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1 **Interpretive Summary:** Structural equations and energy utilization. *By Moraes et al., page 000.*
2 A multivariate model was developed to estimate maintenance requirements and partial
3 efficiencies of utilizing dietary energy and body stores by lactating cows. The model treats
4 energy intake, milk energy output and tissue energy balance as random variables and accounts
5 for the fact that they are mutually interactive traits. The model was used along with a model
6 traditionally utilized for the analysis of energy balance data from lactating cows to show that
7 maintenance requirements and energetic efficiencies of utilizing dietary metabolizable energy
8 have increased in contemporary milk production systems.

9 RUNNING HEAD: STRUCTURAL EQUATIONS AND ENERGY UTILIZATION

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

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31 **ABSTRACT**

32 The objectives of the study were to develop a multivariate framework for analyzing
33 energy balance data from lactating cows and investigate potential changes in maintenance
34 requirements and partial efficiencies of energy utilization by lactating cows over the years. The
35 proposed model accounted for the fact that metabolizable energy intake, milk energy output and
36 tissue energy balance are random variables which mutually interact. The model was specified
37 through structural equations which were implemented in a Bayesian framework. The structural
38 equations, along with a model traditionally used to estimate energetic parameters, were fitted to a
39 large database of indirect calorimetry records from lactating cows. Maintenance requirements
40 and partial efficiencies for both models were similar to values reported in the literature. In
41 particular, the estimated parameters (with 95% Credible Interval in parentheses) for the proposed
42 model were: net energy requirement for maintenance (NE_M) equal to 0.36 (0.34, 0.38) MJ/kg
43 $BW^{0.75}$ d, the efficiency of utilizing dietary energy for milk production (k_L) and tissue gain (k_G)
44 were 0.63 (0.61, 0.64) and 0.70 (0.68, 0.72) respectively. The efficiency of utilizing body stores
45 for milk production (k_T) was 0.89 (0.87, 0.91). Furthermore, additional analyses were conducted
46 for which energetic parameters were allowed to depend on the decade for which studies were
47 conducted. These models investigated potential changes in maintenance requirements and partial
48 efficiencies over the years. Canonical correlation analysis was used to investigate the association
49 between changes in energetic parameters with additional dietary and animal characteristics

50 available in the database. For both models, NE_M , k_L and k_G increased in the more recent decades
51 while k_T remained unchanged. The increase in maintenance requirements in modern milk
52 production systems is consistent with the literature that describes increased fasting heat
53 production in cows of higher genetic merit. The increase in utilization of dietary energy for milk
54 production and tissue gain was partially attributed to the changes in dietary composition, in
55 particular to the increase in dietary ether extract to levels closer to levels currently observed in
56 modern milk production systems. Therefore, the estimated energetic parameters from this study
57 can be used to update maintenance requirements and partial efficiencies of energy utilization in
58 Northern American feeding systems for lactating cows.

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

60 INTRODUCTION

61 The efficiency with which cows utilize dietary energy to execute metabolic and
62 production functions has received great attention over the last five decades (Moe et al., 1971;
63 Kebreab et al., 2003; Strathe et al., 2011). Estimates of energetic efficiencies and maintenance
64 requirements are necessary for the development of feeding systems and for the examination of
65 production systems through quantitative approaches (Moraes et al., 2012). The Northern
66 American (NRC, 2001), the Dutch (Van Es, 1978) and the British (AFRC, 1993) energy
67 evaluation systems for dairy cows rely mainly on data from the 1960s despite dramatic increase
68 in milk production per cow in the past five decades (Shook, 2006; VandeHaar and St-Pierre,
69 2006). Furthermore, cows of high genetic merit have higher gross energetic efficiency than cows
70 of low genetic merit (Veerkamp and Emmans, 1995). Compatibly, genetic selection has
71 increased fasting heat production and energy maintenance requirements in lactating cows

72 (Agnew & Yan, 2000). However, using a European database of indirect calorimetry on lactating
73 dairy cows, Strathe et al. (2011) did not find a relationship between maintenance or efficiency
74 parameters and the year studies were conducted. In this context, in order to cope with increased
75 maintenance requirements and achieve the observed increase in gross energetic efficiency,
76 improvements in energy utilization must have been achieved in at least one of the various
77 processes associated with energy transactions in the lactating cow.

78 Fundamental parameters in energy evaluation systems are partial efficiencies of energy
79 utilization and maintenance requirements. These parameters have been estimated using a variety
80 of modeling approaches for different livestock species. In lactating cows, Moe et al. (1971)
81 proposed a multiple linear regression approach for estimating maintenance requirements and
82 partial efficiencies based on the observation that dietary ME is used with similar efficiencies for
83 maintenance and lactation. Although Kebreab et al. (2003) proposed nonlinear models as
84 alternatives to the multiple regression approach, nonlinear response functions performed similar
85 to the multiple regression models. Strathe et al. (2011) proposed an energy function which
86 generalized the model advocated by Moe et al. (1971). These three models were univariate
87 models in the sense that a response variable (usually milk energy output) is regressed on a set of
88 independent variables which are often assumed to be known and measured without error. In this
89 framework, the uncertainty in the observed data is accounted by the assignment of a probability
90 model for the errors associated with the dependent variable. However, energy balance records
91 have intrinsic variation; for example, measurement error can be expected in fecal, urinary,
92 methane, milk and tissue energy records. In this context, treating energy traits as independent
93 variables of deterministic nature may underestimate the total variability associated with energetic
94 transactions in the lactating cow, as seminally discussed by Van Es (1972). Furthermore, energy

95 traits are expected to be correlated and mutually interact. For example, biological principles
96 imply that increasing milk production will augment energy intake and, at the same time,
97 increasing energy intake will increase the delivery of energy available for milk production.
98 Univariate modeling techniques are often unsuitable for the representation of mutually
99 interactive traits. For instance, parameter estimates are biased if two mutually interactive traits
100 are used in univariate least squares regression for which one trait is used as a covariate to model
101 the other trait (Gianola and Sorensen, 2004). Multivariate models have been proposed for the
102 analysis of energy partitioning in growing animals (Koong, 1977; van Milgen and Noblet, 1999;
103 Strathe et al., 2012). Further, simultaneous and structural equation models have been extensively
104 used in animal breeding (Gianola and Sorensen, 2004; de los Campos et al., 2006; Rosa et al.,
105 2011) and econometrics (Goldberger, 1972; Zellner, 1979; Koop, 2003) but applications in
106 animal nutrition are scarce. Therefore, the objectives of this study were to propose a multivariate
107 framework for analyzing energy balance data from lactating cows and to investigate potential
108 changes in maintenance requirements and energetic efficiencies associated with changes in
109 dietary characteristics and animals traits over the years.

110 **MATERIAL AND METHODS**

111 ***Database***

112 The database comprised 1,038 complete energy balance records from 284 Holstein cows
113 in 40 studies conducted from 1963 to 1995. Records summarize at least four consecutive days of
114 lactating cows in respiration chambers and were collected at the former USDA Energy
115 Metabolism Unit at Beltsville, Maryland. A comprehensive description of the experimental
116 procedures is available from Flatt et al. (1958) and Moe et al. (1972). The database is a subset of

117 the database described by Moraes et al. (2014) comprised by measurements only on Holstein
118 lactating cows. Descriptive statistics of nutrient composition of diets and animal status are
119 presented in Table 1. Milk energy output, ME intake and tissue energy data are presented in
120 Figure 1. The database has a hierarchical structure, such that there are multiple observations on
121 the same animal although animals are not fully nested within studies since those were used in
122 multiple studies.

123 ***General Framework***

124 Models were implemented in a Bayesian framework for which minimally informative
125 prior densities were specified for all parameters and posterior inferences were based on Markov
126 Chain Monte Carlo (MCMC) methods. The Bayesian framework is particularly suited because it
127 naturally accommodates the hierarchical structure of the data and directly estimates standard
128 error of functions of parameters through the MCMC sampling. Models were implemented in the
129 statistical software WinBUGS which utilizes Gibbs sampling, Metropolis-Hastings and slice
130 sampling type algorithms to sample from posterior distributions (Lunn et al., 2000). Two chains
131 with over-dispersed initial values were specified for each parameter and chain mixing, auto-
132 correlation, posterior densities and the Gelman-Rubin diagnostics (Gelman and Rubin, 1992)
133 were used to visually assess chain convergence and determine the required burn in period. The
134 tests of the convergence diagnostic and output analysis (CODA) package (Best et al., 1995) were
135 used to formally assess chains' convergence. Hypothesis testing of energetic parameters was
136 conducted through the construction of 95% Bayesian Credible Intervals (CrI) and Bayesian P -
137 values, defined as $P\text{-value} = 2 \times \min[\Pr(\theta_1 - \theta_2 \geq 0 | \mathbf{y}), \Pr(\theta_1 - \theta_2 < 0 | \mathbf{y})]$, where θ_1 and θ_2 are
138 the parameters being compared and \mathbf{y} is the observed data. Model comparison was performed
139 using deviance information criteria (DIC) as described by Spiegelhalter et al. (2002). The DIC is

140 a model comparison tool which assesses the trade-off between goodness of fit and model
141 complexity and is approximately equal to the Akaike's information criteria in Gaussian models
142 (Ntzoufras, 2009). Specifically, $DIC = E_{\theta|y} [-2 \log p(\mathbf{y} | \boldsymbol{\theta})] + p_D$, i.e., the expected minus twice
143 the log likelihood plus a penalty for the number of effective parameters. In practice, reductions
144 of 5 and 10 DIC units often represent a tendency and a substantive improvement of fit to data,
145 respectively (Spiegelhalter et al. 2002).

146 *Energy Balance Models*

147 Two models were used to describe energy utilization by lactating cows in this study. The
148 first model (Strathe et al., 2011) is a generalization of the model proposed by Moe et al. (1971)
149 and belongs to the family of univariate models because the response represents a single energy
150 trait. The second model belongs to the family of multivariate models for which the response
151 vector is composed of three energy traits that were described through structural equations. In the
152 following notation, q is the metabolizability (MJ ME/MJ GE), ME_M is the ME requirement for
153 maintenance (MJ/kg $BW^{0.75}$ d), NE_M is the net energy requirement for maintenance (MJ/kg
154 $BW^{0.75}$ d), k_L is the efficiency of utilizing dietary ME for milk production (MJ Milk/MJ ME), k_T
155 is the efficiency of utilizing body stores for milk production (MJ Milk/MJ Tissue) and k_G is the
156 efficiency of utilizing dietary ME for tissue gain (MJ Tissue/MJ ME).

157 *Univariate Framework*

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

$$159 \quad EL = \beta_0 + \beta_1 MEI - \beta_2 TG + \beta_3 TL \quad [1]$$

160 where EL denotes the milk energy output (MJ/kg BW^{0.75} d), MEI is the dietary ME intake
 161 (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
 162 BW^{0.75} d) [Note that TL and TG are zero if the cow is in positive or negative tissue energy
 163 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
 164 described in Strathe et al. (2011). The model was implemented through a linear mixed effects
 165 model:

$$166 \quad \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta} + \boldsymbol{\varepsilon} \quad [2]$$

167 where \mathbf{y} is the $n \times 1$ vector of milk energy outputs, \mathbf{X} , \mathbf{Z}_1 and \mathbf{Z}_2 are known design matrices
 168 relating elements of $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$ and $\boldsymbol{\delta}$ to \mathbf{y} . $\boldsymbol{\beta}$ is the $m \times 1$ vector of regression coefficients, $\boldsymbol{\alpha}$ is the
 169 vector of $mn_a \times 1$ animal random regression coefficients, $\boldsymbol{\delta}$ is the vector of $mn_s \times 1$ study random
 170 regression coefficients and $\boldsymbol{\varepsilon}$ is the $n \times 1$ vector of errors. In this notation, n represents the total
 171 number of observations; n_s and n_a are the number of studies and animals. The joint distribution
 172 of the errors and random effects was assumed to be:

$$173 \quad \begin{bmatrix} \boldsymbol{\varepsilon} \\ \boldsymbol{\alpha} \\ \boldsymbol{\delta} \end{bmatrix} \sim N \left\{ \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma^2 \mathbf{I}_n & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_{n_a} \otimes \mathbf{G}_\alpha & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_{n_s} \otimes \mathbf{G}_\delta \end{bmatrix} \right\} \quad [3]$$

174 where \otimes is the Kronecker product, σ^2 is the errors' variance, \mathbf{I} is the identity matrix, \mathbf{G}_α and
 175 \mathbf{G}_δ are unstructured covariance matrices of order m . A comprehensive description of the
 176 Bayesian implementation of this linear mixed model is provided in the Appendix (see Appendix
 177 1).

178 *Multivariate Framework*

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

$$183 \begin{bmatrix} \text{MEI} \\ \text{EL} \\ \text{TE} \end{bmatrix} = \begin{bmatrix} \beta_1 \text{GEI} \\ \beta_2 + \lambda_{21} \text{MEI} + \lambda_{23}^{(1)} \text{TE} I_{\{\text{TE} > 0\}} + \lambda_{23}^{(2)} \text{TE} I_{\{\text{TE} < 0\}} \\ \beta_3 + \lambda_{31} \text{MEI} + \lambda_{32} \text{EL} \end{bmatrix} \quad [4]$$

184 where MEI is the ME intake (MJ/kg BW^{0.75} d), EL is the milk energy output (MJ/kg BW^{0.75} d)
 185 and TE the tissue energy balance (MJ/kg BW^{0.75} d), GEI is the gross energy intake (MJ/kg
 186 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

187 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 $k_G = \frac{\lambda_{21}}{\lambda_{23}^{(1)}}$.

188 The model was implemented through structural equations as described in Gianola and Sorensen
 189 (2004):

$$190 \Lambda \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1 \boldsymbol{\alpha} + \mathbf{Z}_2 \boldsymbol{\delta} + \boldsymbol{\varepsilon} \quad [5]$$

191 where \mathbf{y} is the $3n \times 1$ vector composed of ME intakes, milk energy outputs and tissue energy
 192 balances, \mathbf{X} , \mathbf{Z}_1 and \mathbf{Z}_2 are known design matrices relating elements of $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$ and $\boldsymbol{\delta}$ to \mathbf{y} . $\boldsymbol{\beta}$ is

193 the $m \times 1$ vector of regression coefficients [$m = \sum_{r=1}^3 m_r$, where m_r is the number of regression

194 parameters for the r^{th} response: the responses are ME intake, milk energy output and tissue

195 energy balance], $\boldsymbol{\alpha}$ is the $mn_a \times 1$ vector of animal random regression coefficients, $\boldsymbol{\delta}$ is the mn_s

196 $\times 1$ vector of study random regression coefficients and $\boldsymbol{\varepsilon}$ is the $3n \times 1$ vector of errors. In this
 197 notation, n represents the total number of observations, n_a the number of animals and n_s the
 198 number of studies. Further, $\boldsymbol{\Lambda} = \mathbf{I}_n \otimes \boldsymbol{\Lambda}_0$ where:

$$199 \quad \boldsymbol{\Lambda}_0 = \begin{bmatrix} 1 & -\lambda_{12} & -\lambda_{13} \\ -\lambda_{21} & 1 & -\lambda_{23} \\ -\lambda_{31} & -\lambda_{32} & 1 \end{bmatrix} \quad [6]$$

200 for which the off-diagonal elements are the structural parameters (gradient of one energy trait
 201 with respect to the other). The unknown elements of $\boldsymbol{\Lambda}$ are collected in $\boldsymbol{\lambda}$ which is modeled as
 202 $\boldsymbol{\lambda} = \mathbf{W}\boldsymbol{\lambda}_\mu + \mathbf{Z}_3\boldsymbol{\zeta} + \mathbf{Z}_4\boldsymbol{\xi}$, where \mathbf{W} , \mathbf{Z}_3 and \mathbf{Z}_4 are known incidence matrices relating elements of
 203 $\boldsymbol{\lambda}_\mu$, $\boldsymbol{\zeta}$ and $\boldsymbol{\xi}$ to elements in $\boldsymbol{\lambda}$. $\boldsymbol{\lambda}_\mu$ is the $k \times 1$ vector of population structural coefficients (k
 204 denotes the number of unknowns in $\boldsymbol{\Lambda}_0$), $\boldsymbol{\zeta}$ and $\boldsymbol{\xi}$ are $kn_a \times 1$ and $kn_s \times 1$ vectors of animal and
 205 study random coefficients respectively. The joint distribution of the errors and random effects
 206 was assumed to be:

$$207 \quad \begin{bmatrix} \boldsymbol{\varepsilon} \\ \boldsymbol{\alpha} \\ \boldsymbol{\delta} \\ \boldsymbol{\zeta} \\ \boldsymbol{\xi} \end{bmatrix} \sim N \left\{ \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{I}_n \otimes \mathbf{R} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_{n_a} \otimes \mathbf{G}_\alpha & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_{n_s} \otimes \mathbf{G}_\delta & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_{n_a} \otimes \mathbf{G}_\zeta & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_{n_s} \otimes \mathbf{G}_\xi \end{bmatrix} \right\} \quad [7]$$

208 where \mathbf{R} is an unstructured covariance matrix of order 3, \mathbf{G}_α and \mathbf{G}_δ are unstructured
 209 covariance matrices of order m , and \mathbf{G}_ζ and \mathbf{G}_ξ are unstructured covariance matrices of order k .
 210 We set $\lambda_{12} = 0 = \lambda_{13}$ to create the causal structure described in Figure 2. In this structure, tissue
 211 energy balance and milk energy output have a simultaneous relationship in the sense that it may

212 be expected that cows mobilize tissue reserves to sustain milk production but cows also have
213 increased milk production as a consequence of tissue mobilization. Further, ME intake is
214 assumed to affect milk energy balance and tissue energy in a unidirectional fashion because cows
215 often have pre-determined intake levels in energy balance calorimetric studies. A comprehensive
216 description of the Bayesian implementation of this structural equation model is presented in the
217 Appendix (see Appendix 1).

218 *Changes in Energetic Parameters over the Years*

219 In order to examine potential changes in energetic parameters over the years, further
220 analyses were conducted in which regression and structural parameters were allowed to depend
221 on the decade the study was conducted. A three level nominal factor was created to identify the
222 membership of each record to one of the three intervals: [1963, 1973], [1974, 1983] and [1984,
223 1995]. Therefore, energetic parameters were decade specific and the hypothesis that maintenance
224 requirements and energetic efficiencies have changed over the decades was investigated.
225 Canonical Correlation Analysis (CCA) was then used to investigate the correlations between
226 estimated energetic parameters on the different decades and additional dietary characteristics and
227 animal traits available in the database. The ideal situation would be to identify dietary
228 characteristics and animal traits which affect energetic parameters and model these parameters as
229 a function of such variables within the model fitting process. The strategy of modeling energetic
230 parameters as a function of dietary characteristics has been adopted by the ARC (1980) where k_L
231 is modeled as a linear function of the metabolizability. Similarly, Marcondes et al. (2013)
232 modeled partial efficiencies of ME use for maintenance (k_M) and k_G as functions of animal
233 characteristics in beef steers, although a two stage type of analysis was adopted. In the present
234 study, an attempt was made to model energetic parameters as a function of dietary variables and

235 animal traits simultaneously in the model fitting but none of the relationships were statistically
 236 significant due to large standard errors of the parameters. A possible cause for the lack of
 237 significant relationships among energetic parameters, dietary characteristics and animal traits is
 238 the mostly unknown forms of the relationships which, in this study, were assumed to be linear.
 239 These results are consistent with Strathe et al. (2011) in which no significant effects of the diet
 240 metabolizability was found on NE_M , k_L , and k_T when their full dataset was used in the analysis. It
 241 is important to note, however, that when excluding two experiments for which $q < 0.5$, Strathe et
 242 al. (2011) found k_L to be significantly affected by q . In this context, CCA was used to describe
 243 the association between changes in energetic parameters at different decades with diet and
 244 animal characteristics and to potentially elucidate mechanisms associated with the increased
 245 gross energetic efficiency of dairy cows in modern production systems through physiology, diet
 246 and milk production.

247 The CCA was conducted as follows: Let $\boldsymbol{\theta} = (\text{ME}_{M,ijl}, \text{NE}_{M,ijl}, k_{L,ijl}, k_{T,ijl}, k_{G,ijl})^T$ be the 5
 248 $\times 1$ vector of mixed effects estimated in the Strathe et al. (2011) model for the l^{th} record ($l = 1,$
 249 \dots, n_{ij}) from the i^{th} animal ($i = 1, \dots, n_a$) on the j^{th} study ($j = 1, \dots, n_s$) and
 250 $\boldsymbol{\eta} = (\text{HB}_{ijl}, \text{DIP}_{ijl}, \text{MY}_{ijl}, \text{MP}_{ijl}, \text{MF}_{ijl}, \text{NDF}_{ijl}, \text{CP}_{ijl}, \text{EE}_{ijl}, \text{TEB}_{ijl})^T$ be a 9×1 vector of covariates
 251 associated with this record describing dietary characteristics and animal traits. In this notation,
 252 HB is the heart rate in beats per second, DIP is the days in pregnancy, MY is the milk yield
 253 (kg/d), MP is the milk crude protein (%), MF is the milk fat (%), NDF is the dietary NDF (% of
 254 DM), CP is the dietary crude protein (% of DM), EE is the dietary EE (% of DM) and TEB is the
 255 tissue energy balance (MJ/d). It is assumed that

256
$$\text{Var} \begin{bmatrix} \boldsymbol{\theta} \\ \boldsymbol{\eta} \end{bmatrix} = \begin{bmatrix} \mathbf{V}_{11} & \mathbf{V}_{12} \\ \mathbf{V}_{21} & \mathbf{V}_{22} \end{bmatrix} \quad [8]$$

257 where $\text{Var}(\boldsymbol{\theta}) = \mathbf{V}_{11}$, $\text{Var}(\boldsymbol{\eta}) = \mathbf{V}_{22}$, $\mathbf{V}_{12} = \text{Cov}(\boldsymbol{\theta}, \boldsymbol{\eta}) = \mathbf{V}_{21}^T$ for \mathbf{V}_{11} and \mathbf{V}_{22} of full rank.

258 Canonical correlation analysis seeks vectors \mathbf{a} and \mathbf{b} ($\mathbf{a} \in \mathbb{R}^5$ and $\mathbf{b} \in \mathbb{R}^9$) such that the

259 correlation between the linear combinations $\mathbf{a}^T \boldsymbol{\theta}$ and $\mathbf{b}^T \boldsymbol{\eta}$ are maximized. In particular, the

260 function

261
$$\rho = \max_{\mathbf{a}, \mathbf{b}} \left\{ \frac{\mathbf{a}^T \mathbf{V}_{12} \mathbf{b}}{\sqrt{\mathbf{a}^T \mathbf{V}_{11} \mathbf{a} \mathbf{b}^T \mathbf{V}_{22} \mathbf{b}}} \right\} \quad [9]$$

262 was maximized with generalized eigenvalues. The canonical correlations ($\rho_1 \geq \dots \geq \rho_5$) are the

263 correlations between the canonical variates ($\mathbf{a}_1^T \boldsymbol{\theta}, \dots, \mathbf{a}_5^T \boldsymbol{\theta}$) which are associated with the vector of

264 energetic parameters and the canonical variates ($\mathbf{b}_1^T \boldsymbol{\eta}, \dots, \mathbf{b}_5^T \boldsymbol{\eta}$) associated with the vector of

265 dietary and animal characteristics. Canonical loadings and cross-loadings represent the

266 correlation between each individual variable with its own canonical variate and with the

267 canonical variate of the other set of variables respectively. These measures of correlation are

268 often the ones used to investigate the role of individual variables in the canonical functions

269 because canonical weights are not robust to multicollinearity (Alpert and Peterson, 1972; Hair et

270 al., 1998). In this study, the loadings and cross loadings of the first canonical functions were used

271 to investigate the correlation between estimated energetic parameters in each decade with dietary

272 and animal characteristics. For example, the canonical loadings of variables in $\boldsymbol{\theta}$ represent the

273 correlation between each individual variable from this set and the canonical variate $\mathbf{a}_1^T \boldsymbol{\theta}$ whereas

274 canonical cross-loadings of variables in $\boldsymbol{\theta}$ represent the correlation between each individual

275 variable in $\boldsymbol{\theta}$ with the canonical variate $\mathbf{b}_1^T \boldsymbol{\eta}$. The CCA for the structural equation model is
276 similar to the one described above for the Strathe et al. (2011) model but with
277 $\boldsymbol{\theta} = (\text{ME}_{M,ijm}, \text{NE}_{M,ijm}, k_{L,ijm}, k_{T,ijm}, k_{G,ijm}, q_{ijm})^T$ and $\mathbf{a} \in \mathbb{R}^6$. A detailed description of the CCA
278 implementation is presented in the Appendix (see Appendix 1).

279 **RESULTS AND DISCUSSION**

280 *Energetic Parameters*

281 Posterior means and 95% CrI of parameters estimated by the univariate Strathe et al.
282 (2011) and the multivariate structural equation models are given in Table 2. Diagnostic plots for
283 assessing fit of all models are presented in the Appendix (see Appendix 2). Variance
284 components' posteriors means and associated 95% CrI for all models are also in the Appendix
285 (see Appendix 3). Energetic parameters are summarized by posterior means and 95% CrI in
286 Table 3. Estimates of the efficiency of utilizing dietary ME for producing milk from both models
287 were similar to the k_L proposed by Moe et al. (1972) and adopted by the NRC (2001).
288 Specifically, the k_L of 0.64 adopted by the NRC (2001) was contained in the 95% CrI from both
289 Strathe et al. (2011) and structural equation models. Moreover, the partial efficiencies of utilizing
290 dietary ME for tissue gain from the two models are also in good agreement with the values
291 proposed by Moe et al. (1971). For instance, the k_G estimates of 0.70 and 0.75 in this study were
292 within the theoretical maximum efficiencies [0.7, 0.8] of utilizing dietary energy for growth in
293 ruminants calculated by Baldwin et al. (1980). Further, estimates of k_G in this study were
294 substantially smaller than the ones from Kebreab et al. (2003) and Strathe et al. (2011) who
295 estimated k_G ranging from 0.83 to 0.88 in European dairy cows. The results from this study
296 corroborate findings of Moe et al. (1971) that dietary ME is used as efficiently or better for

297 concurrent growth than for lactation. Moreover, the estimated k_T 's of 0.80 and 0.89 (Table 3) in
298 this study were in good agreement with the efficiencies estimated by Moe et al. (1971).
299 Additionally, these estimates support the results from Moe et al. (1971) that the indirect net
300 efficiency of producing milk from dietary ME through tissue mobilization and subsequent
301 deposition was similar to k_L . For example, in the structural equation model this efficiency would
302 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
303 important to note that in all models from this study $k_T > k_G$ as originally proposed by Moe et al
304 (1971) but challenged by Kebreab et al. (2003) and Strathe et al. (2011). In particular, the
305 implementation of the Strathe et al. (2011) model with our database and the estimation of
306 efficiencies for which $k_T > k_G$ suggests that there are substantial differences between the
307 European (Kebreab et al., 2003; Strathe et al., 2011) and Northern American databases rather
308 than differences in the models used to estimate energetic efficiencies. It can therefore be
309 suggested that, in US Holstein cows, the efficiency of producing milk from body store reserves is
310 substantially higher than the efficiency of utilizing dietary ME for tissue energy gain as initially
311 proposed by Moe et al. (1971).

312 Energy maintenance requirements estimated in the two models are in Table 3. The NE_M
313 from the Strathe et al. (2011) model ($0.35 \text{ MJ/kg BW}^{0.75} \text{ d}$) was in good agreement with the
314 NE_M adopted by the current US feeding system for dairy cows of $0.33 \text{ MJ/kg BW}^{0.75} \text{ d}$ [or 0.08
315 $\text{Mcal/kg BW}^{0.75} \text{ d}$]. However, the NE_M from the structural equation model ($0.36 \text{ MJ/kg BW}^{0.75} \text{ d}$)
316 was slightly larger compared to NRC (2001) because the value of 0.33 was outside its 95% CrI
317 (Table 3). The ME_M from models in this study was $0.57 \text{ MJ/kg BW}^{0.75} \text{ d}$ (Table 3) which was
318 larger than what would be expected using the default NRC (2001) values for NE_M and k_L [ME_M
319 = $NE_M/k_L = 0.33/0.64 = 0.52 \text{ MJ/kg BW}^{0.75} \text{ d}$ using $k_M = k_L$ as suggested by the NRC, (2001)].

320 However, the ME_M was in good agreement with recent estimates by Agnew and Yan (2000)
321 ranging from 0.49 to 0.67 MJ/kg $BW^{0.75}$ d. A potential increase in maintenance requirements for
322 lactating dairy cows in modern milk production systems was discussed in detail by Agnew and
323 Yan (2000). In particular, the process of genetic selection for milk production may have altered
324 animals' metabolic rates and consequently maintenance requirements. For instance, Yan et al.
325 (1997) estimated fasting heat production of Holstein-Friesian cows of 0.45 MJ/kg $BW^{0.75}$ d and
326 Birnie (1999) reported fasting heat production of 0.39 MJ/kg $BW^{0.75}$ d for non-lactating, non-
327 pregnant dairy cows previously fed at maintenance level. Values from both studies were
328 substantially larger than the current NRC (2001) estimate of NE_M (0.33 MJ/kg $BW^{0.75}$ d).
329 Similarly, five decades ago, high producing lactating cows have been recognized to have a
330 proportional 0.20 increase in ME required for maintenance compared to cows with moderate
331 milk production levels (Flatt et al., 1969; Moe et al., 1970; Van Es et al., 1970). Likewise, beef
332 steers with different residual feed intakes were estimated to have considerably different energy
333 requirements for maintenance (Sainz et al., 2013). A difference of 30% in maintenance
334 requirements was observed between steers in the most efficient and least efficient groups. Two
335 major factors were discussed by Agnew and Yan (2000) for explaining changes in maintenance
336 of dairy cows with genetic selection: larger proportions of body weight as protein mass and
337 enlarged organ sizes in high producing lactating cows due to greater nutrient intakes. The fact
338 that modern dairy cows have larger proportions of body protein mass was confirmed by Ferris et
339 al. (1999) who reported that high genetic merit cows were found to have lower backfat thickness,
340 at comparable body weights, than cows of medium and low genetic merits. Similarly, Veerkamp
341 et al. (1994) estimated a higher lipid-free empty body weight proportion in high genetic merit
342 cows. The influence of body weight protein proportion in maintenance requirements may be

343 explained by the substantial energy cost associated with protein turnover (Baldwin et al., 1980;
344 Agnew and Yan, 2000). Furthermore, cows of high genetic merit may have enlarged organ sizes
345 due to a greater activity of digestive and circulatory tissues to digest and transport nutrients
346 (Reynolds, 1996). Organs involved in these metabolic activities have an important contribution
347 to total maintenance requirements (Baldwin et al., 1980; Baldwin et al., 1985).

348 *Changes in Energetic Parameters over the Years*

349 The effect of the study decade was introduced into energetic parameters through a three
350 level nominal factor. We hypothesized that changes in metabolizability, maintenance and
351 efficiency parameters in the past few decades may elucidate potential mechanisms associated
352 with the increased gross energetic efficiency of dairy cows in modern production systems. The
353 estimated mixed effects (i.e., fixed population parameters plus animal and study deviations from
354 the population) from the different decades were associated with additional variables describing
355 dietary characteristics and animal traits through canonical correlation analysis. We quote Pearson
356 (1900): "... where we find correlation we cannot always predict causation." to point out that the
357 results must be interpreted from a correlation perspective because correlation is a necessary but
358 not sufficient condition for causality. Studies from this database were conducted under distinct
359 biological hypotheses examining various nutritional factors associated with energy utilization in
360 dairy cows. However, the division of this database into decades aimed at representing the
361 changes in animals and diets which would have occurred with the advancement of bioenergetics
362 research and the genetic selection process of animals and feedstuffs over the years.

363 Posterior means and 95% CrI of the parameters estimated in all models of different
364 decades are presented in the Appendix (see Appendix 3). Estimated energetic parameters and
365 associated 95% CrI are presented in Table 4. The metabolizability parameter q from the

366 structural equation model was not different between decades suggesting that the metabolizability
367 of diets did not change across decades in this database. In particular, q was not different between
368 the first and second decade ($P = 0.81$) and the first and third decade ($P = 0.41$). Similarly, k_T was
369 not statistically different among decades for any energy function, suggesting that the efficiency
370 with which cows mobilize body stores to produce milk has not changed over the decades in this
371 database. However, ME_M , NE_M , k_L and k_G all increased over the decades for both energy
372 functions (Table 4). Therefore, it can be suggested that maintenance requirements and the
373 efficiency of utilizing dietary ME increased over the decades in this database. The increased
374 maintenance requirement in high producing dairy cows has been discussed above and by Agnew
375 and Yan (2000) comprehensively. In particular, Agnew and Yan (2000) pointed out that high
376 producing cows have enlarged organ sizes to sustain nutrient transport, digestion and absorption
377 at relatively greater nutrient intakes. Boxplots of dietary and animal characteristics from the three
378 decades are presented in Figure 3. For instance, it is evident that heart rate, milk yield and gross
379 energetic efficiency are largest in cows of the third decade (Figure 3). Furthermore, the
380 efficiency of utilizing dietary ME for milk production in the first and second decades were not
381 different in the univariate model ($P = 0.18$) as well as in the structural equation model ($P = 0.06$),
382 although the estimated k_L in the second decade is slightly outside the 95% CrI of the k_L from the
383 first decade. Conversely, k_L in the third decade was greater in both univariate ($P < 0.01$) and
384 structural equations ($P < 0.01$) models compared to the first decade. Similarly, k_G was greater in
385 the second decade than in the first in both univariate ($P = 0.01$) and structural equation models (P
386 $= 0.04$). Moreover, k_G was also greater in the third decade than in the first in both univariate ($P <$
387 0.01) and structural equation ($P < 0.01$) models. Additionally, it is important to notice that
388 models fitted with energetic parameters depending on the study decade were better supported by

389 the data than models fitted without the study decade. A reduction in the DIC was observed for all
390 energy functions when maintenance requirements and energetic efficiencies were decade
391 specific. Specifically, with the Strathe et al. (2011) model the DIC decreased from $-3,852$ to $-$
392 $3,858$ when the parameters were allowed to depend on the study decade. Likewise, in the
393 structural equation model, the DIC decreased from $-16,030$ to $-16,076$ when parameters were
394 allowed to depend on the study decade.

395 Canonical correlation analysis was used to investigate the degree of association between
396 the set of estimated energetic parameters at different decades and a set of variables describing
397 dietary and animal characteristics. Particularly, loadings and cross-loadings from the CCA were
398 used to identify animal and dietary characteristics that have high correlations with the canonical
399 variate associated with the estimated energetic parameters in different decades. The number of
400 canonical correlations extracted is equal to the number of variables in the smaller set. The
401 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
402 parameters from the Strathe et al. (2011) model and
403 $(r_1 = 0.81, r_2 = 0.50, r_3 = 0.40, r_4 = 0.32, r_5 = 0.17, r_6 = 0.10)$ for the parameters from the
404 structural equation model. The first canonical correlations between the two sets of variables in
405 both models suggest that, as expected, the set of dietary animal characteristics were strongly
406 associated with the energetic parameters from the different decades. The loadings and cross-
407 loadings associated with the first canonical functions are presented in Table 5. In both models,
408 canonical loadings of the energetic parameters were high for the ME_M , NE_M , k_L and k_G
409 suggesting that these four energetic parameters were the most important predictors for the first
410 canonical variate associated with the θ vector. Moreover, the canonical loadings of the dietary
411 and animal variables were high for HB, MY, and dietary EE suggesting that these three variables

412 were the most important animal and dietary contributors for the first canonical function.
413 Similarly, the examination of the cross-loadings of the first canonical function suggests that MY,
414 HB and dietary EE were the variables which present higher correlations with the canonical
415 variate associated with the set of energetic parameters. Likewise, energetic parameters that
416 correlated highly with the first canonical variate of the set of dietary and animal related variables
417 were ME_M , NE_M , k_L and k_G . Furthermore, the redundancy coefficient describes the amount of
418 variance in the energetic parameters' canonical variate explained by the animal and diet related
419 canonical variate. These coefficients were 0.48 and 0.39 for the first canonical function for the
420 Strathe et al. (2011) and structural equation models, respectively.

421 Therefore, using the findings that maintenance requirements and dietary partial
422 efficiencies were different between decades and the results from the CCA, combined dietary and
423 animal factors can be used to explain the increase in the efficiency of utilizing dietary energy.
424 Partial efficiencies of ME utilization for milk production and growth are dependent on
425 stoichiometric and thermodynamic relationships between substrates and animal products
426 (Baldwin et al., 1995). For instance, dietary ME utilization is affected by type of diet (Garrett
427 and Johnson, 1983) because changes in dietary composition will alter the pattern of available
428 nutrients for milk and tissue synthesis. Equally, changes in the partial efficiencies of producing
429 milk and depositing tissue energy may occur through changes in milk and tissue gain
430 compositions. Instead, cows' energy balance status may also alter the energetic efficiency of
431 synthesizing milk: cows mobilizing body fat will use more preformed lipids and less volatile
432 fatty acids to produce milk fat than cows in positive energy balance. From this database, it can be
433 suggested that cows in the last decade were of higher genetic merit than cows in the first two
434 decades although pedigree information was not available. Recent studies have reported that

435 partial efficiencies of ME utilization are similar for cows of different genetic merits (Grainer et
436 al., 1985; Veerkamp and Emmans, 1995) and also for cows in studies conducted in different
437 decades (Strathe et al., 2011). In addition, Bauman et al. (1985) suggested that between animal
438 variation in the partial efficiency of utilizing dietary ME for lactation is negligible and proposed
439 alternative strategies for gains in efficiency such as altered nutrient partitioning and dilution of
440 maintenance. Although cows of different genetic merits have been reported to have similar k_L
441 there is increasing evidence that genetic selection has altered the expression of metabolites
442 associated with nutrient utilization pathways. For instance, Holstein-Friesian cows of different
443 genetic backgrounds have been found to have different expression of gluconeogenic enzymes
444 (White et al., 2012). Moreover, changes in subcutaneous adipose tissue metabolism and gene
445 network expression have been reported in cows of different genetic merits (Khan et al., 2013)
446 and the expression of genes involved in the somatotrophic axis have been found to differ in
447 different strains of Holstein-Friesian cows (McCarthy et al., 2009). A key factor determining the
448 efficiency of dietary energy utilization is the source of dietary energy (Smith, 1988; Vandehaar,
449 1998). Diets in the third decade had higher proportion of EE than diets in the first two decades
450 (Figure 3). It can therefore be hypothesized that a larger proportion of the dietary ME content
451 originated from fat in the third decade. Such differences in the nutrients comprising dietary ME
452 would alter the nutrients available for production functions and consequently alter the
453 efficiencies of producing milk and depositing tissue energy. It is important to note that the
454 dietary EE percentages from the first two decades (means = 2.47 and 2.37 % of DM) were in
455 good agreement with the data (Moe et al., 1971; Moe et al., 1972) used as the basis for the
456 energy evaluation system for the current US feeding system for dairy cows (NRC, 2001).
457 However, the dietary EE percentages in the third decade (mean = 3.71 % of DM) were closer to

458 dietary EE percentages from modern milk production systems (Rossow and Aly, 2013). The
459 increase in k_L with increased dietary fat is well established in the literature and it has been
460 traditionally attributed to a decrease in the heat increment (VandeHaar, 1998) and the relatively
461 low energetic cost of the transfer of absorbed fatty acids to milk fat when compared with the cost
462 of de novo synthesis of fatty acids (Bauman et al., 1985).

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

475 CONCLUSIONS

476 A multivariate framework was proposed to analyze energy balance data from lactating
477 cows which accounted for the variation in ME intake, milk energy output and tissue energy
478 balance and allowed for these traits to have simultaneous and recursive relationships. The
479 proposed model was compared to methods traditionally used to estimate maintenance

480 requirements and energetic efficiencies. Maintenance requirements and partial efficiencies of
481 utilizing dietary energy and body stores, estimated in both models, were similar to values
482 proposed in the literature. In particular, for the proposed model, NE_M was $0.36 \text{ MJ/kg BW}^{0.75} \text{ d}$,
483 k_L , k_G , and k_T were 0.63, 0.70 and 0.89 respectively. Additional analyses were conducted in
484 which energetic parameters were allowed to depend on the decade of the study to investigate
485 potential changes in maintenance requirements and partial efficiencies across decades. For both
486 models, NE_M , k_L and k_G increased for the more recent decades while k_T remained unchanged. The
487 increase in maintenance requirements in contemporary milk production systems is consistent
488 with the literature that describes increased fasting heat production in cows of higher genetic
489 merit. The increase in the efficiency of utilizing dietary energy was partially attributed to the
490 changes in dietary composition, in particular to the increase in dietary EE to levels closer to
491 those currently observed in milk production systems. Finally, the estimated energetic parameters
492 from this study can be used to update maintenance requirements and partial efficiencies of
493 energy utilization in Northern American feeding systems.

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625

TABLES AND FIGURES

626 **Table 1.** Descriptive statistics of dietary nutrient composition and animal status¹.

Item ¹	Mean	Min	Max	SD
NDF (% of DM)	33.7	14.9	76.1	7.2
ADF (% of DM)	19.7	7.7	47.1	4.28
ME (MJ/kg DM)	10.9	6.9	14.6	0.9
CP (% of DM)	16.3	5.2	23.5	2.29
EE (% of DM)	2.7	1.0	7.0	1.0
DMI (kg/d)	16.8	6.2	29.4	4.30
GEI (MJ/d)	318.5	113.4	584.7	84.1
MEI (MJ/d)	182.1	66.3	348.2	43.1
FECGE (MJ/d)	109.0	23.4	232.6	34.1
UGE (MJ/d)	10.6	2.9	25.6	3.2
CH ₄ (MJ/d)	16.8	3.8	30.7	5.0
TEB (MJ/d)	2.6	-86.0	78.8	1.33
MILKGE (MJ/d)	68.6	0.3	156.5	29.3
Milk Yield (kg/d)	23.9	0.1	56.6	10.34
Milk CP (%)	3.23	2.30	5.75	0.38
Milk Fat (%)	3.58	1.43	7.60	0.75
DIM	160.2	11	488	81.5
BW (kg)	608.1	350.7	854.1	72.4
AGE (Months)	64.3	25	185	25.5

638 ¹NDF is the dietary neutral detergent fiber, ADF is the dietary acid detergent fiber, ME is the dietary ME content,
639 CP is the dietary crude protein, EE is the dietary ether extract, GEI is the gross energy intake, MEI is the
640 metabolizable energy intake, FECGE is the fecal gross energy output, UGE is the urinary gross energy output, CH₄
641 is the methane emission, TEB is the tissue energy balance, MILKGE is the milk gross energy output and AGE is the
642 cow age in months.

643

644 **Table 2.** Parameters posterior means and 95% Credible Intervals using the Strathe et al. (2011)
 645 and the structural equation (SEqM) models¹.

Parameter	Strathe et al. (2011)	SEqM
β_0	-0.35 (-0.38, -0.32)	-
β_1	0.62 (0.60, 0.64)	0.57 (0.56, 0.58)
β_2	-0.83 (-0.87, -0.79)	-0.36 (-0.38, -0.34)
β_3	-0.80 (-0.84, -0.76)	-0.40 (-0.42, -0.37)
λ_{21}	-	0.63 (0.61, 0.64)
$\lambda_{23}^{(1)}$	-	-0.90 (-0.92, -0.88)
$\lambda_{23}^{(2)}$	-	-0.89 (-0.91, -0.87)
λ_{31}	-	0.70 (0.68, 0.72)
λ_{32}	-	-1.11 (-1.13, -1.09)

646 ¹ β 's are the regression coefficients and λ 's are the structural parameters of the structural equation
 647 model. Note that β 's in the two different models represent different parameters which are not
 648 directly comparable.

649 **Table 3.** Energetic parameters posterior means and 95% Credible Intervals using the Strathe et
 650 al. (2011) and the structural equation (SEqM) models¹.

Parameter	Strathe et al. (2011)	SEqM
q	-	0.57 (0.56, 0.58)
ME_M	0.57 (0.53, 0.60)	0.57 (0.54, 0.59)
NE_M	0.35 (0.32, 0.38)	0.36 (0.34, 0.38)
k_L	0.62 (0.60, 0.64)	0.63 (0.61, 0.64)
k_T	0.80 (0.75, 0.84)	0.89 (0.87, 0.91)
k_G	0.75 (0.70, 0.79)	0.70 (0.68, 0.72)

651 ¹ q is the metabolizability (MJ ME/MJ GE), ME_M is the metabolizable energy requirements for maintenance
 652 (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
 653 intake for milk production (MJ Milk/MJ ME), k_T is the efficiency of utilizing body stores for milk production (MJ
 654 Milk/MJ Tissue) and k_G is the efficiency of utilizing ME intake for tissue gain (MJ Tissue/MJ ME).

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657 **Table 4.** Energetic parameters posterior means and 95% Credible Intervals using the Strathe et
658 al. (2011) and the structural equation (SEqM) models for the three decades for which studies
659 were conducted.

Parameter ¹	Decade	Strathe et al. (2011)	SEqM
q	1963 - 1973	-	0.56 (0.55, 0.58)
q	1974 - 1983	-	0.57 (0.55, 0.59)
q	1984 - 1995	-	0.57 (0.55, 0.59)
ME_M	1963 - 1973	0.50 (0.47, 0.54)	0.51 (0.48, 0.54)
ME_M	1974 - 1983	0.58 (0.53, 0.63)	0.59 (0.55, 0.63)
ME_M	1984 - 1995	0.70 (0.64, 0.75)	0.74 (0.70, 0.78)
NE_M	1963 - 1973	0.30 (0.27, 0.33)	0.31 (0.28, 0.33)
NE_M	1974 - 1983	0.36 (0.32, 0.41)	0.37 (0.34, 0.41)
NE_M	1984 - 1995	0.48 (0.42, 0.53)	0.52 (0.47, 0.56)
k_L	1963 - 1973	0.60 (0.58, 0.62)	0.60 (0.58, 0.62)
k_L	1974 - 1983	0.62 (0.59, 0.65)	0.63 (0.60, 0.65)
k_L	1984 - 1995	0.68 (0.65, 0.71)	0.70 (0.68, 0.73)
k_T	1963 - 1973	0.82 (0.76, 0.87)	0.90 (0.89, 0.92)
k_T	1974 - 1983	0.81 (0.73, 0.87)	0.90 (0.88, 0.93)
k_T	1984 - 1995	0.79 (0.70, 0.86)	0.90 (0.88, 0.92)
k_G	1963 - 1973	0.68 (0.63, 0.73)	0.66 (0.64, 0.69)
k_G	1974 - 1983	0.79 (0.72, 0.87)	0.70 (0.67, 0.73)
k_G	1984 - 1995	0.83 (0.77, 0.91)	0.78 (0.75, 0.80)

660 ¹ q is the metabolizability (MJ ME/MJ GE), ME_M is the metabolizable energy requirements for maintenance
661 (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
662 intake for milk production (MJ Milk/MJ ME), k_T is the efficiency of utilizing body stores for milk production (MJ
663 Milk/MJ Tissue) and k_G is the efficiency of utilizing ME intake for tissue gain (MJ Tissue/MJ ME).

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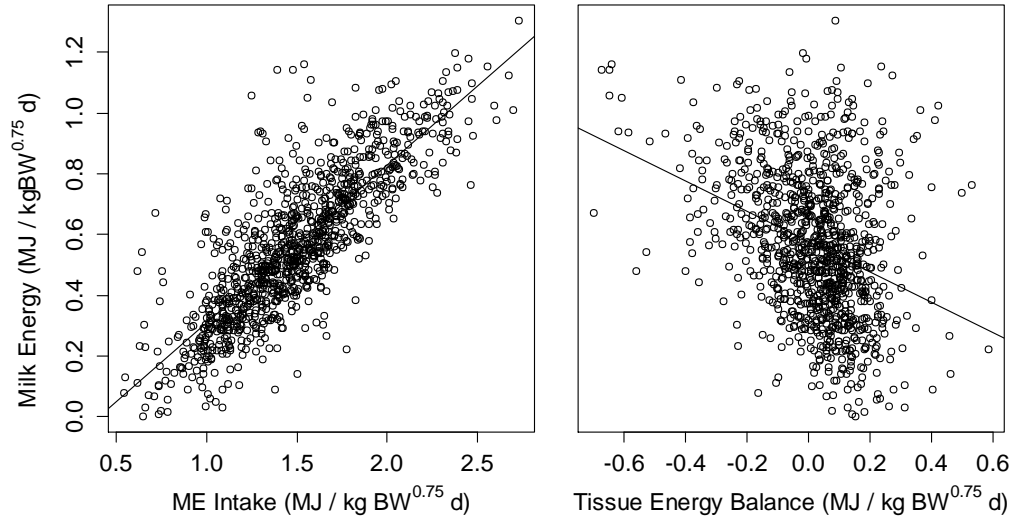
666 **Table 5.** Canonical loadings and cross-loadings for the first canonical variate of the dietary and
667 animal characteristics and estimated energetic parameters in Strathe et al. (2011) and structural
668 equation (SEqM) models.

Variable ¹	Strathe et al. (2011)		SEqM	
	Loading	Cross-loading	Loading	Cross-loading
η				
HB	0.76	0.64	-0.77	-0.63
DIP	-0.29	-0.25	0.30	0.24
MY	0.87	0.73	-0.88	-0.72
MP	-0.27	-0.23	0.26	0.21
MF	-0.04	-0.03	0.04	0.03
NDF	<0.01	<0.01	0.03	0.03
CP	0.52	0.44	-0.56	-0.45
EE	0.72	0.61	-0.68	-0.55
TEB	0.03	0.03	-0.04	-0.03
θ				
ME _M	0.88	0.73	-0.93	-0.75
NE _M	0.93	0.78	-0.96	-0.78
k_L	0.90	0.75	-0.93	-0.75
k_G	0.94	0.79	-0.93	-0.75
k_T	-0.32	-0.26	0.07	0.05
q	-	-	-0.28	-0.23

669 ¹ η is the vector of dietary and animal characteristics and θ is the vector of estimated energetic parameters in each
670 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
671 the milk crude protein (%), MF is the milk fat (%), NDF is the dietary NDF (% of DM), CP is the dietary crude
672 protein (% of DM), EE is the dietary EE (% of DM) and TEB is the tissue energy balance (MJ/d). Further, q is the
673 metabolizability (MJ ME/MJ GE), ME_M is the ME requirement for maintenance (MJ/kg BW^{0.75} d), NE_M is the net
674 energy requirement for maintenance (MJ/kg BW^{0.75} d), k_L is the efficiency of utilizing dietary ME for milk
675 production (MJ Milk/MJ ME), k_T is the efficiency of utilizing body stores for milk production (MJ Milk/MJ Tissue)
676 and k_G is the efficiency of utilizing dietary ME for tissue gain (MJ Tissue/MJ ME).

677

678 **Figure 1.** Daily milk energy output (MJ/kg BW^{0.75} d) versus daily ME intake (MJ/kg BW^{0.75} d)
679 or daily tissue energy balance (MJ/kg BW^{0.75} d) with linear trend lines included.



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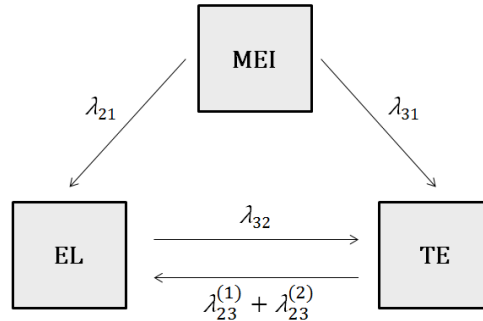
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690 **Figure 2.** Schematic diagram representing the structural equation model with recursive and
 691 simultaneous relationships of energy traits.

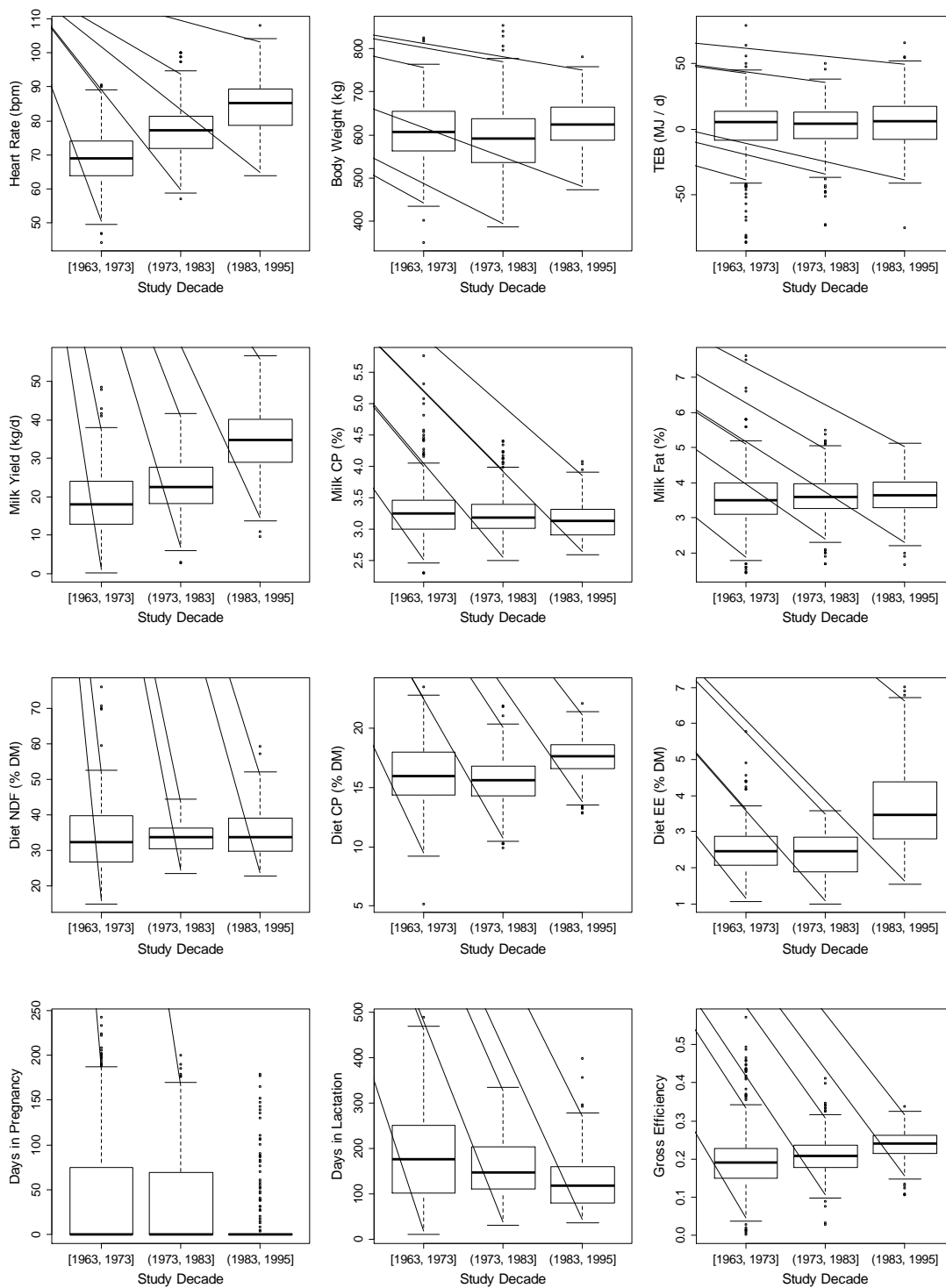


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693 Note: MEI is the metabolizable energy intake (MJ/kg BW^{0.75} d), EL is the milk energy output
 694 (MJ/kg BW^{0.75} d) and TE is the tissue energy balance (MJ/kg BW^{0.75} d). We use the notation
 695 from Gianola and Sorensen (2004) where λ 's are the structural parameters representing the
 696 gradients of one energy trait with respect to another and not fluxes. In this notation, λ_{23} is the
 697 sum of two parameters which individually represent the gradient when cows are in positive or
 698 negative tissue energy balance. It is important to note that in Equation [4], $\lambda_{23}^{(1)}$ vanishes when
 699 the cow is in negative tissue energy balance whereas $\lambda_{23}^{(2)}$ vanishes when the cow is in positive
 700 tissue energy balance.

701

702 **Figure 3.** Boxplots of dietary characteristics and animal traits for the three decades.



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