 1989; Baldwin 1995). Various factors affect k_g in growing cattle, for example, composition of the gain (i.e. protein versus fat) plays a major role in determining k_g because fat deposition is often more energetically efficient than protein deposition. The database from this study originated from calorimetric studies for which carcass composition, and consequently tissue gain composition, was not directly available. Thus, k_g was not factorised into partial efficiencies of fat and protein deposition. However, the effects of gain composition on k_g have been studied extensively (e.g. Williams and Jenkins 2003; Tedeschi *et al.* 2004; Marcondes *et al.* 2013). Further, a comprehensive examination of additional factors which affect efficiency of energy utilisation for gain in growing cattle is reported by Garrett (1980).

Finally, the ability of the models in describing RE in this database was checked with the use of posterior predictive distributions. In particular, the correlations between observed values and posterior predictions were 0.89 and 0.90 for the piecewise linear and non-parametric models suggesting that both models are reasonably consistent with the data. Further, posterior predictions plotted against ME intake (Fig. 2) suggest good agreement between observed RE and posterior predictions. Posterior means of parameters from each energy retention model and variance components as well as their 95% credible intervals are in Table 3.

Analysis with informative prior for NE_M

The same energy retention models were fitted with the specification of an informative prior distribution for NE_M. In this framework the data was used to update the prior knowledge on energetic parameters and the inference was based on the posterior density, which contains substantial prior knowledge on NE_M. Maintenance requirements and partial efficiencies estimated in these models are in Table 2. Estimates of ME_M and k_g were practically unchanged with the specification of an informative prior distribution for NE_M and were within the range of typical values reported in the literature. However, NE_M and k_m for the piecewise linear and non-parametric models were substantially smaller than the ones estimated when using a non-informative prior distribution for NE_M (Table 2). Comparing these models with the ones fitted using a non-informative prior distribution through the information criterion showed that both models provided a worse fit to the data as suggested by larger DIC for the piecewise linear model (–2936 vs –2930) and for the non-parametric model (–2965 vs –2956) (Table 2). Furthermore, the plots of posterior predictions and observed values against ME intake (Fig. 2) suggested that RE

Table 3. Posterior means and 95% credible intervals for parameters estimated in the piecewise linear and non-parametric energy retention models

Non-informative represents models fitted using non-informative prior distributions for the energetic parameters and informative represents models fitted using informative prior distributions for the NE_M according to Baldwin (1995). β_0, β_1 and β_2 are the parameters of the energy retention models describing the relationship between retained energy and metabolisable energy intake, κ is the breakpoint from the piecewise linear model, $\sigma_{\alpha_0}^2$, $\sigma_{\alpha_1}^2$ and $\sigma_{\alpha_2}^2$ are variance components associated with animal random effects, $\sigma_{\gamma_0}^2$, $\sigma_{\gamma_1}^2$ and $\sigma_{\gamma_2}^2$ are variance components associated with study random effects, σ_b^2, σ_a^2 and σ_s^2 are variance components associated with random effects of spline bases in the non-parametric model and σ^2 is the error's variance

Parameter	Piecewise linear		Non-parametric	
	Non-informative	Informative	Non-informative	Informative
β_0	–0.50 (–0.60, –0.40)	–0.40 (–0.46, –0.34)	–0.49 (–0.60, –0.39)	–0.40 (–0.46, –0.34)
β_1	0.94 (0.76, 1.13)	0.77 (0.65, 0.89)	0.95 (0.75, 1.16)	0.78 (0.65, 0.92)
β_2	–0.40 (–0.60, –0.21)	–0.23 (–0.36, –0.09)	–	–
κ	0.52 (0.51, 0.54)	0.53 (0.51, 0.56)	–	–
$\sigma_{\alpha_0}^2$	0.0004 (0.0002, 0.0006)	0.0004 (0.0002, 0.0006)	0.0004 (0.0002, 0.0006)	0.0004 (0.0002, 0.0006)
$\sigma_{\alpha_1}^2$	0.0003 (0.0002, 0.0006)	0.0003 (0.0002, 0.0006)	0.0003 (0.0001, 0.0006)	0.0003 (0.0001, 0.0006)
$\sigma_{\alpha_2}^2$	0.0006 (0.0002, 0.0012)	0.0006 (0.0002, 0.0013)	–	–
$\sigma_{\gamma_0}^2$	0.0035 (0.0012, 0.0087)	0.0033 (0.0010, 0.0081)	0.0024 (0.0006, 0.0060)	0.0025 (0.0006, 0.0063)
$\sigma_{\gamma_1}^2$	0.0019 (0.0003, 0.0065)	0.0017 (0.0003, 0.0059)	0.0018 (0.0003, 0.0066)	0.0019 (0.0003, 0.0069)
$\sigma_{\gamma_2}^2$	0.0076 (0.0011, 0.0225)	0.0076 (0.0011, 0.0231)	–	–
σ_b^2	–	–	0.0139 (0.0024, 0.0426)	0.0094 (0.0014, 0.0311)
σ_a^2	–	–	0.0001 (0.00005, 0.0002)	0.0001 (0.0001, 0.0002)
σ_s^2	–	–	0.0021 (0.0005, 0.0057)	0.0020 (0.0005, 0.0054)
σ^2	0.0008 (0.0007, 0.0009)	0.0008 (0.0007, 0.0009)	0.0008 (0.0007, 0.0009)	0.0008 (0.0007, 0.0009)

fitted curve regularly over-predicted RE at ME intake below ME_M when compared with models containing non-informative priors. More specifically, the majority of the RE observations lie below the predicted curve for ME intake ranging from 0.4 to 0.5 MJ/kg $BW^{0.75}$.day [plots (*c*) and (*d*) in Fig. 2], suggesting that the fitted models predicted RE values consistently greater than observed at this range of ME intake. Therefore, the cost of using prior knowledge was, on average, over-prediction of RE at lower levels of ME intake. This suggests that the RE, below ME_M, may be over-predicted, resulting in an estimated NE_M that is on average smaller than suggested by these data. However, the use of an informative prior distribution provides estimates of energetic parameters for the nutritionist who prefers to use a compromised estimate of energetic parameters from this database and prior knowledge of bioenergetics research. Posterior means of parameters from each energy retention model, with informative prior distribution for NE_M, and variance components as well as their 95% credible intervals are given in Table 3.

Heat production models

Analysis with non-informative priors

Four models were used to describe HP with the use of non-informative prior distributions for the energetic parameters. The first model is the one proposed by Lofgreen and Garrett (1968), which models the logarithm of HP as a linear function of the ME intake. The NE_M estimated under this model was 0.36 MJ/kg $BW^{0.75}$.day with 95% credible interval [0.33, 0.40] MJ/kg $BW^{0.75}$.day. This credible interval does not contain the 0.32 MJ/kg $BW^{0.75}$.day NE_M from Lofgreen and Garrett (1968), suggesting that the estimate NE_M from the logarithmic model is larger than previously proposed by the same authors. However, it should be noted that when plotting the posterior predictions and observed values as a function of ME intake (Fig. 3), the logarithmic transformed HP deviate considerably from linearity, particularly at lower ME intakes. Therefore, a linear model may not be suitable for the logarithmic transformed data or a logarithmic transformation may not be necessary to describe this dataset with a linear response function.

In this context, three other models were used to describe HP as a function of ME intake for which NE_M estimates are in Table 4. As expected, the estimate from the modified Lofgreen

and Garrett model of 0.37 MJ/kg $BW^{0.75}$.day was practically the same as the estimate from the logarithmic regression. The NE_M in the linear model was smaller than the one from the modified Lofgreen and Garrett model (0.29 MJ/kg $BW^{0.75}$.day). In particular, the 95% credible interval [0.25, 0.33] MJ/kg $BW^{0.75}$.day contained the NE_M of 0.32 MJ/kg $BW^{0.75}$.day proposed by Lofgreen and Garrett (1968) but does not contain the NE_M estimates from the logarithmic regression in this database. The NE_M estimate from the non-parametric model, was substantially larger than estimates from the other HP models (0.49 MJ/kg $BW^{0.75}$.day). Its 95% credible interval [0.39, 0.61] MJ/kg $BW^{0.75}$.day did not include the NE_M proposed by Lofgreen and Garrett (1968) and from any of the other HP models utilised in our study.

Comparison of models using the DIC (Table 4) showed that the non-parametric model had the smallest DIC (–2962), followed
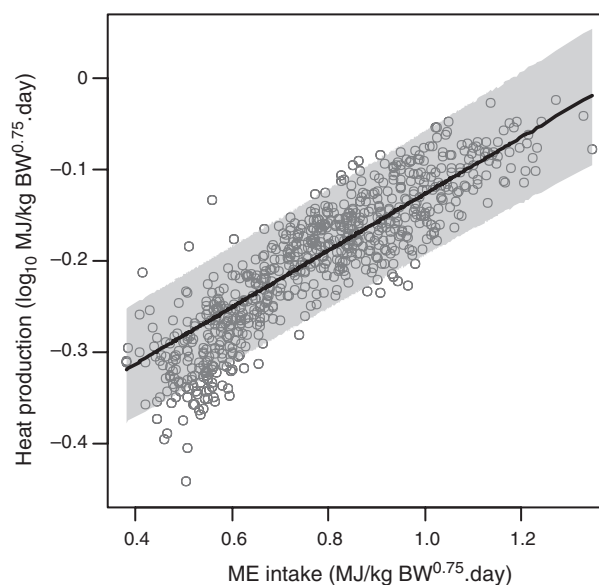

Fig. 3. Posterior predictive distributions of the Lofgreen and Garrett (1968) heat production model plotted as a function of metabolisable energy (ME) intake. All variables are scaled to kg $BW^{0.75}$. The line represents the posterior median and the grey-shaded area is the 95% credible interval for the predictions. Note that non-informative prior distributions were used in this analysis and the estimated NE_M was 0.36 (MJ/kg $BW^{0.75}$).

Table 4. Parameter posterior means and standard deviations in parentheses for the modified Lofgreen and Garrett (L and G), linear and non-parametric heat production models, correlation between observed and predicted values and deviance information criteria (DIC)

Non-informative represents models fitted using non-informative prior distributions for the energetic parameters and informative represents models fitted using informative prior distributions for the NE_M according to Lofgreen and Garrett (1968). NE_M, the daily net energy requirement for maintenance (MJ/kg $BW^{0.75}$.day); σ^2, the error's variance; $r(\mathbf{y^{rep}}, \mathbf{y})$, the correlation between observed values and posterior predictive distributions medians; DIC, a model comparison tool, which trades-off between a measure of goodness of fit and model complexity. Models with smaller DIC represent a better fit to the data and reductions of 5 and 10 DIC units often represent a tendency and a substantive improvement of fit to data (Spiegelhalter *et al.* 2002)

Parameter	Modified L and G		Linear		Non-parametric	
	Non-informative	Informative	Non-informative	Informative	Non-informative	Informative
NE_M	0.37 (0.02)	0.34 (0.01)	0.29 (0.02)	0.31 (0.01)	0.49 (0.05)	0.33 (0.01)
σ^2	0.00088 (0.00005)	0.00089 (0.00005)	0.00088 (0.00005)	0.00087 (0.00005)	0.00075 (0.00005)	0.00077 (0.00005)
$r(\mathbf{y^{rep}}, \mathbf{y})$	0.89	0.89	0.89	0.89	0.90	0.90
DIC	–2878.01	–2876.57	–2893.30	–2898.52	–2962.00	–2945.60

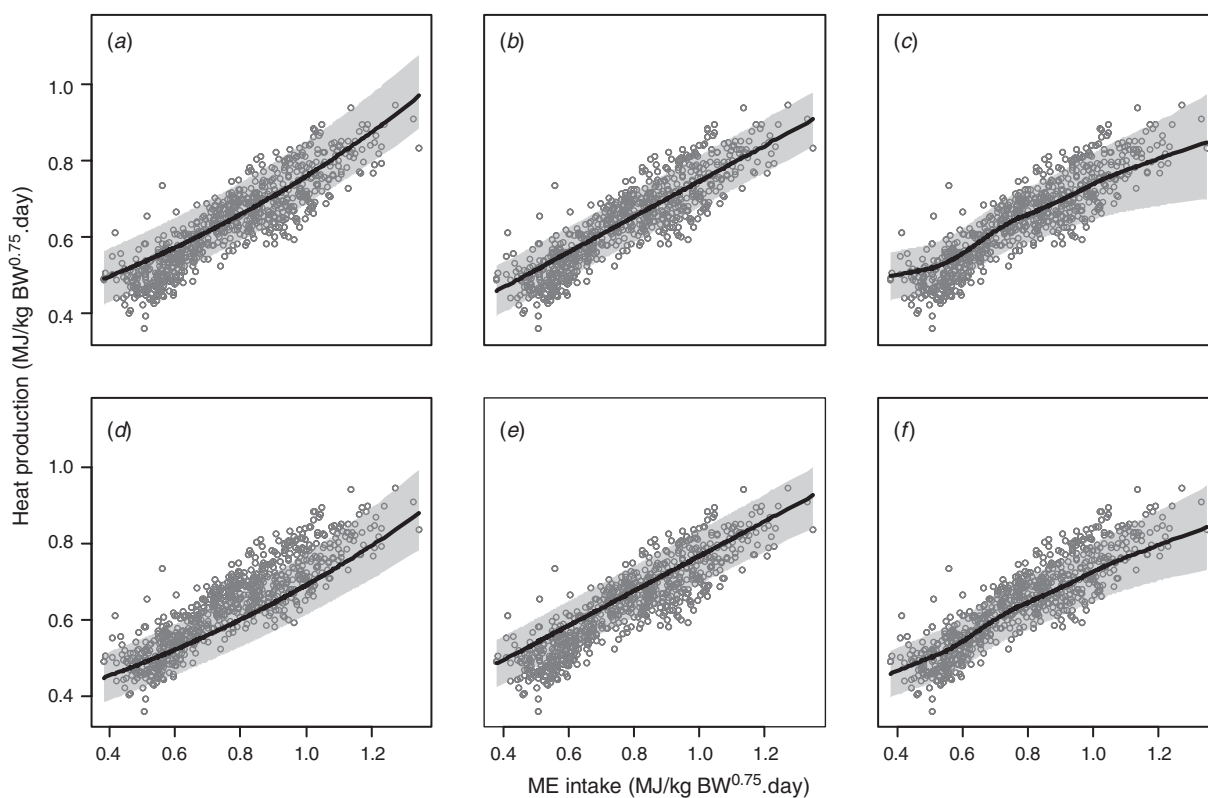**Fig. 4.** Posterior predictive distributions of the heat production models plotted as a function of ME intake. All variables are scaled to kg BW$^{0.75}$. The line represents the posterior predictions medians and the grey-shaded area is the 95% credible interval for the predictions. The graph shows (*a*) the modified Lofgreen and Garrett (1968) model with non-informative prior, (*b*) the linear model with non-informative prior, (*c*) the non-parametric model with non-informative prior, (*d*) the modified Lofgreen and Garrett (1968) model with informative prior, (*e*) the linear model with informative prior and (*f*) the non-parametric model with informative prior.

by the linear model (–2893) and lastly the modified Lofgreen and Garrett model (–2878). Therefore, the DIC suggests that the non-parametric model was the best choice although the non-parametric model, by design, has a greater ability to fit to the data. Consequently, the DIC in the non-parametric model is expected to be substantially smaller than in the parametric models because of its greater flexibility even though it is expected to be penalised more severely for model complexity. Furthermore, the visual inspection of posterior predictions plotted as a function of ME intake (Fig. 4) revealed the principles behind each HP curve to extrapolate to the point of zero ME intake. These principles may be used to select which NE$_M$ estimate should be used based on biological grounds. The modified Lofgreen and Garrett model utilises of a logarithmic transformation as a more realistic manner to extrapolate to the point on the zero ME intake (Lofgreen and Garrett 1968). The linear HP model utilises a linear relationship between HP and ME intake, which is assumed to be the same over all levels of ME intake, to extrapolate to zero ME intake. The non-parametric HP model utilises a linear relationship of HP and ME intake, which is assumed to be the same on the neighbourhood of the minimum ME intake, to extrapolate to zero ME intake. The span of the neighbourhood is determined by the curve first breakpoint, which was specified according to the quantiles of the data, as described in the previous sections. The relationship between HP

and ME intake seemed to be roughly linear over all levels of intake in this database (Fig. 1). Further, the NE$_M$ estimate from the linear model (0.29 MJ/kg BW$^{0.75}$.day) was in good agreement with FHP reported by Lofgreen and Garrett (1968) and Baldwin (1995). Therefore, it can be suggested that NE$_M$ estimated by FHP in this database was 0.29 MJ/kg BW$^{0.75}$.day with a 95% credible interval [0.25, 0.33]. For this model, it is easy to show that ME$_M$ = $\beta_0/(1-\beta_1)$ and k_m = $(1-\beta_1)$ where β_0 and β_1 were the parameters from Eqn 15. Consequently, ME$_M$ was 0.53 MJ/kg BW$^{0.75}$.day with 95% credible interval [0.47, 0.60] and k_m was equal to 0.54 with 95% credible interval [0.50, 0.58]. Therefore, although NE$_M$ and k_m were substantially greater in RE models than in HP models, the ME$_M$ estimates are virtually identical between the two approaches. Lastly, the posterior predictive distributions indicated that all models were reasonably consistent with the data, as suggested by the large correlations between posterior predictions and observed values ($r(\mathbf{y^{rep}}, \mathbf{y}) \geq$ 0.89). Posterior means of parameters from each HP model and variance components as well as their 95% credible intervals are in Table 5.

Analysis with informative priors for NE$_M$

The same HP models of the previous section were fitted with the use of an informative prior distribution for the NE$_M$. In

Table 5. Posterior means and 95% credible intervals for parameters estimated in the modified Lofgreen and Garrett (L and G), linear and non-parametric heat production models

Non-informative represents models fitted using non-informative prior distributions for the energetic parameters and informative represents models fitted using informative prior distributions for the NE_M according to Lofgreen and Garrett (1968). β_0 and β_1 are the parameters from the heat production models describing the relationship between heat production and metabolisable energy intake. $\sigma_{\alpha_0}^2$ and $\sigma_{\alpha_1}^2$ are the variance components associated with animal random effects, $\sigma_{\gamma_0}^2$ and $\sigma_{\gamma_1}^2$ are variance components associated with study random effects, σ_b^2, σ_a^2, σ_s^2 are variance components of the random effects associated with the spline bases in the non-parametric model and σ^2 is the error's variance

Parameter	Modified L and G		Linear		Non-parametric	
	Non-informative	Informative	Non-informative	Informative	Non-informative	Informative
β_0	−0.43	−0.47	0.29	0.31	0.49	0.33
	(−0.47, −0.39)	(−0.50, −0.45)	(0.25, 0.33)	(0.29, 0.33)	(0.39, 0.61)	(0.31, 0.35)
β_1	0.30	0.31	0.46	0.45 (0.41, 0.49)	0.04	0.35
	(0.26, 0.33)	(0.27, 0.34)	(0.43, 0.49)		(−0.19, 0.25)	(0.27, 0.42)
$\sigma_{\alpha_0}^2$	0.0002	0.0002	0.0004	0.0004	0.0004	0.0004
	(0.0001, 0.0003)	(0.0001, 0.0003)	(0.0002, 0.0006)	(0.0002, 0.0006)	(0.0002, 0.0006)	(0.0002, 0.0006)
$\sigma_{\alpha_1}^2$	0.0002	0.0002 (0.0001, 0.0003)	0.0003	0.0003	0.0003	0.0003
	(0.0001, 0.0003)		(0.0002, 0.0006)	(0.0002, 0.0006)	(0.0001, 0.0006)	(0.0001, 0.0006)
$\sigma_{\gamma_0}^2$	0.0054	0.0069	0.0032	0.0044	0.0025	0.0026
	(0.0018, 0.0131)	(0.0020, 0.0174)	(0.0010, 0.0090)	(0.0015, 0.0107)	(0.0007, 0.0063)	(0.0007, 0.0071)
$\sigma_{\gamma_1}^2$	0.0040	0.0039	0.0022	0.0031	0.0018	0.0020
	(0.0010, 0.0106)	(0.0010, 0.0104)	(0.0004, 0.0073)	(0.0006, 0.0094)	(0.0003, 0.0064)	(0.0003, 0.0069)
σ_b^2	–	–	–	–	0.0162	0.0061
					(0.0030, 0.0532)	(0.0008, 0.0225)
σ_a^2	–	–	–	–	0.0001	0.0001
					(0.0001, 0.0002)	(0.0001, 0.0002)
σ_s^2	–	–	–	–	0.0020	0.0021
					(0.0005, 0.0057)	(0.0005, 0.0060)
σ^2	0.0009	0.0009	0.0009	0.0009	0.0007	0.0008
	(0.0008, 0.0010)	(0.0008, 0.0010)	(0.0008, 0.0010)	(0.0008, 0.0010)	(0.0007, 0.0008)	(0.0007, 0.0009)

particular, NE_M (FHP) was assumed to follow a Gaussian distribution with mean 0.32 MJ/kg $BW^{0.75}$.day and standard deviation 0.01. This created the [0.30, 0.34] MJ/kg $BW^{0.75}$. day 95% confidence interval for NE_M as suggested by results from Lofgreen and Garrett (1968). NE_M estimates for all models (Table 4) were in good agreement with those proposed by Lofgreen and Garrett (1968). Comparison of these models with the corresponding models fitted with non-informative prior distributions, suggested that the ability of fitting the data were not altered with the use of informative priors in the modified Lofgreen and Garrett and the linear models (Table 4). In particular the DIC were similar for the modified Lofgreen and Garrett model (–2877 vs –2878) and for the linear HP model (–2899 vs –2893). However, for the non-parametric model the inclusion of prior information decreased the ability of the model in fitting the data as shown by substantial increase in the DIC (–2946 vs –2962).

Posterior predictions of HP plotted against ME intake (Fig. 4) suggest that HP is mostly under-predicted by the modified Lofgreen and Garrett model when informative priors for the NE_M are specified [plot (*d*) Fig. 4]. The linear HP model seems to slightly over-predict HP, as most of the observations fall below the fitted curve [plot (*e*) Fig. 4]. The non-parametric model, when compared with the non-parametric model with non-informative prior, seems to have a steeper slope at the neighbourhood of the minimum ME intake resulting in a smaller intercept and consequently NE_M. In summary, the use of prior information on the NE_M when fitting HP models reduced the ability of the parametric models in describing the data as

shown by the posterior predictive distributions. Further, in the non-parametric HP model the DIC increased substantially, when including prior information on NE_M. The estimates from these models, however, provide energetic parameters that compromise between information provided by this database and prior knowledge of bioenergetics on growing cattle. Posterior means of parameters from each HP model and variance components as well as their 95% credible intervals are given in Table 5.

Conclusions

Maintenance requirements and partial efficiencies of utilising dietary ME were estimated in various models with different strategies in specifying prior distributions and also with varying energy responses (RE vs HP). Biological principles associated with each model differ; consequently estimates of NE_M and k_m were spread over a wide range. In particular, two main classes of models were fitted: energy retention and HP models. For each class, Bayesian models were fitted with the use of informative or non-informative prior distributions. With the use of non-informative prior distributions, the inference is mostly influenced by the data while with the use of informative prior distributions prior knowledge on energetic parameters has a substantial influence on maintenance and efficiency estimates. In particular, when using HP models, NE_M and k_m estimates were substantially smaller than when using RE models. The k_m from the energy retention models ranged from 0.77 to 0.94 whereas it was 0.54 in the HP model. These differences may be explained by the fact that in RE models NE_M represents FCAT while in HP

models it represents FHP. Further, HP seems to be well explained by a linear function of ME intake in this database and the ME_M from this HP model was similar to the ones from RE models (ME_M = 0.53 MJ/kg $BW^{0.75}$.day). Estimates of NE_M from HP models ranged from 0.29 to 0.49 MJ/kg $BW^{0.75}$.day. The NE_M from the linear HP model ranged from 0.29 to 0.31 MJ/kg $BW^{0.75}$.day and due to the good ability of this model in describing this database, it is suggested that FHP in heifers and steers in this database was 0.29 MJ/kg $BW^{0.75}$.day. Further, NE_M estimates in the energy retention models ranged from 0.40 to 0.50 MJ/kg $BW^{0.75}$.day, suggesting that the FCAT in the heifers and steers in this database is within this range. The k_g was slightly greater in the non-parametric model when compared with the piecewise linear model but was not substantially affected when prior information was included in the Bayesian model. In summary, ME_M was similar among models; NE_M and k_m were larger in energy retention models because of biological principles associated with energetic calculations. Finally, introducing prior information on the NE_M generally reduced the ability of the models in describing the data but provided estimates of energetic parameters that were a compromise between information provided by this database and previous knowledge on energy utilisation by growing cattle.

Acknowledgements

References

Agricultural and Food Research Council (1993) 'Energy and protein requirements of ruminants.' (CAB International: Wallingford, UK)

Agricultural Research Council (1980) 'The nutrient requirements of ruminant livestock.' (Commonwealth Agricultural Bureaux: Slough, UK)

Baldwin RL (1995) 'Modeling ruminant digestion and metabolism.' (Chapman and Hall: London)

Best N, Cowles MK, Vines SK (1995) 'CODA manual version 0.30.' (MRC Biostatistics Unit: Cambridge, UK)

Blaxter KL (1980) The efficiency of energy utilisation by beef cattle. *Annales de Zootechnie* **29**, 145–159. doi:10.1051/animres:19800509

Blaxter KL, Boyne AW (1978) The estimation of the nutritive value of feeds as energy sources for ruminants and the derivation of feeding systems. *The Journal of Agricultural Science* **90**, 47–68. doi:10.1017/S0021859600048589

Cantet RJC, Birchmeier AN, Canaza Cayo AW, Fioretti C (2005) Semiparametric animal models via penalized splines as alternatives to models with contemporary groups. *Journal of Animal Science* **83**, 2482–2494.

Carstens GE, Johnson DE, Johnson KA, Hotovy SK, Szymanski TJ (1989) Genetic variation in energy expenditures of monozygous twin beef cattle at 9 and 20 months of age. In 'Proceedings of the 11th symposium on energy metabolism on farm animals'. (Eds J van der Honing, WH Close) Publication No. 43. pp. 312–315. (European Association for Animal Production Publication: Wageningen, The Netherlands)

Chiogna M, Gaetan C (2007) Semiparametric zero-inflated Poisson models with application to animal abundance studies. *Environmetrics* **18**, 303–314. doi:10.1002/env.830

Commonwealth Scientific and Industrial Research Organization (2007) 'Nutrient requirements of domesticated ruminants.' (CSIRO: Melbourne)

Crainiceanu CM, Ruppert D, Wand MP (2005) Bayesian analysis for penalized spline regression using WinBUGS. *Journal of Statistical Software* **14**(14).

Faridi A, Golian A, France J (2012) Evaluating the egg production of broiler breeder hens in response to dietary nutrient intake from 31 to 60 weeks of age through neural network models. *Canadian Journal of Animal Science* **92**, 473–481. doi:10.4141/cjas2012-020

Faridi A, Golian A, Mottaghitalab M, Lopez S, France J (2013) Predicting the metabolizable energy content of corn for ducks: a comparison of support vector regression with other methods. *Spanish Journal of Agricultural Research* **11**, 1036–1043. doi:10.5424/sjar/2013114-4220

Ferrell CL, Jenkins TG (1985) Energy utilization by Hereford and Simmental males and females. *Animal Production* **41**, 53–61. doi:10.1017/S0003356100017542

Flatt WP, Van Soest PJ, Sykes JF, Moore LA (1958) A description of the Energy Metabolism Laboratory at the US Department of Agriculture Research Center in Beltsville, Maryland. In 'Proceedings of the 1st symposium on energy metabolism. Vol. 8'. (Eds GA Thorbek, H Aersoe) pp. 53–64. (European Association of Animal Production: Copenhagen, Denmark)

France J, Dhanoa MS, Cammell SB, Gill M, Beever DE, Thornley JHM (1989) On the use of response functions in energy balance analysis. *Journal of Theoretical Biology* **140**, 83–99. doi:10.1016/S0022-5193(89)80031-1

Frisch JE, Vercoe JE (1977) Food intake, eating rate, weight gains, metabolic rate and efficiency of feed utilization in *Bos taurus* and *Bos indicus* crossbred cattle. *Animal Production* **25**, 343–358. doi:10.1017/S0003356100016755

Garrett WN (1980) Factors influencing energetic efficiency of beef production. *Journal of Animal Science* **51**, 1434–1440.

Garrett WN, Johnson DE (1983) Nutritional energetics of ruminants. *Journal of Animal Science* **57**(Suppl. 2), 478–497.

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Statistical Science* **7**, 457–472. doi:10.1214/ss/1177011136

Gelman A, Carlin J, Stern H, Rubin D (2004) 'Bayesian data analysis.' 2nd edn. Texts in Statistical Science. (Chapman and Hall: London)

Gurrin LC, Scurrah KJ, Hazelton ML (2005) Tutorial in biostatistics: spline smoothing with linear mixed models. *Statistics in Medicine* **24**, 3361–3381. doi:10.1002/sim.2193

Jenkins TG, Ferrell CL (1983) Nutrient requirements to maintain weight of mature, nonlactating, nonpregnant cows of four diverse breed types. *Journal of Animal Science* **56**, 761–770.

Kebreab E, France J, Agnew RE, Yan T, Dhanoa MS, Dijkstra J, Beever DE, Reynolds CK (2003) Alternatives to linear analysis of energy balance data from lactating cows. *Journal of Dairy Science* **86**, 2904–2913. doi:10.3168/jds.S0022-0302(03)73887-9

Lofgreen GP, Garrett WN (1968) A system for expressing net energy requirements and feed values for growing and finishing beef cattle. *Journal of Animal Science* **27**, 793–806.

Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* **10**, 325–337. doi:10.1023/A:1008929526011

Marcondes MI, Tedeschi LO, Valadares Filho SC, Gionbelli MP (2013) Predicting efficiency of use of metabolizable energy to net energy for gain and maintenance of Nellore cattle. *Journal of Animal Science* **91**, 4887–4898. doi:10.2527/jas.2011-4051

Meyer K (2005) Random regression analyses using B-splines to model growth of Australian Angus cattle. *Genetics, Selection, Evolution* **37**, 473–500. doi:10.1186/1297-9686-37-6-473

Moe PW, Flatt WP, Tyrrell H (1972) Net energy value of feeds for lactation. *Journal of Dairy Science* **55**, 945–958. doi:10.3168/jds.S0022-0302(72)85601-7

Moraes LE, Wilen JE, Robinson PH, Fadel JG (2012) A linear programming model to optimize diets in environmental policy scenarios. *Journal of Dairy Science* **95**, 1267–1282. doi:10.3168/jds.2011-4651

Moraes LE, Strathe AB, Fadel JG, Casper DP, Kebreab E (2014) Prediction of enteric methane emissions from cattle. *Global Change Biology* **20**, 2140–2148. doi:10.1111/gcb.12471

National Research Council (2000) 'Nutrient requirements of beef cattle.' 7th revised edn. (National Academy of Sciences: Washington, DC)

Ntzoufras I (2009) 'Bayesian modeling using WinBUGS.' (John Wiley and Sons: New York)

Old CA, Garrett WN (1985) Efficiency of feed energy utilization for protein and fat gain in Hereford and Charolais steers. *Journal of Animal Science* **60**, 766–771.

Pinheiro J, Bates DM (2000) 'Mixed effects models in S and SPLUS. Statistics and computing.' (Springer: New York)

Ruppert D (2002) Selecting the number of knots for penalized splines. *Journal of Computational and Graphical Statistics* **11**, 735–757. doi:10.1198/106186002853

Spiegelhalter DJ, Best N, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society. Series B. Methodological* **64**, 583–639. doi:10.1111/1467-9868.00353

Strathe AB, Danfær A, Sørensen H, Kebreab E (2010) A multilevel nonlinear mixed-effects approach to model growth in pigs. *Journal of Animal Science* **88**, 638–649. doi:10.2527/jas.2009-1822

Strathe AB, Dijkstra J, France J, Lopez S, Yan T, Kebreab E (2011) A Bayesian approach to analyse energy balance data from lactating dairy cows. *Journal of Dairy Science* **94**, 2520–2531.

Tedeschi LO, Boin C, Fox DG, Leme PR, Alleoni GF, Lanna DPD (2002) Energy requirement for maintenance and growth of Nellore bulls and steers fed high-forage diets. *Journal of Animal Science* **80**, 1671–1682.

Tedeschi LO, Fox DG, Guiroy PJ (2004) A decision support system to improve individual cattle management. 1. A mechanistic, dynamic model for animal growth. *Agricultural Systems* **79**, 171–204. doi:10.1016/S0308-521X(03)00070-2

Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology* **84**, 2034–2041. doi:10.1890/02-0472

Wand MP (2003) Smoothing and mixed models. *Computational Statistics* **18**, 223–249.

Williams CB, Jenkins TG (2003) A dynamic model of metabolizable energy utilization in growing and mature cattle. II. Metabolizable energy utilization for gain. *Journal of Animal Science* **81**, 1382–1389.