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Interpretive Summary: Structural equations and energy utilization. By Moraes et al., page 000.

A multivariate model was developed to estimate maintenance requirements and partial efficiencies of utilizing dietary energy and body stores by lactating cows. The model treats energy intake, milk energy output and tissue energy balance as random variables and accounts for the fact that they are mutually interactive traits. The model was used along with a model traditionally utilized for the analysis of energy balance data from lactating cows to show that maintenance requirements and energetic efficiencies of utilizing dietary metabolizable energy have increased in contemporary milk production systems.

RUNNING HEAD: STRUCTURAL EQUATIONS AND ENERGY UTILIZATION

Multivariate and univariate analysis of energy balance data from lactating dairy cows

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ABSTRACT

The objectives of the study were to develop a multivariate framework for analyzing energy balance data from lactating cows and investigate potential changes in maintenance requirements and partial efficiencies of energy utilization by lactating cows over the years. The proposed model accounted for the fact that metabolizable energy intake, milk energy output and tissue energy balance are random variables which mutually interact. The model was specified through structural equations which were implemented in a Bayesian framework. The structural equations, along with a model traditionally used to estimate energetic parameters, were fitted to a large database of indirect calorimetry records from lactating cows. Maintenance requirements and partial efficiencies for both models were similar to values reported in the literature. In particular, the estimated parameters (with 95% Credible Interval in parentheses) for the proposed model were: net energy requirement for maintenance (NE_M) equal to 0.36 (0.34, 0.38) MJ/kg BW^{0.75} d, the efficiency of utilizing dietary energy for milk production (k_L) and tissue gain (k_G) were 0.63 (0.61, 0.64) and 0.70 (0.68, 0.72) respectively. The efficiency of utilizing body stores for milk production (k_T) was 0.89 (0.87, 0.91). Furthermore, additional analyses were conducted for which energetic parameters were allowed to depend on the decade for which studies were conducted. These models investigated potential changes in maintenance requirements and partial efficiencies over the years. Canonical correlation analysis was used to investigate the association between changes in energetic parameters with additional dietary and animal characteristics.
available in the database. For both models, NE$_M$, $k_L$ and $k_G$ increased in the more recent decades while $k_T$ remained unchanged. The increase in maintenance requirements in modern milk production systems is consistent with the literature that describes increased fasting heat production in cows of higher genetic merit. The increase in utilization of dietary energy for milk production and tissue gain was partially attributed to the changes in dietary composition, in particular to the increase in dietary ether extract to levels closer to levels currently observed in modern milk production systems. Therefore, the estimated energetic parameters from this study can be used to update maintenance requirements and partial efficiencies of energy utilization in Northern American feeding systems for lactating cows.

**Key words:** energy, maintenance, efficiency, structural equations

**INTRODUCTION**

The efficiency with which cows utilize dietary energy to execute metabolic and production functions has received great attention over the last five decades (Moe et al., 1971; Kebreab et al., 2003; Strathe et al., 2011). Estimates of energetic efficiencies and maintenance requirements are necessary for the development of feeding systems and for the examination of production systems through quantitative approaches (Moraes et al., 2012). The Northern American (NRC, 2001), the Dutch (Van Es, 1978) and the British (AFRC, 1993) energy evaluation systems for dairy cows rely mainly on data from the 1960s despite dramatic increase in milk production per cow in the past five decades (Shook, 2006; VandeHaar and St-Pierre, 2006). Furthermore, cows of high genetic merit have higher gross energetic efficiency than cows of low genetic merit (Veerkamp and Emmans, 1995). Compatibly, genetic selection has increased fasting heat production and energy maintenance requirements in lactating cows.
(Agnew & Yan, 2000). However, using a European database of indirect calorimetry on lactating dairy cows, Strathe et al. (2011) did not find a relationship between maintenance or efficiency parameters and the year studies were conducted. In this context, in order to cope with increased maintenance requirements and achieve the observed increase in gross energetic efficiency, improvements in energy utilization must have been achieved in at least one of the various processes associated with energy transactions in the lactating cow.

Fundamental parameters in energy evaluation systems are partial efficiencies of energy utilization and maintenance requirements. These parameters have been estimated using a variety of modeling approaches for different livestock species. In lactating cows, Moe et al. (1971) proposed a multiple linear regression approach for estimating maintenance requirements and partial efficiencies based on the observation that dietary ME is used with similar efficiencies for maintenance and lactation. Although Kebreab et al. (2003) proposed nonlinear models as alternatives to the multiple regression approach, nonlinear response functions performed similar to the multiple regression models. Strathe et al. (2011) proposed an energy function which generalized the model advocated by Moe et al. (1971). These three models were univariate models in the sense that a response variable (usually milk energy output) is regressed on a set of independent variables which are often assumed to be known and measured without error. In this framework, the uncertainty in the observed data is accounted by the assignment of a probability model for the errors associated with the dependent variable. However, energy balance records have intrinsic variation; for example, measurement error can be expected in fecal, urinary, methane, milk and tissue energy records. In this context, treating energy traits as independent variables of deterministic nature may underestimate the total variability associated with energetic transactions in the lactating cow, as seminally discussed by Van Es (1972). Furthermore, energy
traits are expected to be correlated and mutually interact. For example, biological principles imply that increasing milk production will augment energy intake and, at the same time, increasing energy intake will increase the delivery of energy available for milk production. Univariate modeling techniques are often unsuitable for the representation of mutually interactive traits. For instance, parameter estimates are biased if two mutually interactive traits are used in univariate least squares regression for which one trait is used as a covariate to model the other trait (Gianola and Sorensen, 2004). Multivariate models have been proposed for the analysis of energy partitioning in growing animals (Koong, 1977; van Milgen and Noblet, 1999; Strathe et al., 2012). Further, simultaneous and structural equation models have been extensively used in animal breeding (Gianola and Sorensen, 2004; de los Campos et al., 2006; Rosa et al., 2011) and econometrics (Goldberger, 1972; Zellner, 1979; Koop, 2003) but applications in animal nutrition are scarce. Therefore, the objectives of this study were to propose a multivariate framework for analyzing energy balance data from lactating cows and to investigate potential changes in maintenance requirements and energetic efficiencies associated with changes in dietary characteristics and animals traits over the years.

MATERIAL AND METHODS

Database

The database comprised 1,038 complete energy balance records from 284 Holstein cows in 40 studies conducted from 1963 to 1995. Records summarize at least four consecutive days of lactating cows in respiration chambers and were collected at the former USDA Energy Metabolism Unit at Beltsville, Maryland. A comprehensive description of the experimental procedures is available from Flatt et al. (1958) and Moe et al. (1972). The database is a subset of
the database described by Moraes et al. (2014) comprised by measurements only on Holstein lactating cows. Descriptive statistics of nutrient composition of diets and animal status are presented in Table 1. Milk energy output, ME intake and tissue energy data are presented in Figure 1. The database 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.

**General Framework**

Models were implemented in a Bayesian framework for which minimally informative prior densities were specified for all parameters and posterior inferences were based on Markov Chain Monte Carlo (MCMC) methods. The Bayesian framework is particularly suited because it naturally accommodates the hierarchical structure of the data and directly estimates standard error of functions of parameters through the MCMC sampling. Models were implemented in the statistical software WinBUGS which utilizes Gibbs sampling, Metropolis-Hastings and slice sampling type algorithms to sample from posterior distributions (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 (CODA) package (Best et al., 1995) were used to formally assess chains’ convergence. Hypothesis testing of energetic parameters was conducted through the construction of 95% Bayesian Credible Intervals (CrI) and Bayesian $P$-values, defined as $P-value = 2 \times \min \{ \Pr(\theta_1 - \theta_2 \geq 0 | y), \ Pr(\theta_1 - \theta_2 < 0 | y) \}$, where $\theta_1$ and $\theta_2$ are the parameters being compared and $y$ is the observed data. 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). Specifically, 
\[
\text{DIC} = E_{\theta y} \left[ -2 \log p(y|\theta) \right] + p_D , \text{ i.e., the expected minus twice the log likelihood plus a penalty for the number of effective parameters. In practice, reductions of 5 and 10 DIC units often represent a tendency and a substantive improvement of fit to data, respectively (Spiegelhalter et al. 2002).}
\]

**Energy Balance Models**

Two models were used to describe energy utilization by lactating cows in this study. The first model (Strathe et al., 2011) is a generalization of the model proposed by Moe et al. (1971) and belongs to the family of univariate models because the response represents a single energy trait. The second model belongs to the family of multivariate models for which the response vector is composed of three energy traits that were described through structural equations. In the following notation, \( q \) is the metabolizability (MJ ME/MJ GE), \( \text{ME}_M \) is the ME requirement for maintenance (MJ/kg BW\(^{0.75} \) d), \( \text{NE}_M \) is the net energy requirement for maintenance (MJ/kg BW\(^{0.75} \) d), \( k_L \) is the efficiency of utilizing dietary ME for milk production (MJ Milk/MJ ME), \( k_T \) is the efficiency of utilizing body stores for milk production (MJ Milk/MJ Tissue) and \( k_G \) is the efficiency of utilizing dietary ME for tissue gain (MJ Tissue/MJ ME).

**Univariate Framework**

The energy function proposed by Strathe et al. (2011) is described as:

\[
\text{EL} = \beta_0 + \beta_1 \text{MEI} - \beta_2 \text{TG} + \beta_3 \text{TL} \tag{1}
\]
where EL denotes the milk energy output (MJ/kg BW^{0.75} d), MEI is the dietary ME intake (MJ/kg BW^{0.75} d), TG is the tissue gain (MJ/kg BW^{0.75} d) and TL is the tissue loss (MJ/kg BW^{0.75} d) [Note that TL and TG are zero if the cow is in positive or negative tissue energy balance, respectively]. In this model, \( NE_M = -\beta_0 \), \( ME_M = -\frac{\beta_0}{\beta_1} \), \( k_L = \beta_1 \), \( k_T = \beta_3 \) and \( k_G = \frac{\beta_1}{\beta_2} \) as described in Strathe et al. (2011). The model was implemented through a linear mixed effects model:

\[
y = X\beta + Z_1\alpha + Z_2\delta + \epsilon \tag{2}
\]

where \( y \) is the \( n \times 1 \) vector of milk energy outputs, \( X \), \( Z_1 \) and \( Z_2 \) are known design matrices relating elements of \( \beta \), \( \alpha \) and \( \delta \) to \( y \). \( \beta \) is the \( m \times 1 \) vector of regression coefficients, \( \alpha \) is the vector of \( mn_a \times 1 \) animal random regression coefficients, \( \delta \) is the vector of \( mn_s \times 1 \) study random regression coefficients and \( \epsilon \) is the \( n \times 1 \) vector of errors. In this notation, \( n \) represents the total number of observations; \( n_s \) and \( n_a \) are the number of studies and animals. The joint distribution of the errors and random effects was assumed to be:

\[
\begin{bmatrix}
\epsilon \\
\alpha \\
\delta
\end{bmatrix}
\sim N
\left( 
\begin{bmatrix}
0 \\
0 \\
0
\end{bmatrix}, 
\begin{bmatrix}
\sigma^2 I_n \\
\sigma^2 I_{n_a} \otimes G_\alpha \\
\sigma^2 I_{n_s} \otimes G_\delta
\end{bmatrix}
\right)
\tag{3}
\]

where \( \otimes \) is the Kronecker product, \( \sigma^2 \) is the errors’ variance, \( I \) is the identity matrix, \( G_\alpha \) and \( G_\delta \) are unstructured covariance matrices of order \( m \). A comprehensive description of the Bayesian implementation of this linear mixed model is provided in the Appendix (see Appendix 1).

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Multivariate Framework

The multivariate framework proposed in this study differs from traditional univariate models of energy utilization in two main aspects: i) ME intake, milk energy and tissue energy are all treated as random variables and ii) ME intake, milk energy and tissue energy are mutually interactive random variables. The energy functions proposed in this study are:

\[
\begin{bmatrix}
\text{MEI} \\
\text{EL} \\
\text{TE}
\end{bmatrix} = \begin{bmatrix}
\beta_1 \text{GEI} \\
\beta_2 + \lambda_{21} \text{MEI} + \lambda_{23}^{(1)} \text{TE} \text{I}_{(\text{TE} > 0)} + \lambda_{23}^{(2)} \text{TE} \text{I}_{(\text{TE} < 0)} \\
\beta_3 + \lambda_{31} \text{MEI} + \lambda_{32} \text{EL}
\end{bmatrix}
\]

where MEI is the ME intake (MJ/kg BW^0.75 d), EL is the milk energy output (MJ/kg BW^0.75 d) and TE the tissue energy balance (MJ/kg BW^0.75 d), GEI is the gross energy intake (MJ/kg BW^0.75 d) and \( I_{(B)} \) denotes the indicator function for the event B; that is, \( I_{(B)} = 1 \) if B is true and 0 otherwise. In this model, \( q = \beta_1 \), \( \text{NE}_M = -\beta_2 \), \( \text{ME}_M = -\frac{\beta_2}{\lambda_{21}} \), \( k_L = \lambda_{21} \), \( k_T = \lambda_{23}^{(2)} \) and \( k_G = \frac{\lambda_{21}}{\lambda_{23}^{(1)}} \).

The model was implemented through structural equations as described in Gianola and Sorensen (2004):

\[\Lambda \mathbf{y} = X \mathbf{\beta} + Z_1 \mathbf{\alpha} + Z_2 \mathbf{\delta} + \mathbf{\epsilon}\]

where \( \mathbf{y} \) is the \( 3n \times 1 \) vector composed of ME intakes, milk energy outputs and tissue energy balances, \( X \), \( Z_1 \) and \( Z_2 \) are known design matrices relating elements of \( \mathbf{\beta} \), \( \mathbf{\alpha} \) and \( \mathbf{\delta} \) to \( \mathbf{y} \). \( \mathbf{\beta} \) is the \( m \times 1 \) vector of regression coefficients \( m = \sum_{r=1}^{s} m_r \), where \( m_r \) is the number of regression parameters for the \( r^{th} \) response: the responses are ME intake, milk energy output and tissue energy balance], \( \mathbf{\alpha} \) is the \( mn_a \times 1 \) vector of animal random regression coefficients, \( \mathbf{\delta} \) is the \( mn_s \)
× 1 vector of study random regression coefficients and \( \varepsilon \) is the \( 3n \times 1 \) vector of errors. In this notation, \( n \) represents the total number of observations, \( n_a \) the number of animals and \( n_s \) the number of studies. Further, \( \Lambda = I_n \otimes \Lambda_0 \) where:

\[
\Lambda_0 = \begin{bmatrix}
1 & -\lambda_{12} & -\lambda_{13} \\
-\lambda_{21} & 1 & -\lambda_{23} \\
-\lambda_{31} & -\lambda_{32} & 1
\end{bmatrix}
\]

for which the off-diagonal elements are the structural parameters (gradient of one energy trait with respect to the other). The unknown elements of \( \Lambda \) are collected in \( \lambda \) which is modeled as

\[
\lambda = W\mu + Z_3\zeta + Z_4\xi,
\]

where \( W, Z_3 \) and \( Z_4 \) are known incidence matrices relating elements of \( \lambda_\mu, \zeta \) and \( \xi \) to elements in \( \lambda \). \( \lambda_\mu \) is the \( k \times 1 \) vector of population structural coefficients (\( k \) denotes the number of unknowns in \( \Lambda_0 \)), \( \zeta \) and \( \xi \) are \( kn_a \times 1 \) and \( kn_s \times 1 \) vectors of animal and study random coefficients respectively. The joint distribution of the errors and random effects was assumed to be:

\[
\begin{bmatrix}
\varepsilon \\
\alpha \\
\delta \\
\zeta \\
\xi
\end{bmatrix} \sim N
\begin{bmatrix}
0 \\
0 \\
0 \\
0 \\
0
\end{bmatrix},
\begin{bmatrix}
I_n \otimes R & 0 & 0 & 0 & 0 \\
0 & I_{n_a} \otimes G_\alpha & 0 & 0 & 0 \\
0 & 0 & I_{n_s} \otimes G_\delta & 0 & 0 \\
0 & 0 & 0 & I_{n_a} \otimes G_\zeta & 0 \\
0 & 0 & 0 & 0 & I_{n_s} \otimes G_\xi
\end{bmatrix}
\]

where \( R \) is an unstructured covariance matrix of order 3, \( G_\alpha \) and \( G_\delta \) are unstructured covariance matrices of order \( m \), and \( G_\zeta \) and \( G_\xi \) are unstructured covariance matrices of order \( k \).

We set \( \lambda_{12} = 0 = \lambda_{13} \) to create the causal structure described in Figure 2. In this structure, tissue energy balance and milk energy output have a simultaneous relationship in the sense that it may
be expected that cows mobilize tissue reserves to sustain milk production but cows also have increased milk production as a consequence of tissue mobilization. Further, ME intake is assumed to affect milk energy balance and tissue energy in a unidirectional fashion because cows often have pre-determined intake levels in energy balance calorimetric studies. A comprehensive description of the Bayesian implementation of this structural equation model is presented in the Appendix (see Appendix 1).

Changes in Energetic Parameters over the Years

In order to examine potential changes in energetic parameters over the years, further analyses were conducted in which regression and structural parameters were allowed to depend on the decade the study was conducted. A three level nominal factor was created to identify the membership of each record to one of the three intervals: [1963, 1973], [1974, 1983] and [1984, 1995]. Therefore, energetic parameters were decade specific and the hypothesis that maintenance requirements and energetic efficiencies have changed over the decades was investigated. Canonical Correlation Analysis (CCA) was then used to investigate the correlations between estimated energetic parameters on the different decades and additional dietary characteristics and animal traits available in the database. The ideal situation would be to identify dietary characteristics and animal traits which affect energetic parameters and model these parameters as a function of such variables within the model fitting process. The strategy of modeling energetic parameters as a function of dietary characteristics has been adopted by the ARC (1980) where $k_L$ is modeled as a linear function of the metabolizability. Similarly, Marcondes et al. (2013) modeled partial efficiencies of ME use for maintenance ($k_M$) and $k_G$ as functions of animal characteristics in beef steers, although a two stage type of analysis was adopted. In the present study, an attempt was made to model energetic parameters as a function of dietary variables and
animal traits simultaneously in the model fitting but none of the relationships were statistically
significant due to large standard errors of the parameters. A possible cause for the lack of
significant relationships among energetic parameters, dietary characteristics and animal traits is
the mostly unknown forms of the relationships which, in this study, were assumed to be linear.
These results are consistent with Strathe et al. (2011) in which no significant effects of the diet
metabolizability was found on NE_M, k_L, and k_T when their full dataset was used in the analysis. It
is important to note, however, that when excluding two experiments for which q < 0.5, Strathe et
al. (2011) found k_L to be significantly affected by q. In this context, CCA was used to describe
the association between changes in energetic parameters at different decades with diet and
animal characteristics and to potentially elucidate mechanisms associated with the increased
gross energetic efficiency of dairy cows in modern production systems through physiology, diet
and milk production.

The CCA was conducted as follows: Let \( \theta = (ME_{M,ijl}, NE_{M,ijl}, k_{L,ijl}, k_{T,ijl}, k_{G,ijl})^T \) be the 5
\( \times 1 \) vector of mixed effects estimated in the Strathe et al. (2011) model for the \( l \)th record (\( l = 1, \ldots, n_{ij} \)) from the \( i \)th animal (\( i = 1, \ldots, n_a \)) on the \( j \)th study (\( j = 1, \ldots, n_s \)) and
\( \eta = (HB_{ijl}, DIP_{ijl}, MY_{ijl}, MP_{ijl}, MF_{ijl}, NDF_{ijl}, CP_{ijl}, EE_{ijl}, TEB_{ijl})^T \) be a 9 \( \times 1 \) vector of covariates
associated with this record describing dietary characteristics and animal traits. In this notation,
HB is the heart rate in beats per second, DIP is the days in pregnancy, MY is the milk yield
(kg/d), MP is the milk crude protein (%), MF is the milk fat (%), NDF is the dietary NDF (% of
DM), CP is the dietary crude protein (% of DM), EE is the dietary EE (% of DM) and TEB is the
tissue energy balance (MJ/d). It is assumed that
where \( \text{Var}(\theta) = V_{11}, \ \text{Var}(\eta) = V_{22}, \ \text{Cov}(\theta, \eta) = V_{12}^T \) for \( V_{11} \) and \( V_{22} \) of full rank.

Canonical correlation analysis seeks vectors \( a \) and \( b \) (\( a \in \mathbb{R}^5 \) and \( b \in \mathbb{R}^9 \)) such that the correlation between the linear combinations \( a^T \theta \) and \( b^T \eta \) are maximized. In particular, the function

\[
\rho = \max_{a, b} \left\{ \frac{a^T V_{12} b}{\sqrt{a^T V_{11} a b^T V_{22} b}} \right\}
\]

was maximized with generalized eigenvalues. The canonical correlations \( \rho_1 \geq \ldots \geq \rho_5 \) are the correlations between the canonical variates \( (a_1^T \theta, \ldots, a_5^T \theta) \) which are associated with the vector of energetic parameters and the canonical variates \( (b_1^T \eta, \ldots, b_5^T \eta) \) associated with the vector of dietary and animal characteristics. Canonical loadings and cross-loadings represent the correlation between each individual variable with its own canonical variate and with the canonical variate of the other set of variables respectively. These measures of correlation are often the ones used to investigate the role of individual variables in the canonical functions because canonical weights are not robust to multicollinearity (Alpert and Peterson, 1972; Hair et al., 1998). In this study, the loadings and cross loadings of the first canonical functions were used to investigate the correlation between estimated energetic parameters in each decade with dietary and animal characteristics. For example, the canonical loadings of variables in \( \theta \) represent the correlation between each individual variable from this set and the canonical variate \( a_1^T \theta \) whereas canonical cross-loadings of variables in \( \theta \) represent the correlation between each individual
variable in $\theta$ with the canonical variate $b_i^T \eta$. The CCA for the structural equation model is similar to the one described above for the Strathe et al. (2011) model but with

$$\theta = (ME_{M,ijm}, NE_{M,ijm}, k_{L,ijm}, k_{T,ijm}, k_{G,ijm}, q_{ijm})^T$$

and $a \in \mathbb{R}^6$. A detailed description of the CCA implementation is presented in the Appendix (see Appendix 1).

RESULTS AND DISCUSSION

Energetic Parameters

Posterior means and 95% CrI of parameters estimated by the univariate Strathe et al. (2011) and the multivariate structural equation models are given in Table 2. Diagnostic plots for assessing fit of all models are presented in the Appendix (see Appendix 2). Variance components’ posteriors means and associated 95% CrI for all models are also in the Appendix (see Appendix 3). Energetic parameters are summarized by posterior means and 95% CrI in Table 3. Estimates of the efficiency of utilizing dietary ME for producing milk from both models were similar to the $k_L$ proposed by Moe et al. (1972) and adopted by the NRC (2001). Specifically, the $k_L$ of 0.64 adopted by the NRC (2001) was contained in the 95% CrI from both Strathe et al. (2011) and structural equation models. Moreover, the partial efficiencies of utilizing dietary ME for tissue gain from the two models are also in good agreement with the values proposed by Moe et al. (1971). For instance, the $k_G$ estimates of 0.70 and 0.75 in this study were within the theoretical maximum efficiencies [0.7, 0.8] of utilizing dietary energy for growth in ruminants calculated by Baldwin et al. (1980). Further, estimates of $k_G$ in this study were substantially smaller than the ones from Kebreab et al. (2003) and Strathe et al. (2011) who estimated $k_G$ ranging from 0.83 to 0.88 in European dairy cows. The results from this study corroborate findings of Moe et al. (1971) that dietary ME is used as efficiently or better for
concurrent growth than for lactation. Moreover, the estimated $k_T$’s of 0.80 and 0.89 (Table 3) in this study were in good agreement with the efficiencies estimated by Moe et al. (1971). Additionally, these estimates support the results from Moe et al. (1971) that the indirect net efficiency of producing milk from dietary ME through tissue mobilization and subsequent deposition was similar to $k_L$. For example, in the structural equation model this efficiency would be $0.89 \times 0.70 = 0.62$, which is similar to the estimated $k_L$ of 0.63 from this model. Finally, it is important to note that in all models from this study $k_T > k_G$ as originally proposed by Moe et al (1971) but challenged by Kebreab et al. (2003) and Strathe et al. (2011). In particular, the implementation of the Strathe et al. (2011) model with our database and the estimation of efficiencies for which $k_T > k_G$ suggests that there are substantial differences between the European (Kebreab et al., 2003; Strathe et al., 2011) and Northern American databases rather than differences in the models used to estimate energetic efficiencies. It can therefore be suggested that, in US Holstein cows, the efficiency of producing milk from body store reserves is substantially higher than the efficiency of utilizing dietary ME for tissue energy gain as initially proposed by Moe et al. (1971).

Energy maintenance requirements estimated in the two models are in Table 3. The NE$\text{M}$ from the Strathe et al. (2011) model (0.35 MJ/kg BW$^{0.75}$ d) was in good agreement with the NE$\text{M}$ adopted by the current US feeding system for dairy cows of 0.33 MJ/kg BW$^{0.75}$ d [or 0.08 Mcal/kg BW$^{0.75}$ d]. However, the NE$\text{M}$ from the structural equation model (0.36 MJ/kg BW$^{0.75}$ d) was slightly larger compared to NRC (2001) because the value of 0.33 was outside its 95% CrI (Table 3). The ME$\text{M}$ from models in this study was 0.57 MJ/kg BW$^{0.75}$ d (Table 3) which was larger than what would be expected using the default NRC (2001) values for NE$\text{M}$ and $k_L$ [ME$\text{M}$ = NE$\text{M}$/k$\text{L}$ = 0.33/0.64 = 0.52 MJ/kg BW$^{0.75}$ d using $k_M = k_L$ as suggested by the NRC, (2001)].
However, the ME\textsubscript{M} was in good agreement with recent estimates by Agnew and Yan (2000) ranging from 0.49 to 0.67 MJ/kg BW\textsuperscript{0.75} d. A potential increase in maintenance requirements for lactating dairy cows in modern milk production systems was discussed in detail by Agnew and Yan (2000). In particular, the process of genetic selection for milk production may have altered animals’ metabolic rates and consequently maintenance requirements. For instance, Yan et al. (1997) estimated fasting heat production of Holstein-Friesian cows of 0.45 MJ/kg BW\textsuperscript{0.75} d and Birnie (1999) reported fasting heat production of 0.39 MJ/kg BW\textsuperscript{0.75} d for non-lactating, non-pregnant dairy cows previously fed at maintenance level. Values from both studies were substantially larger than the current NRC (2001) estimate of NE\textsubscript{M} (0.33 MJ/kg BW\textsuperscript{0.75} d).

Similarly, five decades ago, high producing lactating cows have been recognized to have a proportional 0.20 increase in ME required for maintenance compared to cows with moderate milk production levels (Flatt et al., 1969; Moe et al., 1970; Van Es et al., 1970). Likewise, beef steers with different residual feed intakes were estimated to have considerably different energy requirements for maintenance (Sainz et al., 2013). A difference of 30% in maintenance requirements was observed between steers in the most efficient and least efficient groups. Two major factors were discussed by Agnew and Yan (2000) for explaining changes in maintenance of dairy cows with genetic selection: larger proportions of body weight as protein mass and enlarged organ sizes in high producing lactating cows due to greater nutrient intakes. The fact that modern dairy cows have larger proportions of body protein mass was confirmed by Ferris et al. (1999) who reported that high genetic merit cows were found to have lower backfat thickness, at comparable body weights, than cows of medium and low genetic merits. Similarly, Veerkamp et al. (1994) estimated a higher lipid-free empty body weight proportion in high genetic merit cows. The influence of body weight protein proportion in maintenance requirements may be
explained by the substantial energy cost associated with protein turnover (Baldwin et al., 1980; Agnew and Yan, 2000). Furthermore, cows of high genetic merit may have enlarged organ sizes due to a greater activity of digestive and circulatory tissues to digest and transport nutrients (Reynolds, 1996). Organs involved in these metabolic activities have an important contribution to total maintenance requirements (Baldwin et al., 1980; Baldwin et al., 1985).

**Changes in Energetic Parameters over the Years**

The effect of the study decade was introduced into energetic parameters through a three level nominal factor. We hypothesized that changes in metabolizability, maintenance and efficiency parameters in the past few decades may elucidate potential mechanisms associated with the increased gross energetic efficiency of dairy cows in modern production systems. The estimated mixed effects (i.e., fixed population parameters plus animal and study deviations from the population) from the different decades were associated with additional variables describing dietary characteristics and animal traits through canonical correlation analysis. We quote Pearson (1900): “… where we find correlation we cannot always predict causation.” to point out that the results must be interpreted from a correlation perspective because correlation is a necessary but not sufficient condition for causality. Studies from this database were conducted under distinct biological hypotheses examining various nutritional factors associated with energy utilization in dairy cows. However, the division of this database into decades aimed at representing the changes in animals and diets which would have occurred with the advancement of bioenergetics research and the genetic selection process of animals and feedstuffs over the years.

Posterior means and 95% CrI of the parameters estimated in all models of different decades are presented in the Appendix (see Appendix 3). Estimated energetic parameters and associated 95% CrI are presented in Table 4. The metabolizability parameter $q$ from the
structural equation model was not different between decades suggesting that the metabolizability of diets did not change across decades in this database. In particular, $q$ was not different between the first and second decade ($P = 0.81$) and the first and third decade ($P = 0.41$). Similarly, $k_T$ was not statistically different among decades for any energy function, suggesting that the efficiency with which cows mobilize body stores to produce milk has not changed over the decades in this database. However, $\text{ME}_M$, $\text{NE}_M$, $k_L$ and $k_G$ all increased over the decades for both energy functions (Table 4). Therefore, it can be suggested that maintenance requirements and the efficiency of utilizing dietary ME increased over the decades in this database. The increased maintenance requirement in high producing dairy cows has been discussed above and by Agnew and Yan (2000) comprehensively. In particular, Agnew and Yan (2000) pointed out that high producing cows have enlarged organ sizes to sustain nutrient transport, digestion and absorption at relatively greater nutrient intakes. Boxplots of dietary and animal characteristics from the three decades are presented in Figure 3. For instance, it is evident that heart rate, milk yield and gross energetic efficiency are largest in cows of the third decade (Figure 3). Furthermore, the efficiency of utilizing dietary ME for milk production in the first and second decades were not different in the univariate model ($P = 0.18$) as well as in the structural equation model ($P = 0.06$), although the estimated $k_L$ in the second decade is slightly outside the 95% CrI of the $k_L$ from the first decade. Conversely, $k_L$ in the third decade was greater in both univariate ($P < 0.01$) and structural equations ($P < 0.01$) models compared to the first decade. Similarly, $k_G$ was greater in the second decade than in the first in both univariate ($P = 0.01$) and structural equation models ($P = 0.04$). Moreover, $k_G$ was also greater in the third decade than in the first in both univariate ($P < 0.01$) and structural equation ($P < 0.01$) models. Additionally, it is important to notice that models fitted with energetic parameters depending on the study decade were better supported by
the data than models fitted without the study decade. A reduction in the DIC was observed for all energy functions when maintenance requirements and energetic efficiencies were decade specific. Specifically, with the Strathe et al. (2011) model the DIC decreased from –3.852 to –3.858 when the parameters were allowed to depend on the study decade. Likewise, in the structural equation model, the DIC decreased from –16,030 to –16,076 when parameters were allowed to depend on the study decade.

Canonical correlation analysis was used to investigate the degree of association between the set of estimated energetic parameters at different decades and a set of variables describing dietary and animal characteristics. Particularly, loadings and cross-loadings from the CCA were used to identify animal and dietary characteristics that have high correlations with the canonical variate associated with the estimated energetic parameters in different decades. The number of canonical correlations extracted is equal to the number of variables in the smaller set. The canonical correlations were \( r_1 = 0.84, r_2 = 0.45, r_3 = 0.33, r_4 = 0.17, r_5 = 0.10 \) for the parameters from the Strathe et al. (2011) model and \( r_1 = 0.81, r_2 = 0.50, r_3 = 0.40, r_4 = 0.32, r_5 = 0.17, r_6 = 0.10 \) for the parameters from the structural equation model. The first canonical correlations between the two sets of variables in both models suggest that, as expected, the set of dietary animal characteristics were strongly associated with the energetic parameters from the different decades. The loadings and cross-loadings associated with the first canonical functions are presented in Table 5. In both models, canonical loadings of the energetic parameters were high for the \( \text{ME}_M, \text{NE}_M, k_L \) and \( k_G \) suggesting that these four energetic parameters were the most important predictors for the first canonical variate associated with the \( \Theta \) vector. Moreover, the canonical loadings of the dietary and animal variables were high for \( \text{HB}, \text{MY}, \) and dietary EE suggesting that these three variables...
were the most important animal and dietary contributors for the first canonical function. Similarly, the examination of the cross-loadings of the first canonical function suggests that MY, HB and dietary EE were the variables which present higher correlations with the canonical variate associated with the set of energetic parameters. Likewise, energetic parameters that correlated highly with the first canonical variate of the set of dietary and animal related variables were $\text{ME}_M$, $\text{NE}_M$, $k_L$ and $k_G$. Furthermore, the redundancy coefficient describes the amount of variance in the energetic parameters’ canonical variate explained by the animal and diet related canonical variate. These coefficients were 0.48 and 0.39 for the first canonical function for the Strathe et al. (2011) and structural equation models, respectively.

Therefore, using the findings that maintenance requirements and dietary partial efficiencies were different between decades and the results from the CCA, combined dietary and animal factors can be used to explain the increase in the efficiency of utilizing dietary energy. Partial efficiencies of ME utilization for milk production and growth are dependent on stoichiometric and thermodynamic relationships between substrates and animal products (Baldwin et al., 1995). For instance, dietary ME utilization is affected by type of diet (Garrett and Johnson, 1983) because changes in dietary composition will alter the pattern of available nutrients for milk and tissue synthesis. Equally, changes in the partial efficiencies of producing milk and depositing tissue energy may occur through changes in milk and tissue gain compositions. Instead, cows’ energy balance status may also alter the energetic efficiency of synthesizing milk: cows mobilizing body fat will use more preformed lipids and less volatile fatty acids to produce milk fat than cows in positive energy balance. From this database, it can be suggested that cows in the last decade were of higher genetic merit than cows in the first two decades although pedigree information was not available. Recent studies have reported that
partial efficiencies of ME utilization are similar for cows of different genetic merits (Grainer et al., 1985; Veerkamp and Emmans, 1995) and also for cows in studies conducted in different decades (Strathe et al., 2011). In addition, Bauman et al. (1985) suggested that between animal variation in the partial efficiency of utilizing dietary ME for lactation is negligible and proposed alternative strategies for gains in efficiency such as altered nutrient partitioning and dilution of maintenance. Although cows of different genetic merits have been reported to have similar $k_L$ there is increasing evidence that genetic selection has altered the expression of metabolites associated with nutrient utilization pathways. For instance, Holstein-Friesian cows of different genetic backgrounds have been found to have different expression of gluconeogenic enzymes (White et al., 2012). Moreover, changes in subcutaneous adipose tissue metabolism and gene network expression have been reported in cows of different genetic merits (Khan et al., 2013) and the expression of genes involved in the somatotropic axis have been found to differ in different strains of Holstein-Friesian cows (McCarthy et al., 2009). A key factor determining the efficiency of dietary energy utilization is the source of dietary energy (Smith, 1988; Vandehaar, 1998). Diets in the third decade had higher proportion of EE than diets in the first two decades (Figure 3). It can therefore be hypothesized that a larger proportion of the dietary ME content originated from fat in the third decade. Such differences in the nutrients comprising dietary ME would alter the nutrients available for production functions and consequently alter the efficiencies of producing milk and depositing tissue energy. It is important to note that the dietary EE percentages from the first two decades (means = 2.47 and 2.37 % of DM) were in good agreement with the data (Moe et al., 1971; Moe et al., 1972) used as the basis for the energy evaluation system for the current US feeding system for dairy cows (NRC, 2001). However, the dietary EE percentages in the third decade (mean = 3.71 % of DM) were closer to
dietary EE percentages from modern milk production systems (Rossow and Aly, 2013). The increase in $k_L$ with increased dietary fat is well established in the literature and it has been traditionally attributed to a decrease in the heat increment (VandeHaar, 1998) and the relatively low energetic cost of the transfer of absorbed fatty acids to milk fat when compared with the cost of de novo synthesis of fatty acids (Bauman et al., 1985).

Furthermore, it is important to note that from a practical feeding perspective, the increase in maintenance requirements in modern milk production systems may be partially balanced by the simultaneous increase in the efficiency of dietary ME utilization. For example, assuming no tissue gain or loss and a BW of 600 kg, the ME$_M$ and $k_L$ values of the SEqM model result in total ME expenditure to be in balance in these 3 decades at an energy corrected milk production of about 38 kg/d. Compared with the third decade, animals in the first decade are more efficient at energy corrected milk production levels below 38 kg/d, and less efficient at energy corrected milk production levels above 38 kg/d. Finally, it is also important to note that maintenance requirements and efficiency estimates are inherently correlated within a model, as pointed out by Moe (1981) who described lower efficiencies as a consequence of lower maintenance costs. Therefore, only the estimated energetic parameters for a given model and decade should be used in the prediction of energy utilization by lactating cows.

**CONCLUSIONS**

A multivariate framework was proposed to analyze energy balance data from lactating cows which accounted for the variation in ME intake, milk energy output and tissue energy balance and allowed for these traits to have simultaneous and recursive relationships. The proposed model was compared to methods traditionally used to estimate maintenance
requirements and energetic efficiencies. Maintenance requirements and partial efficiencies of utilizing dietary energy and body stores, estimated in both models, were similar to values proposed in the literature. In particular, for the proposed model, \( \text{NE}_M \) was 0.36 MJ/kg BW\(^{0.75} \) d, \( k_L, k_G, \) and \( k_T \) were 0.63, 0.70 and 0.89 respectively. Additional analyses were conducted in which energetic parameters were allowed to depend on the decade of the study to investigate potential changes in maintenance requirements and partial efficiencies across decades. For both models, \( \text{NE}_M, k_L \) and \( k_G \) increased for the more recent decades while \( k_T \) remained unchanged. The increase in maintenance requirements in contemporary milk production systems is consistent with the literature that describes increased fasting heat production in cows of higher genetic merit. The increase in the efficiency of utilizing dietary energy was partially attributed to the changes in dietary composition, in particular to the increase in dietary EE to levels closer to those currently observed in milk production systems. Finally, the estimated energetic parameters from this study can be used to update maintenance requirements and partial efficiencies of energy utilization in Northern American feeding systems.

**ACKNOWLEDGEMENTS**

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**REFERENCES**


Table 1. Descriptive statistics of dietary nutrient composition and animal status\(^1\).

<table>
<thead>
<tr>
<th>Item(^1)</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDF (% of DM)</td>
<td>33.7</td>
<td>14.9</td>
<td>76.1</td>
<td>7.2</td>
</tr>
<tr>
<td>ADF (% of DM)</td>
<td>19.7</td>
<td>7.7</td>
<td>47.1</td>
<td>4.6</td>
</tr>
<tr>
<td>ME (MJ/kg DM)</td>
<td>10.9</td>
<td>6.9</td>
<td>14.6</td>
<td>0.9</td>
</tr>
<tr>
<td>CP (% of DM)</td>
<td>16.3</td>
<td>5.2</td>
<td>23.5</td>
<td>2.9</td>
</tr>
<tr>
<td>EE (% of DM)</td>
<td>2.7</td>
<td>1.0</td>
<td>7.0</td>
<td>1.0</td>
</tr>
<tr>
<td>DMI (kg/d)</td>
<td>16.8</td>
<td>6.2</td>
<td>29.4</td>
<td>4.0</td>
</tr>
<tr>
<td>GEI (MJ/d)</td>
<td>318.5</td>
<td>113.4</td>
<td>584.7</td>
<td>84.1</td>
</tr>
<tr>
<td>MEI (MJ/d)</td>
<td>182.1</td>
<td>66.3</td>
<td>348.2</td>
<td>46.3</td>
</tr>
<tr>
<td>FECGE (MJ/d)</td>
<td>109.0</td>
<td>23.4</td>
<td>232.6</td>
<td>34.1</td>
</tr>
<tr>
<td>UGE (MJ/d)</td>
<td>10.6</td>
<td>2.9</td>
<td>25.6</td>
<td>36.2</td>
</tr>
<tr>
<td>CH(_4) (MJ/d)</td>
<td>16.8</td>
<td>3.8</td>
<td>30.7</td>
<td>5.0</td>
</tr>
<tr>
<td>TEB (MJ/d)</td>
<td>2.6</td>
<td>-86.0</td>
<td>78.8</td>
<td>19</td>
</tr>
<tr>
<td>MILKGE (MJ/d)</td>
<td>68.6</td>
<td>0.3</td>
<td>156.5</td>
<td>29.3</td>
</tr>
<tr>
<td>Milk Yield (kg/d)</td>
<td>23.9</td>
<td>0.1</td>
<td>56.6</td>
<td>16.3</td>
</tr>
<tr>
<td>Milk CP (%)</td>
<td>3.23</td>
<td>2.30</td>
<td>5.75</td>
<td>0.38</td>
</tr>
<tr>
<td>Milk Fat (%)</td>
<td>3.58</td>
<td>1.43</td>
<td>7.60</td>
<td>0.93</td>
</tr>
<tr>
<td>DIM</td>
<td>160.2</td>
<td>11</td>
<td>488</td>
<td>81.5</td>
</tr>
<tr>
<td>BW (kg)</td>
<td>608.1</td>
<td>350.7</td>
<td>854.1</td>
<td>72.4</td>
</tr>
<tr>
<td>AGE (Months)</td>
<td>64.3</td>
<td>25</td>
<td>185</td>
<td>25.5</td>
</tr>
</tbody>
</table>

\(^1\)NDF is the dietary neutral detergent fiber, ADF is the dietary acid detergent fiber, ME is the dietary ME content, CP is the dietary crude protein, EE is the dietary ether extract, GEI is the gross energy intake, MEI is the metabolizable energy intake, FECGE is the fecal gross energy output, UGE is the urinary gross energy output, CH\(_4\) is the methane emission, TEB is the tissue energy balance, MILKGE is the milk gross energy output and AGE is the cow age in months.
Table 2. Parameters posterior means and 95% Credible Intervals using the Strathe et al. (2011) and the structural equation (SEqM) models.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Strathe et al. (2011)</th>
<th>SEqM</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>$-0.35 (-0.38, -0.32)$</td>
<td>-</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>0.62 (0.60, 0.64)</td>
<td>0.57 (0.56, 0.58)</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>$-0.83 (-0.87, -0.79)$</td>
<td>$-0.36 (-0.38, -0.34)$</td>
</tr>
<tr>
<td>$\beta_3$</td>
<td>$-0.80 (-0.84, -0.76)$</td>
<td>$-0.40 (-0.42, -0.37)$</td>
</tr>
<tr>
<td>$\lambda_{21}$</td>
<td>-</td>
<td>0.63 (0.61, 0.64)</td>
</tr>
<tr>
<td>$\lambda_{21}^{(1)}$</td>
<td>-</td>
<td>$-0.90 (-0.92, -0.88)$</td>
</tr>
<tr>
<td>$\lambda_{21}^{(2)}$</td>
<td>-</td>
<td>$-0.89 (-0.91, -0.87)$</td>
</tr>
<tr>
<td>$\lambda_{31}$</td>
<td>-</td>
<td>0.70 (0.68, 0.72)</td>
</tr>
<tr>
<td>$\lambda_{32}$</td>
<td>-</td>
<td>$-1.11 (-1.13, -1.09)$</td>
</tr>
</tbody>
</table>

$\beta$’s are the regression coefficients and $\lambda$’s are the structural parameters of the structural equation model. Note that $\beta$’s in the two different models represent different parameters which are not directly comparable.
Table 3. Energetic parameters posterior means and 95% Credible Intervals using the Strathe et al. (2011) and the structural equation (SEqM) models.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Strathe et al. (2011)</th>
<th>SEqM</th>
</tr>
</thead>
<tbody>
<tr>
<td>( q )</td>
<td>0.57 (0.53, 0.60)</td>
<td>0.57 (0.54, 0.59)</td>
</tr>
<tr>
<td>ME_M</td>
<td>0.57 (0.53, 0.60)</td>
<td>0.57 (0.54, 0.59)</td>
</tr>
<tr>
<td>NE_M</td>
<td>0.35 (0.32, 0.38)</td>
<td>0.36 (0.34, 0.38)</td>
</tr>
<tr>
<td>( k_L )</td>
<td>0.62 (0.60, 0.64)</td>
<td>0.63 (0.61, 0.64)</td>
</tr>
<tr>
<td>( k_T )</td>
<td>0.80 (0.75, 0.84)</td>
<td>0.89 (0.87, 0.91)</td>
</tr>
<tr>
<td>( k_G )</td>
<td>0.75 (0.70, 0.79)</td>
<td>0.70 (0.68, 0.72)</td>
</tr>
</tbody>
</table>

\( q \) is the metabolizability (MJ ME/MJ GE), ME_M is the metabolizable energy requirements for maintenance (MJ/kg^{0.75} d), NE_M is the net energy requirement for maintenance (MJ/kg^{0.75} d), \( k_L \) is the efficiency of utilizing ME intake for milk production (MJ Milk/MJ ME), \( k_T \) is the efficiency of utilizing body stores for milk production (MJ Milk/MJ Tissue) and \( k_G \) is the efficiency of utilizing ME intake for tissue gain (MJ Tissue/MJ ME).
Table 4. Energetic parameters posterior means and 95% Credible Intervals using the Strathe et al. (2011) and the structural equation (SEqM) models for the three decades for which studies were conducted.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Decade</th>
<th>Strathe et al. (2011)</th>
<th>SEqM</th>
</tr>
</thead>
<tbody>
<tr>
<td>q</td>
<td>1963-1973</td>
<td>-</td>
<td>0.56 (0.55, 0.58)</td>
</tr>
<tr>
<td>q</td>
<td>1974-1983</td>
<td>-</td>
<td>0.57 (0.55, 0.59)</td>
</tr>
<tr>
<td>q</td>
<td>1984-1995</td>
<td>-</td>
<td>0.57 (0.55, 0.59)</td>
</tr>
<tr>
<td>ME_M</td>
<td>1963-1973</td>
<td>0.50 (0.47, 0.54)</td>
<td>0.51 (0.48, 0.54)</td>
</tr>
<tr>
<td>ME_M</td>
<td>1974-1983</td>
<td>0.58 (0.53, 0.63)</td>
<td>0.59 (0.55, 0.63)</td>
</tr>
<tr>
<td>ME_M</td>
<td>1984-1995</td>
<td>0.70 (0.64, 0.75)</td>
<td>0.74 (0.70, 0.78)</td>
</tr>
<tr>
<td>NE_M</td>
<td>1963-1973</td>
<td>0.30 (0.27, 0.33)</td>
<td>0.31 (0.28, 0.33)</td>
</tr>
<tr>
<td>NE_M</td>
<td>1974-1983</td>
<td>0.36 (0.32, 0.41)</td>
<td>0.37 (0.34, 0.41)</td>
</tr>
<tr>
<td>NE_M</td>
<td>1984-1995</td>
<td>0.48 (0.42, 0.53)</td>
<td>0.52 (0.47, 0.56)</td>
</tr>
<tr>
<td>k_L</td>
<td>1963-1973</td>
<td>0.60 (0.58, 0.62)</td>
<td>0.60 (0.58, 0.62)</td>
</tr>
<tr>
<td>k_L</td>
<td>1974-1983</td>
<td>0.62 (0.59, 0.65)</td>
<td>0.63 (0.60, 0.65)</td>
</tr>
<tr>
<td>k_L</td>
<td>1984-1995</td>
<td>0.68 (0.65, 0.71)</td>
<td>0.70 (0.68, 0.73)</td>
</tr>
<tr>
<td>k_T</td>
<td>1963-1973</td>
<td>0.82 (0.76, 0.87)</td>
<td>0.90 (0.89, 0.92)</td>
</tr>
<tr>
<td>k_T</td>
<td>1974-1983</td>
<td>0.81 (0.73, 0.87)</td>
<td>0.90 (0.88, 0.93)</td>
</tr>
<tr>
<td>k_T</td>
<td>1984-1995</td>
<td>0.79 (0.70, 0.86)</td>
<td>0.90 (0.88, 0.92)</td>
</tr>
<tr>
<td>k_G</td>
<td>1963-1973</td>
<td>0.68 (0.63, 0.73)</td>
<td>0.66 (0.64, 0.69)</td>
</tr>
<tr>
<td>k_G</td>
<td>1974-1983</td>
<td>0.79 (0.72, 0.87)</td>
<td>0.70 (0.67, 0.73)</td>
</tr>
<tr>
<td>k_G</td>
<td>1984-1995</td>
<td>0.83 (0.77, 0.91)</td>
<td>0.78 (0.75, 0.80)</td>
</tr>
</tbody>
</table>

1. q is the metabolizability (MJ ME/MJ GE), ME_M is the metabolizable energy requirements for maintenance (MJ/kg^0.75 d), ME_M is the net energy requirement for maintenance (MJ/kg^0.75 d), k_L is the efficiency of utilizing ME intake for milk production (MJ Milk/MJ ME), k_T is the efficiency of utilizing body stores for milk production (MJ Milk/MJ Tissue) and k_G is the efficiency of utilizing ME intake for tissue gain (MJ Tissue/MJ ME).
Table 5. Canonical loadings and cross-loadings for the first canonical variate of the dietary and animal characteristics and estimated energetic parameters in Strathe et al. (2011) and structural equation (SEqM) models.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Strathe et al. (2011)</th>
<th>SEqM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Loading</td>
<td>Cross-loading</td>
</tr>
<tr>
<td>η HB</td>
<td>0.76</td>
<td>0.64</td>
</tr>
<tr>
<td>DIP</td>
<td>-0.29</td>
<td>-0.25</td>
</tr>
<tr>
<td>MY</td>
<td>0.87</td>
<td>0.73</td>
</tr>
<tr>
<td>MP</td>
<td>-0.27</td>
<td>-0.23</td>
</tr>
<tr>
<td>MF</td>
<td>-0.04</td>
<td>-0.03</td>
</tr>
<tr>
<td>NDF</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>CP</td>
<td>0.52</td>
<td>0.44</td>
</tr>
<tr>
<td>EE</td>
<td>0.72</td>
<td>0.61</td>
</tr>
<tr>
<td>TEB</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>θ ME_M</td>
<td>0.88</td>
<td>0.73</td>
</tr>
<tr>
<td>NE_M</td>
<td>0.93</td>
<td>0.78</td>
</tr>
<tr>
<td>k_L</td>
<td>0.90</td>
<td>0.75</td>
</tr>
<tr>
<td>k_G</td>
<td>0.94</td>
<td>0.79</td>
</tr>
<tr>
<td>k_T</td>
<td>-0.32</td>
<td>-0.26</td>
</tr>
<tr>
<td>q</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

1 η is the vector of dietary and animal characteristics and θ is the vector of estimated energetic parameters in each decade. HB is the heart rate in beats per second, DIP is the days in pregnancy, MY is the milk yield (kg/d), MP is the milk crude protein (%), MF is the milk fat (%), NDF is the dietary NDF (% of DM), CP is the dietary crude protein (% of DM), EE is the dietary EE (% of DM) and TEB is the tissue energy balance (MJ/d). Further, q is the metabolizability (MJ ME/MJ GE), ME_M is the ME requirement for maintenance (MJ/kg BW^{0.75} d), NE_M is the net energy requirement for maintenance (MJ/kg BW^{0.75} d), k_L is the efficiency of utilizing dietary ME for milk production (MJ Milk/MJ ME), k_T is the efficiency of utilizing body stores for milk production (MJ Milk/MJ Tissue) and k_G is the efficiency of utilizing dietary ME for tissue gain (MJ Tissue/MJ ME).
Figure 1. Daily milk energy output (MJ/kg BW$^{0.75}$ d) versus daily ME intake (MJ/kg BW$^{0.75}$ d) or daily tissue energy balance (MJ/kg BW$^{0.75}$ d) with linear trend lines included.
**Figure 2.** Schematic diagram representing the structural equation model with recursive and simultaneous relationships of energy traits.

Note: MEI is the metabolizable energy intake (MJ/kg BW^{0.75} d), EL is the milk energy output (MJ/kg BW^{0.75} d) and TE is the tissue energy balance (MJ/kg BW^{0.75} d). We use the notation from Gianola and Sorensen (2004) where λ's are the structural parameters representing the gradients of one energy trait with respect to another and not fluxes. In this notation, λ_{23} is the sum of two parameters which individually represent the gradient when cows are in positive or negative tissue energy balance. It is important to note that in Equation [4], λ_{23}^{(1)} vanishes when the cow is in negative tissue energy balance whereas λ_{23}^{(2)} vanishes when the cow is in positive tissue energy balance.
Figure 3. Boxplots of dietary characteristics and animal traits for the three decades.

Note: TEB is the tissue energy balance (MJ/d) and Gross Efficiency is equal to the ratio of the milk energy output and the gross energy intake.