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# Energetic efficiency and the first law: the California net energy system revisited

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**ABSTRACT:** Models of energy utilization used in livestock production predict input:output relationships well, for all the wrong reasons. Predictive accuracy in such models is not due to fidelity to biochemistry and laws of thermodynamics, but because they were developed to predict accurately, often with little regard to biochemical consistency. Relatively static linear statistical models limit thermodynamically relevant descriptions of energy utilization, especially maintenance, in growing beef cattle and are inadequate research tools, in either ordinary least squares (OLS) or Bayesian frameworks. Metabolizable energy intake (MEI) at recovered energy (RE) = 0 (ME<sub>m</sub>) and efficiencies of ME utilization for maintenance (k<sub>m</sub>) and gain (k<sub>g</sub>) were estimated for 3 independent data sets using OLS or Bayesian frameworks. Estimates of ME<sub>m</sub> differed (P < 0.05) between OLS and Bayesian estimates and were not unique, indicating model misspecification. Bayesian estimates of ME<sub>m</sub> were monotonic, positive, and nonlinear f(MEI); the range was from 6.74 to 14.8 Mcal/d. Estimates of k<sub>m</sub>, the ratio of heat energy (HE) at MEI = 0 to ME<sub>m</sub>, for the 3 data sets averaged 0.590 for OLS solutions, or 0.616 for the first derivative (k<sub>m</sub>, dHE/dMEI for RE = 0) of

a first-order function. The first derivative (dHE/dMEI) of the OLS function was > 1.0 for MEI > 22.1 Mcal/d, counter to the laws of thermodynamics and indicated model misspecification. The Bayesian estimate of k<sub>m</sub> (0.420) differed (P < 0.05) from the OLS estimate and was consistent with the efficiency of ATP synthesis. Efficiency of ME use for gain for RE > 0 (k<sub>g</sub>, OLS solutions) averaged 0.397, solutions were nonunique and single-variable OLS models were misspecified (P < 0.050) for 2 of the 3 data sets. The OLS estimate of k<sub>g</sub> differed (P < 0.05) from the estimate of k<sub>g</sub> (0.676) determined in a Bayesian framework; the latter was calculated as dRE/dMEI for RE > 0. For OLS estimates k<sub>m</sub> > k<sub>g</sub>; for estimates determined in a Bayesian framework k<sub>m</sub> < k<sub>g</sub>, the former is inconsistent, while the latter is consistent with the thermodynamic favorability of reactions underlying maintenance and gain. Our results show that the use of relatively fixed coefficients of maintenance in current feeding standards, mathematical descriptions of metabolic processes and concepts regarding efficiencies of energy utilization in those systems need modification to be consistent with animal biology and the laws of thermodynamics.

**Key words:** beef cattle, efficiency, maintenance

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## INTRODUCTION

Lofgreen and Garrett (1968) described relationships among metabolizable energy intake

(MEI), heat energy (HE), and recovered energy (RE) using empirical linear models; estimators were determined in ordinary least squares (OLS) frameworks. Estimates of efficiencies of ME utilization for maintenance (k<sub>m</sub>) and gain (k<sub>g</sub>) (k<sub>m</sub> > k<sub>g</sub>) were consistent with contemporary dogma, but differ from those based on maintenance as an ATP requirement and of the synthesis

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of biomass, in which  $k_m < k_g$ , the latter is consistent with thermodynamic favorability of reactions underlying the mechanisms. The [NRC \(1984\)](#) described  $k_m$  and  $k_g$  as varying with ME density, but provided static estimates for HE at MEI = 0 ( $H_eE$ ) and MEI at RE = 0 ( $ME_m$ ). [Koong et al. \(1983\)](#) suggested that  $H_eE$  and  $ME_m$  are dynamic, varying with metabolic state, previous nutritional history, growth trajectory, diet type, and feeding level.

In any animal, maintenance and gain are concomitant processes; [Lofgreen and Garrett \(1968\)](#) described maintenance and gain as hierarchical processes. While the net energy system and estimators within it have been very useful in improving efficiency of animal feeding, in large part, many estimators were developed as mathematical solutions to mathematical problems and were not intended to be specific, constant, or final estimates directly related to metabolic processes.

This study was undertaken to evaluate data and concepts forming the basis for prediction of input–output relationships in growing beef cattle ([Lofgreen and Garrett, 1968](#)) using tools and techniques unavailable to investigators in the 1960s. We hypothesized that if the processes comprising maintenance and gain are described as a concomitant first-order function of MEI and a statistical relationship exists, then efficiencies of ME utilization may be described that are consistent with theoretical and thermodynamic favorability of the biochemical reactions underlying maintenance and gain.

## MATERIALS AND METHODS

### *Units of Measurement*

Energy terms are those found in “Nutritional Energetics of Domestic Animals and Glossary of Energy Terms ([NRC, 1981](#)). Energy is not a nutrient, but rather a dynamic property of feed and energy utilization by animals must conform to the first law of thermodynamics; energy can be neither created nor destroyed, only transformed. In 1981, the Subcommittee on Biological Energy published a monograph ([NRC, 1981](#)) describing utilization of dietary energy; the reader is encouraged to visit this publication and the review on energy systems by [Ferrell and Oltjen \(2008\)](#).

Metabolizable energy intake is intake energy not excreted in feces, urine or as energy containing gasses; MEI = sum of HE (heat energy produced by an organism) and RE (recovered energy). Metabolizable energy intake represents the

physiological fuel used at the cellular level ([Baldwin, 1995](#)).

### *Animal Measurements*

Data were obtained from the literature ([Garrett et al., 1964](#); [Lofgreen and Garrett, 1968](#)) and from a study conducted at the USDA Beltsville Agricultural Research Center (reported in part in: [Reynolds and Tyrrell, 1989](#) and [Reynolds et al, 1991](#); data provided courtesy of Christopher K. Reynolds, University of Reading, UK, personal communication). Data found in Table 1 of [Lofgreen and Garrett \(1968\)](#) were obtained from 5 comparative slaughter studies involving a total of 208 steers and heifers. Diets contained from 2 to 100% roughage and were fed at levels of intake from maintenance to ad libitum. Metabolizable energy intakes were from  $0.100 \text{ Mcal ME/BW}^{0.750} \times \text{d}^{-1}$  to  $0.335 \text{ Mcal ME/BW}^{0.750} \times \text{d}^{-1}$  (6.41 to 25.6 Mcal/d) and energy retention was from  $-0.0069$  to  $0.078 \text{ Mcal/BW}^{0.750} \times \text{d}^{-1}$  ( $-0.449$  to 6.19 Mcal/d). Data from Table 1 in [Lofgreen and Garrett \(1968\)](#) were used for parameter estimation of OLS models and external evaluation of a first-order function.

Data from Table 2 of [Lofgreen and Garrett \(1968\)](#) were used as the basis for first-order model development and parameter estimation for OLS models. Those data were from a comparative slaughter study ([Garrett et al., 1964](#)) in which Hereford steers ( $n = 118$ ) and heifers ( $n = 118$ ) were fed a basal diet consisting of (100% DM basis) 50% alfalfa hay, 25% oat hay, 24% cottonseed meal, 1% dicalcium phosphate and Vitamin A added to provide 910 IU/kg. Cattle were fed this diet at approximately maintenance (reported by [Garrett et al., 1964](#) as  $0.075 \text{ BW}^{0.750}$ ,  $n = 50$  of either sex) or were fed the basal diet with either steam flaked barley or steam flaked milo ad libitum (“large gain”,  $n = 50$  of either sex) or the basal diet plus enough grain to produce approximately half the gain of ad libitum fed cattle (“intermediate gain”,  $n = 18$  of either sex). Metabolizable energy intakes were from  $0.140 \text{ Mcal ME/BW}^{0.750} \times \text{d}^{-1}$  to  $0.301 \text{ Mcal ME/BW}^{0.750} \times \text{d}^{-1}$  (8.94 to 23.9 Mcal/d) and energy retention was from 0.010 to 0.092 ( $\text{Mcal/BW}^{0.750} \times \text{d}^{-1}$ ) or from 0.686 to 6.88 Mcal/d. Energy retention was measured in both trials as described by [Lofgreen \(1964\)](#). In the growing animal, RE is the energy accreted in body tissue, but RE refers to any net productive utilization of energy. Each data point described in Table 1 or Table 2 of [Lofgreen and Garrett \(1968\)](#) is the mean of either 6 or 8 animals. In this report, results from analysis of data found in [Lofgreen and](#)

Garrett (1968) Tables 1 and 2 are referred to as **LG1** (Table 1 data) or **LG2** (Table 2 data). Data from the USDA Beltsville Agricultural Research Center (**BARC** data) were for a study in which 59 cross-bred heifers (colloquially termed #1 Okies) were fed diets that were either (100% DM basis) 74.5% ground alfalfa hay, 21.1% ground corn and 3.7% soybean meal (n = 30) or 24.5% ground alfalfa hay, 63.2% ground corn and 11.0% soybean meal (n = 29). Diets were fed at slightly greater than estimated maintenance (0.140 Mcal ME/BW<sup>0.750</sup> × d<sup>-1</sup>; 10.7 Mcal ME/d) or at approximately twice that required for maintenance (0.270 Mcal ME/BW<sup>0.750</sup> × d<sup>-1</sup>; 18.4 Mcal ME/d). Dietary nitrogen content (2.78%) was greater than required for cattle fed at greater ME intakes because of greater nitrogen content of alfalfa hay and to meet the nitrogen requirements for cattle fed at lesser ME intakes. Energy

and nitrogen balance measurements were made for 7 d in respiration chambers; respiratory calorimetry estimates HE from gaseous exchange and RE is determined by difference (MEI – HE) unlike studies reported by Lofgreen and Garrett (1968) in which RE was measured by comparative slaughter. The first law, conservation of energy, requires that MEI = HE + RE; measurement of MEI and RE allowed Lofgreen and Garrett (1968) to calculate HE and for the calculation of RE = MEI – HE, for BARC data. In the growing animal, sources of HE may be basal metabolism, locomotion, net costs of fat and protein synthesis, digestion and absorption to name a few. In the growing animal, HE is partitioned into either ME<sub>m</sub> or heat of product formation (H<sub>r</sub>E); H<sub>r</sub>E is a consequence of the second law of thermodynamics; entropy must increase for a reaction to proceed. Entropy is a measure of

**Table 1.** Estimates of energy utilization for Model 1 using data from Lofgreen and Garrett (1968) and Reynolds et al., (1991)<sup>1</sup>

Parameter estimate	Data set		
	LG1 <sup>2</sup>	LG2 <sup>3</sup>	BARC <sup>4</sup>
HE at MEI = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.0774	0.0820	0.0529
95% CI about HE at MEI = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.0715 to 0.0837	0.0788 to 0.0853	0.0479 to 0.0585
95% prediction interval about HE at MEI = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.660 to 0.907	0.0762 to 0.0883	0.0414 to 0.0676
HE at MEI = 0 (Mcal/d)	5.08	5.43	4.20
95% CI about HE at MEI = 0 (Mcal/d)	4.71 to 5.48	5.23 to 5.66	3.36 to 5.04
95% prediction interval about HE at MEI = 0 (Mcal/d)	4.29 to 6.00	5.00 to 5.92	2.04 to 6.37
MEI at HE = MEI (ME <sub>m</sub> , Mcal/ BW <sup>0.750</sup> × d <sup>-1</sup> )	0.124	0.124	0.108
95% CI about ME <sub>m</sub> (Mcal/ BW <sup>0.750</sup> × d <sup>-1</sup> )	0.114 to 0.134	0.122 to 0.126	0.104 to 0.113
95% prediction interval about ME <sub>m</sub> (Mcal/ BW <sup>0.750</sup> × d <sup>-1</sup> )	0.106 to 0.145	0.116 to 0.132	0.0864 to 0.136
MEI at HE = MEI (ME <sub>m</sub> , Mcal/d)	7.99	8.20	9.05
95% CI about ME <sub>m</sub> (Mcal/d)	7.58 to 8.43	8.03 to 8.39	8.64 to 9.46
95% prediction interval about ME <sub>m</sub> (Mcal/d)	6.78 to 9.42	7.59 to 8.87	7.02 to 11.1
k <sub>m</sub> for data scaled by BW <sup>0.750</sup>	0.626	0.663	0.488
k <sub>m</sub> for data unscaled by BW <sup>0.750</sup>	0.635	0.663	0.464

<sup>1</sup>log HE = H<sub>e</sub>E + b × MEI; HE = heat energy, H<sub>e</sub>E = heat energy at ME intake (MEI) = 0, b = parameter estimate (dimensionless).

<sup>2</sup>Data from Lofgreen and Garrett (1968) Table 1.

<sup>3</sup>Data from Lofgreen and Garrett (1968) Table 2.

<sup>4</sup>Data courtesy of Christopher K. Reynolds, University of Reading, UK from studies reported in part Reynolds et al. (1991).

**Table 2.** Effect of forage intake on apparent ME utilization<sup>1</sup>

Parameter estimate	Forage intake	
	100%	2 to 40%
MEI at RE = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.140	0.119
95% CI about MEI at RE = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.135 to 0.146	0.114 to 0.125
95% prediction interval about MEI at RE = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.129 to 0.153	0.106 to 0.135
MEI at RE = 0 (Mcal/d) FI <sup>a</sup> (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	0.134	0.119
95% CI about MEI at RE = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> ) FI <sup>a</sup>	0.128 to 0.139	0.115 to 0.124
95% prediction interval about MEI at RE = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> ) FI <sup>a</sup>	0.122 to 0.147	0.106 to 0.134

<sup>1</sup>log HE = H<sub>e</sub>E + b × MEI; HE = heat energy, H<sub>e</sub>E = heat energy at ME intake (MEI) = 0, b = parameter estimate (dimensionless), data from Lofgreen and Garrett (1968) Table 1

<sup>a</sup>FI = forced intercept of 0.077 Mcal/BW<sup>0.750</sup> × d<sup>-1</sup>

energy unavailable to do work; the second law simply states that since no reaction is 100% efficient, you can't even break even.

### Mathematical Representations of Energy Transactions

The following models were evaluated:

$$\log HE_i = H_e E + b x MEI_i + r_i \quad \text{Model 1}$$

where:

$HE_i$  = total energy losses as heat (either as Mcal/BW<sup>0.750</sup> × d<sup>-1</sup> or Mcal/d) by the *i*th individual

$H_e E$  = log HE at MEI = 0 (either as Mcal ME/BW<sup>0.750</sup> × d<sup>-1</sup> or as Mcal ME/d)

$MEI_i$  = ME intake (either as Mcal ME/BW<sup>0.750</sup> × d<sup>-1</sup> or as Mcal ME/d) by the *i*th individual

$b$  = parameter estimate (no dimension)

$r_i$  = (observed– predicted) (either as Mcal/BW<sup>0.750</sup> × d<sup>-1</sup> or Mcal/d) by the *i*th individual

$$RE_i = a + k_g x MEI_i + r_i \quad \text{Model 2}$$

where:

$RE_i$  = recovered energy (either as Mcal ME/BW<sup>0.750</sup> × d<sup>-1</sup> or as Mcal ME/d) by the *i*th individual

$a$  = RE at MEI = 0 (either as Mcal /BW<sup>0.750</sup> × d<sup>-1</sup> or as Mcal /d); all other abbreviations have been defined.

The laws of thermodynamics place limits on the efficiency of energy utilization, defined as the ratio of useful work by a system to the energy supplied to that system; therefore the limits of  $k_m$  and  $k_g$  must necessarily be from 0 to 1. Lofgreen and Garrett (1968) did not estimate  $k_g$  as described in Model 2. First,  $k_m$  was determined as  $f(\text{ME}, \text{Mcal/kg})$ ;  $k_g$  was then calculated as  $f(k_m)$  (Moe and Tyrrell, 1973).

$$RE_i = \left[ MEI_i - \left( a_1 e^{k_1 MEI_i} + a_2 e^{k_2 MEI_i} \right) \right] \times k_g + r_i \quad \text{Model 3}$$

where:

$a_n$  = state variables (Mcal MEI/d or Mcal MEI/BW<sup>0.75</sup> × d<sup>-1</sup>)

$k_n$  = rate constants ((Mcal MEI/d)<sup>-1</sup> or ((Mcal MEI/BW<sup>0.75</sup> × d<sup>-1</sup>)<sup>-1</sup>); all other abbreviations have been defined

Solutions for Models 1 and 2 were calculated using the lm package in R (R Core Team, 2013) for all 3 data sets; parametric stability of Model 1 was further evaluated using WinBUGS in R (R Core Team, 2013); for Model 1, informed priors were:  $H_e E = \log(0.077 \text{ Mcal/BW}^{0.750} \times \text{d}^{-1})$

and  $b = 0.00165$  so that  $ME_m = 0.124 \text{ Mcal/BW}^{0.750} \times \text{d}^{-1}$ .

For Model 3, WinBUGS in R was employed (R Core Team, 2013) for data from Table 2 of Lofgreen and Garrett (1968). In Bayesian analysis, inferences are based on posterior densities which combine information on prior densities and that for observed data; for this study prior densities were based on information from prior knowledge determined from biochemical pathways describing utilization of ME in growing and finishing beef cattle (Baldwin, 1968, 1995; Kennedy and Calvert, 2014). Prior knowledge for use in Model 3 provided substantial information for the model (state variables and rate constants); priors were established so that  $k_m \sim 0.4$  and  $k_g \sim 0.65$ . For all models, energy data were either scaled by BW<sup>0.750</sup> or were raw (unscaled).

For all Markov chain Monte Carlo (MCMC) simulations, 100,000 simulations were performed as a “burn-in”; it was assumed that chain ( $n = 4$ ) convergence was achieved after 100,000 simulations. Parameter estimation was evaluated for the next 100,000 simulations. Model validity (Models 1 and 2) was evaluated, internally, by OLS regression of predicted values against observed values, by bootstrapping (Efron, 1979) and by Lin's concordance coefficient (Lin, 1989) an estimate used to evaluate the degree to which pairs of observations fall on the line of unity. Predictive accuracy of Model 3 was evaluated internally by OLS regression of predicted values against observed values and externally using data from LG1 (Lofgreen and Garrett, 1968) and data from BARC. When, for single-variable OLS regressions of **PREDICTED** =  $f(\text{OBSERVED})$ , if slopes differed significantly from 1 or intercepts from 0, the models were considered invalid. Models 1 and 2 were further considered invalid if bootstrapped parameter estimates were different from OLS parameter estimates. Model 3 was externally invalid if the model failed to predict RE for LG1 and BARC or if estimates of  $k_m$  and  $k_g$  were biologically or thermodynamically impossible ( $k_m$  or  $k_g$  less than 0 or greater than 1). Appropriateness of Models 1 and 2 were further evaluated using lack of fit tests (Mason et al., 2003). The finding of a significant *F* ratio for a lack of fit test for OLS models is an indication that the response between predictor and response variables is not linear.

It is assumed in OLS models that error terms follow a normal probability distribution; it may be expected then that corresponding residuals are a sample from the normal density. To determine if this expectation was met, observed MEI (Models 1 and 2, scaled by BW<sup>0.750</sup> and unscaled) were

tested in order (LG1, LG2 and BARC data) for log HE (observed – predicted) and RE (observed – predicted), again scaled by  $BW^{0.750}$  and unscaled. The runs statistic (Swed and Eisenhart, 1943) was employed to test the assumption that errors are randomly distributed by examining signs of the corresponding residuals. Tests for skewness (D'Agostino, 1970) and kurtosis (Anscombe and Glynn, 1983) of the residuals were computed in the moments utility of R (R Core Team, 2013) in which the probability distribution of the third (skewness) and fourth (kurtosis) central moments were determined (Komsta and Novometsky, 2007). Residual plots ( $r_i$  vs. MEI<sub>*i*</sub>) for Models 1 and 2, LG1, LG1, and BARC data, scaled by  $BW^{0.750}$  and unscaled, were evaluated to determine if residual distribution appeared to be random, or if patterns existed (Gunst and Mason, 1980; Baldwin, 1995).

## RESULTS AND DISCUSSION

### *Determination of H<sub>e</sub>E and ME<sub>m</sub>*

Estimated H<sub>e</sub>E for LG1 data was less ( $P < 0.050$ ) than that for LG2 data; both of these estimates were greater ( $P < 0.050$ ) than the estimate of H<sub>e</sub>E for BARC (Table 1). For all 3 data sets the model was internally valid ( $P < 0.050$ ) when evaluated (single-variable OLS) as **PREDICTED** = f(**OBSERVED**);  $\rho_c$  (Lin's concordance coefficient) were 0.937, 0.989, and 0.964 for LG1, LG2, and BARC data, respectively. Lin's concordance coefficient of 1.0 indicates perfect concordance and  $\rho_c$  of 0 indicates a complete lack of relationship between vectors **PREDICTED** and **OBSERVED**. For Model 1, no bootstrapped estimator was same as the OLS parameter estimate ( $P < 0.050$ ) indicating model misspecification; a nonlinear relationship exists between log HE and MEI. Although response data are transformed (log HE as opposed to HE) the relationship is linear, or additive (Gunst and Mason, 1980). Transformation of the response variable may lead to linearization of the relationship with some predictor variables while, at the same time changing the relationship with others (Gunst and Mason, 1980). For the OLS regression of  $HE = f(\log MEI)$ , using unscaled LG1 and LG2 data, HE calculated for  $MEI < \sim 3.6$  Mcal/d is less than 0; when calculated for BARC data,  $HE < 0$  for  $MEI < \sim 4.5$  Mcal/d. Such solutions are possible mathematically, but are biologically impossible. Perhaps Lofgreen and Garrett (1968) recognized this fact and chose to transform HE. Only H<sub>e</sub>E (OLS estimate) reported for LG1 data from did not

differ from  $H_eE = 0.077 \times BW^{0.750}$  (Mcal/d) reported by Lofgreen and Garrett (1968) and found in NRC (1984). For LG1 data, Lofgreen and Garrett (1968) reported log HE at  $MEI = 0$  ( $kcal/BW^{0.750} \times d^{-1}$ ) to be 1.8851 (antilog =  $0.07675$  Mcal/ $BW^{0.750} \times d^{-1}$ ) with limits from 0.0718 to 0.082 Mcal/ $BW^{0.750} \times d^{-1}$ . The range reported by Lofgreen and Garrett (1968) is the intercept  $\pm$  root mean square residual. Estimates from the lm package in R (R Core Team, 2013) for the same data, were slightly different; H<sub>e</sub>E was estimated to be  $1.8867 \pm 0.0341$  (95% CI = 0.0715 to 0.0837 Mcal/ $BW^{0.750} \times d^{-1}$ ). Although estimates are slightly different in magnitude, conclusions regarding energy utilization would remain similar.

### *Transformation and CI*

It should be noted that transformation of HE to log HE causes 95% CI of HE for Model 1, expressed as  $Mcal/BW^{0.750} \times d^{-1}$ , to be narrower at  $MEI = 0$  ( $0.0122$  Mcal/ $BW^{0.750} \times d^{-1}$ ) than at  $0.343$  Mcal/ $BW^{0.750} \times d^{-1}$ , a point equidistant from mean MEI; at that point the 95% CI is  $0.0332$  Mcal/ $BW^{0.750} \times d^{-1}$ . For the equation  $HE = 78.97 \times e^{0.00371MEI}$  (LG1 data), estimated H<sub>e</sub>E ( $0.0790$  kcal/ $BW^{0.750} \times d^{-1}$ ) is not different from the Model 1 estimate of H<sub>e</sub>E for LG1 data. The CI (95%) for the previous equation, at  $MEI = 0$ , is 0.0690 to 0.0889 Mcal/ $BW^{0.750} \times d^{-1}$ , 1.64 times greater than the interval for Model 1. Conclusions regarding variability in heat production may differ when response variables are log transformed. Although it would have been very easy for Lofgreen and Garrett (1968) to describe HE as  $78.97 \times e^{0.00371MEI}$ , at that time, it was difficult to find solutions to such functions (Willcox, 1971), thus the use of Model 1 by Lofgreen and Garrett (1968) provided a known compromise between the best description of the underlying biology and a practical solution.

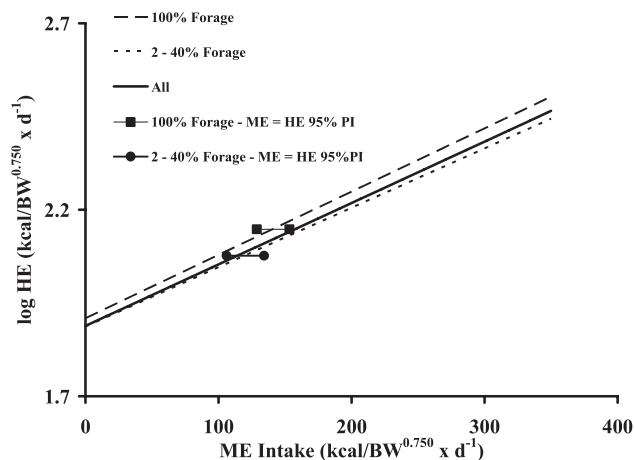
### *Suitability of Forced Intercept*

Lofgreen and Garrett (1968) reported that for LG1 heifers fed 100% forage diets ad libitum, ME<sub>m</sub> was  $0.131$  Mcal/ $BW^{0.750}$  for a forced intercept of  $\log 77$  kcal/ $BW^{0.750} \times d^{-1}$ . The solution to the equation:  $HE = \log(77) + 0.00174 \times MEI$  (kcal/ $BW^{0.750} \times d^{-1}$ ), for the point at which  $HE = MEI$ , using the nls package in R (R Core Team, 2013) was  $0.130$  Mcal/ $BW^{0.750}$ ; essentially the same. Glen Lofgreen used a Marchant rotary calculator (W. N. Garrett, University of California, Davis, late Professor Emeritus of Animal Science, personal

communication) for data analysis; the lack of computing power did not appear to significantly affect conclusions for some OLS analyses. For LG1 data, estimates of  $H_cE$  and  $ME_m$  for OLS equations with and without a forced intercept ( $\log(77) \text{ kcal/BW}^{0.750} \times \text{d}^{-1}$ ) were not different and parametric stability was similar; the ratio of residual mean square (forced intercept model/OLS intercept model) was 1 to 4 decimal places; for that data set, the use of a fixed additive constant was appropriate. For LG2 and BARC data, when the intercept for the OLS regression  $\log HE = f(\text{MEI})$  was forced to be  $\log(77)$ ,  $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$ , residual mean squares were greater by a factor of 1.32 (LG2 data) and 1.75 (BARC data) compared to OLS solutions for HE at  $\text{MEI} = 0$ . Predicted  $\log HE$  was not equal to observed  $\log HE$  ( $P < 0.050$ ) for LG2 and BARC data when the Model 1 intercept was forced as  $\log(77)$ ,  $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$ . This finding indicates the use of  $0.077 \times \text{BW}^{0.750}$  (Mcal/d) as an estimate of HE at  $\text{MEI} = 0$  Mcal/d lacks global applicability and reduces parametric stability.

### Stability of Model 1 Parameter Estimates

In OLS regressions, a key assumption is that parameter estimates are stable across the range of data; that is, for Model 1, estimates of  $H_cE$  and  $b$  should be unique. An OLS evaluation of LG1 data, for cattle consuming 100% forage diets, ( $n = 9$ ) and all others ( $n = 22$ ) indicated  $H_cE$  and  $b$  were not different for either subset. However, even though parameter estimates were similar,  $\text{MEI}$  at energy equilibrium ( $\text{RE} = 0$ ) was different ( $P < 0.050$ ); for cattle consuming 100% forage compared to those consuming 2 to 40% forage (Table 2). These data are graphically presented in Fig. 1. Increasing forage content appears to be associated with an increase in  $ME_m$ . As was previously noted, apparent lack of symmetry for intervals (either confidence or prediction) about the estimates is due to the fact that response variable is  $\log(HE)$ ; intervals about  $\log(ME_m)$  are symmetrical. Lack of parametric stability was also found for Model 1 (LG1 data) when the intercept was forced as  $\log(77)$  ( $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$ ); estimates of  $ME_m$  differed ( $P < 0.050$ ) as well (Table 2). Old and Garrett (1987) reported increased variability in  $H_cE$  when  $H_cE$  was forced as  $\log(77)$  ( $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$ ); variability about the estimate was from 20 to 500% greater when compared to OLS estimates without a forced intercept. Reynolds et al. (1991) also noted increased maintenance costs for cattle consuming diets with greater forage content; across the range of diet types and  $\text{MEI}$ ,  $ME_m$  may not be



**Figure 1.** Log heat energy (HE) ( $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$ ) vs. ME intake ( $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$ ) for LG1 data. Cattle consuming 100% forage ( $n = 9$ ):  $\log HE = 1.90925 + 0.001697 \times \text{MEI}$ ; cattle consuming 2 – 40% forage ( $n = 22$ ):  $\log HE = 1.88673 + 0.001592 \times \text{MEI}$ ; all cattle ( $n = 31$ ):  $\log HE = 1.888659 + 0.001647 \times \text{MEI}$ . Means and 95% prediction intervals (PI) about  $HE = \text{ME intake}$  were 140, 129 to 153  $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$  (100% forage); 119, 106 to 134  $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$  (2 to 40% forage); 119, 104 to 137  $\text{kcal/BW}^{0.750} \times \text{d}^{-1}$  (all cattle).

a constant. Our analysis indicated, for BARC data (unscaled by  $\text{BW}^{0.750}$ ), diet forage concentration had no effect on the estimate of  $H_cE$ . Consistent with the observation by Reynolds et al. (1991), the point at which  $HE = \text{MEI}$ , or  $ME_m$ , was less ( $P < 0.050$ ) for cattle consuming diets containing lesser amount of forage, similar to our observations for LG1 data. Classically, estimated efficiencies of ME utilization for maintenance were similar; for greater and lesser forage intakes, these were 0.659 and 0.674, respectively. Solutions for a first-order function (using raw BARC data for cattle fed at either greater or lesser forage intakes)  $HE = H_cE \times e^{(k\text{MEI})}$ , indicated differences in HE at similar  $\text{MEI}$ . Metabolizable energy intake at  $HE = \text{MEI}$  was greater ( $P < 0.050$ ) for cattle fed a greater concentration of forage (9.93 Mcal/d) compared to those fed a lesser concentration of forage (8.99 Mcal/d). Other investigators have noted that maintenance costs are not constant. Ferrell et al. (1986) commented on differences in heat production due to differences in DMI, gut fill, and gut mass. Williams and Jenkins (2003a) and Williams and Jenkins (2003b) reported as well that maintenance in growing and mature cattle may be variable. Due to lack of stability in  $H_cE$  and  $ME_m$ ,  $k_m$  is dynamic (NRC, 1984) to account for variability in estimates of the point at which  $\text{RE} = 0$ , given that  $H_cE$  is fixed in the system described by Lofgreen and Garrett (1968). The efficiency of ME utilization for maintenance, as calculated by Lofgreen and Garrett (1968), is not the ratio of work performed to energy provided (dimensionless), but rather a rate. Energy status of a system is independent

of the pathway (Nash, 1970), most certainly then, for the same reactants and products the efficiency must be the same, regardless of the thermodynamic favorability of a reaction. Dynamic estimates of  $k_m$  may be considered to be at odds with the laws of thermodynamics. Although our analysis was limited to cattle growth data sets, the same lack of specificity for lactating and adult animals has long been recognized as a limitation to predictions of efficiencies of energy utilization (Tyrrell, 1980). In lactating animals, the inability of a single value for “maintenance” to describe the situation is even more limiting than in growth; as has been identified in the lactation models of Baldwin (1995), the previous NRC for dairy cattle (NRC, 2001) and in more sophisticated analyses of metabolic functions in dairy cattle and sows (McNamara et al., 1991; McNamara and Baldwin, 1994, 2000; McNamara, 2015; McNamara and Pettigrew, 2002).

Lofgreen and Garrett (1968) assumed that the estimate of  $H_e$   $0.077 \text{ Mcal/BW}^{0.750} \times \text{d}^{-1}$  was the true parameter and that it was unique across the range of cattle types and MEI. If this assumption was correct then the parameter estimate  $b$ , fixed as 0.00165 (OLS solution, LG1 data), should be stable for a fixed  $H_e$ . Results from Markov chain Monte Carlo simulation indicated a lack of parametric stability for the parameter estimate  $b$  calculated for data from LG1, LG2, and BARC. Employing informed priors such that a 95% credible interval (CrI) about the intercept 0.077 ( $\text{Mcal/BW}^{0.750} \times \text{d}^{-1}$ ) was from 0.0716 to 0.0828 ( $\text{Mcal/BW}^{0.750} \times \text{d}^{-1}$ ) and the parameter estimate  $b = 0.00165$ , similar to those reported by Lofgreen and Garrett (1968), minimum 95% CrI for the parameter estimate  $b$  were 0.0011 to 0.0022 for LG1 data, 0.0000513 to 0.00308 for LG2 data, and 0.0000820 to 0.00279 for BARC data. CrIs thus determined are 1.64-, 53.9-, and 27.0-fold greater for LG1, LG2, and BARC data than CI estimated in OLS frameworks for an unforced slope and intercept. Lack of parametric stability for the parameter estimate  $b$  is a clear indication that Model 1 poorly describes the relationship between  $\log HE$  and MEI when an  $H_e$  of  $0.077 \text{ (Mcal/BW}^{0.750} \times \text{d}^{-1})$  and an  $ME_m$  of  $0.124 \text{ Mcal ME/BW}^{0.750} \times \text{d}^{-1}$  is forced. This analysis is further evidence that the theoretical relationship between HE and MEI described by Lofgreen and Garrett (1968) and in the NRC (1984) appears to be poorly characterized in a single-variable OLS framework.

Significant lack-of-fit  $F$  ratios ( $P < 0.050$ ) were found for all 3 data sets; misspecification of a linear model is an indication that the relationship between

predictor and response variable is nonlinear. Lack of linearity in the relationship between  $\log HE$  and MEI is further indication that  $ME_m$  may be variable. Bootstrapped parameter estimates, lack of parametric stability in MCMC simulation and lack of fit tests indicated that Model 1 fails to adequately describe  $\log HE$  as a linear function of MEI. Furthermore, coefficients of determination may inadequately represent appropriateness of model structure. For Model 1,  $R^2$  were 0.937, 0.978, and 0.931 for data from LG1, LG2, and BARC, respectively, yet as previously noted the model failed to pass all tests of validity.

### *Use of Ratios to Describe Energy Relationships*

When MEI intake and  $\log HE$  were not scaled by  $BW^{0.750}$ , the criterion for internal validity (slope of  $\log HE_{\text{predicted}}$  vs.  $\log HE_{\text{observed}}$  not different from 1 or intercept not different from 0) was met for all 3 data sets, however, bootstrapped estimators were different ( $P < 0.050$ ) from OLS estimators. As was the case with data scaled by  $BW^{0.750}$ , Model 1 evaluated with raw data also failed that test (bootstrapping) of internal validity. Coefficients of determination for unscaled LG1, LG2, and BARC data were 0.949, 0.982, and 0.940, respectively, these are slightly greater than coefficients of determination for data scaled by  $BW^{0.750}$ . Bernier et al. (1987) also noted greater coefficients of determination for data not scaled by  $BW^{0.750}$ .

Standardized regression coefficients (Model 1) were estimated for data from LG1, LG2 and BARC for data scaled by  $BW^{0.750}$  and raw; the mean square residual (Model 1) was reduced when data were not scaled. The mean square residual was reduced, compared to the scaled analysis by 17.7, 19.4, and 0.700% for LG1, LG2, and BARC, respectively. The magnitude of prediction intervals at mean HE was greater by 10.3, 10.2, and 0% for LG1, LG2, and BARC for the scaled analysis. Scaling energy inputs (MEI) and outputs (HE) by  $BW^{0.750}$  may reduce accuracy of prediction.

### *Variability in $k_m$*

Heat production was not measured for LG1 and LG2 data, HE was estimated as  $MEI - RE$ , both of which were measured, therefore measurement error of MEI and RE is reflected in HE. Since  $MEI = 0$  was not in the range evaluated, variability about the estimate  $H_e$  may be more appropriately characterized by a prediction interval, rather than by a CI; Lofgreen and Garrett (1968) reported root



mean square residual. Prediction intervals for  $H_cE$  (scaled by  $BW^{0.750}$ ) were 2.02, 1.88, and 2.47 times greater than CI for LG1, LG2, and BARC data, respectively (Table 1). Uncertainty in the estimate of  $H_cE$  affects estimates of  $ME_m$ , calculated as the point at which  $RE = 0$ , and therefore  $k_m$ , defined as the ratio  $H_cE:ME_m$ . The robust nature of these estimates is critical to ensure accurate descriptions of input–output relationships determined using the California Net Energy System (CNES). Ordinary least squares (Model 1) estimates of  $ME_m$  are found in Table 1 and prediction intervals about the point estimate for  $HE = MEI$  (Table 1) indicated that solutions may be unique to each data set. Therefore, Model 1 is not robust. Old and Garrett (1987), using Model 1, reported a 95% CI for  $HE = MEI$  of 0.101 to 0.124 (Mcal/ $BW^{0.750} \times d^{-1}$ ); greater  $ME_m$  (for that study) were found when  $H_cE$  was forced as 0.077 (Mcal/ $BW^{0.750} \times d^{-1}$ ). Efficiencies of ME utilization (OLS) for maintenance were also numerically different from bootstrapped estimates, further indicating that linear, constant systems inadequately describe energy utilization. Estimates of  $k_m$  reported by Old and Garrett (1987) using either a forced intercept ( $\log HE$ , kcal/ $BW^{0.750} \times d^{-1} = 1.8865$ ) or an intercept model were from 0.626 to 0.684, similar to those found in this study. The first derivative (dHE/dMEI) of the function described by Model 1, for data scaled by  $BW^{0.750}$ , calculated at  $MEI = 0$  (Mcal/ $BW^{0.750} \times d^{-1}$ ) were 0.393, 0.359, and 0.497 for data from LG1, LG1, and BARC, respectively. When calculated at  $ME_m$ , dHE/dMEI were 0.469, 0.411, and 0.717 for data from LG1, LG1, and BARC, respectively. Only the estimate for BARC data was similar to the classic estimate of  $k_m$ , an observation consistent with improper model specification; neither  $H_cE$  nor  $ME_m$  appear to be fixed values. Differences in dHE/dMEI from  $MEI = 0$  to  $RE = 0$  may reflect differences in fuels used for metabolic processes, not all HE can be accounted for as MEI. The true parameter  $k_m$ , which is the efficiency of ME utilization for maintenance, may be poorly estimated as  $H_cE/ME_m$  since at  $MEI = 0$  heat produced as a result of the ingestion of food ( $H_iE$ ) = 0 (Lofgreen and Garrett, 1968; NRC, 1981).

Model 1 estimates for data not scaled by  $BW^{0.750}$  may be found in Table 1. Estimates of  $H_cE$  and  $ME_m$  are more similar when data are not scaled by  $BW^{0.750}$ . Estimators may be biased when expressed as ratios (Dinkel et al., 1965; Atchley et al., 1976); for this study, bias in  $b$  is reduced for raw when compared to scaled data. The standard error of  $b$  is proportionally less by 9.82, 10.4, and 7.51% for LG1, LG2, and BARC data when comparing

raw data and data scaled by  $BW^{0.750}$ . The rates of change of HE with respect to MEI at  $MEI = 0$  (Mcal/d) were 0.288, 0.272, and 0.270 for LG1, LG2, and BARC data, respectively. For the point at which  $MEI = HE$  (Mcal/d), dHE/dMEI, or  $k_m$ , were 0.454, 0.411, and 0.405 for LG1, LG2, and BARC data, respectively. Heat energy per unit of MEI, as described by Model 1, is not constant over the range of MEI from  $H_cE$  to  $ME_m$  but was more similar at a given MEI for unscaled data indicating better model specification. It should be noted that  $BW^{0.750}$  was originally used interspecifically for comparison of  $H_cE$  in animals ranging in size from mice to elephants (Kleiber, 1961), and may be different within a given specie. This analysis indicates, for the data evaluated, predictor and response variables should not be scaled by  $BW^{0.750}$ .

Heat production of fasting mammals has been estimated to be 0.070 Mcal/ $BW^{0.750}$  (Kleiber, 1961) and the OLS estimate of 0.077 Mcal/ $BW^{0.750}$  reported by Lofgreen and Garrett (1968) may have been considered appropriate for growing and finishing beef cattle, given costs of locomotion and other energy expenditures for cattle housed in open corrals. As was previously noted, Lofgreen and Garrett (1968) extrapolated outside the range of observed ME intakes to estimate HE at ME intake of 0. It is likely that heat production during short-term feed deprivation, characterized by Kleiber (1961), differs from long-term starvation. Soboleva et al. (1999) noted that changes in ME intake are not fully reflected by changes in metabolic rate for as many as 14 d, while Oltjen et al. (2003) reported a 20-d lag period. It is well accepted by those working in the field of energetics that at approximately the same time animals adapt to  $MEI = 0$ , they die. Therefore, the assumption that either short-term feed removal or extrapolation beyond the data range approximates  $H_cE$  for cattle consuming  $ME > RE = 0$  may not be correct. While estimates of  $H_cE$  determined using Model 1 are similar to those reported by Lofgreen and Garrett (1968), variability in the estimators  $H_cE$  and HE at  $RE = 0$  indicate bias in those estimates. Use of OLS parameter estimates to calculate  $ME_m$  and  $k_m$  result in values that are nonunique and unstable; it appears unlikely any linear model approximates the true relationship; parameter estimates thus determined are likely to be biologically and thermodynamically irrelevant.

Use of semi-log plots by Lofgreen and Garrett (1968) and others describing the relationship between HE and MEI, indicates that metabolic processes (maintenance and gain in growing and finishing cattle) over the range of MEI are

continually variable and distinct (Baldwin, 1995). Baldwin (1968) used theoretical estimates of caloric relationships to describe energy utilization and proposed that the efficiency of biological processes associated with maintenance should be that for ATP synthesis (Baldwin, 1995). Schiemann (1969) wrote “The maintenance requirement is a requirement for ATP-equivalents” and van Milgen (2002, 2006) noted the same. Consumption of ME in all animals provides fuel for processes associated with whole-organism service functions, maintenance of ionic gradients in the kidney, heart work, nervous function and respiration. Fuel (MEI) is also used for repair functions including lipid and protein turnover and sodium transport in the maintenance of membrane potentials (Baldwin, 1995). Baldwin (1995) estimated that service functions account for approximately 36 to 45% of maintenance and repair functions for 31 to 42% of maintenance. In this paper we use the term “service and repair” functions to describe the aforementioned processes. These processes are distinct from net synthesis of biomass, yet occur concomitantly in cattle in a positive energy balance. The characterization of maintenance by Armsby and Moulton (1925) is remarkably similar to that of Baldwin (1995): “The concept of maintenance must involve the idea of preserving the existing status of the animal while doing no work and producing no product. There should be an exact balance between income and outgo of ash, nitrogen, hydrogen and energy, showing that there was neither a loss nor a gain of protein, fat, carbohydrate or mineral matter. Strictly there should be no translocation of material within the animal itself.” Implicit in this statement is the notion that biochemical transactions associated with maintenance of biomass are different from those associated with gain of biomass. However, unlike the assumption of a discrete estimate of maintenance (a fixed point at which MEI = HE), the rate of biochemical processes providing for service and repair functions may vary continuously over the entire range of ME intake. Indeed, the very concept of maintenance as a state for which RE = 0 is a condition seldom, if ever, found in production animals (NRC, 1981). The difference between an animal at RE = 0 and one for which RE > 0 is, obviously, net accumulation of biomass or net work. All metabolic processes which are not net synthetic are necessarily service and repair functions; therefore, turnover is not assignable to gain as there is no net work.

Webster et al. (1974) proposed that ME<sub>m</sub> is not a static function as did Koong et al. (1983); Williams and Jenkins (2003a) showed that ME<sub>m</sub> increased as ME intake increased, albeit in a linear fashion. It might be expected that ME<sub>m</sub> is dynamic; increased energy intakes, resulting in increased adiposity, increase energy expenditures via infusions of leptin (and other compounds) induced hypothalamically mediated energetic responses (Jousse et al. 2011). Data from Labussierre et al. (2011) in growing pigs and cattle indicated that ME<sub>m</sub> requirements of those animals were influenced by feeding level. Estimates of k<sub>m</sub> using classical energetic methodologies (Model 1) differ from those calculated from the stoichiometry of biochemical pathways, in part, due to failure to properly partition ME utilized for maintenance, or service and repair functions, and gain; again, a large portion of the former can be accounted for as energy expended in the maintenance of ionic gradients or in turnover of cellular proteins.

Service and repair functions utilize the reaction: ATP → ADP + P<sub>i</sub>, therefore efficiencies associated with service and repair functions may be similar to synthetic efficiency of ATP (or similar entities), consistent with Baldwin (1968), Schiemann (1969), van Milgen (2002, 2006). The efficiency of ATP synthesis is variable across tissues and is a function of substrate oxidized as well as P<sub>i</sub> (inorganic phosphate), ADP and ATP concentrations. Gibbs free energy (ΔG) for ATP has been reported in hepatocytes as either −12.2 kcal/mol (Jibb and Richards, 2008) or −8.44 kcal/mol (Morikofer and Walter, 1992) and in skeletal muscle as either −10.3 kcal/mol (Morikofer and Walter, 1992) or −9.92 kcal/mol (Siegel et al., 2012). Rich (2003) reported that 30 mol of ATP are produced per mol of glucose oxidized (heat of combustion (ΔH<sub>c</sub>) = 674 kcal/mol), therefore from 37.6 to 53.5% of the energy in glucose is conserved in ATP. Oxidation of acetate is slightly less efficient (8 mol ATP per mol, ΔH<sub>c</sub> = 209 kcal/mol) and from 32.2 to 45.8% of the energy in acetate is conserved in ATP. Oxidation of a mol of stearic acid (ΔH<sub>c</sub> = 2712 kcal/mol) to CO<sub>2</sub> and H<sub>2</sub>O yields 120 mol (net) of ATP. The reaction captures from 37.3 to 54.2% of ΔH<sub>c</sub> of stearate; therefore, the range in efficiency of ATP synthesis is virtually identical for glucose and stearate oxidation.

Maintenance is defined as the state RE = 0 (NRC, 1981); given such a definition the efficiency of ME utilization for maintenance (k<sub>m</sub>) may only be calculable at that point. For cattle consuming ME such that RE < 0, sources of energy contributing to the total energy economy of the animal

are not exclusively ME; for  $RE > 0$  there is a blend of metabolic processes. Baldwin (1995) described  $k_m$  as  $\sim 0.90$ ; Moraes et al., (2014), in a Bayesian framework, used an informed prior,  $k_m = 0.94$ , similar to that described by Baldwin (1995) and reported a CrI that included 1.0; Moraes et al., (2014) also reported efficiencies greater than 1.0 (CrI = 0.76 to 1.13). Baldwin (1995) and Moraes et al. (2014) estimates of  $k_m$  differ greatly from the efficiency of ATP synthesis. If work is performed by a system, the change in energy ( $\Delta E$ ) is equal to heat ( $q$ ) minus work ( $w$ ). In the system described by Moraes et al. (2014), for  $k_m$  not different from 1.0,  $q$  and  $w = 0$ ; a state of equilibrium exists. Efficiencies greater than 1.0 are inconsistent with the first law of thermodynamics, which states that you can't get something for nothing. A  $k_m > 1.00$  means something is gotten for nothing and is necessarily prohibited by the first law. Estimates of  $k_m$  reported by Baldwin (1995) and Moraes et al. (2014) are similar to HE from bond breakage, such as glycogen  $\rightarrow$  glucose, and may only partially represent metabolic processes associated with maintenance.

Old and Garrett (1987) described the relationship between RE and MEI as a quadratic function; estimates of  $ME_m$  were 0.0953 Mcal ME/ $BW^{0.750} \times d^{-1}$  (Hereford steers) and 0.100 Mcal ME/ $BW^{0.750} \times d^{-1}$  (Charolais steers). Recovered energy at MEI = 0 was  $-0.0402$  Mcal/ $BW^{0.750} \times d^{-1}$  for Hereford steers and  $-0.046$  Mcal/ $BW^{0.750} \times d^{-1}$  for Charolais steers; these estimates differ ( $P < 0.05$ ) from  $H_eE$  calculated for the same data using Model 1. When calculated as the first derivative of equations (body energy spared by consumption of ME) reported by Old and Garrett (1987) for MEI =  $ME_m$  ( $\pm 0.010$  Mcal ME/ $BW^{0.750} \times d^{-1}$ ), estimates of  $k_m$  averaged 0.385 and 0.406 Hereford and Charolais steers, respectively. Old and Garrett (1987) reported an ME (Mcal/kg) of 2.72; based on the NRC (1984) estimating equation,  $k_m = 0.659$ , a value in the range for classically derived estimates determined for this study. Estimates of  $k_m$  for MEI at  $RE \sim 0$  (quadratic function) are consistent with theoretical values for efficiency of ATP synthesis (Schiemann, 1969; van Milgen (2002, 2006), but such results may be unique to that study. When the quadratic equation described by Old and Garrett (1987) was used with data from this study, parametric stability was lacking and 95% CI about the parameter estimate for the squared term included 0 indicating that a single-variable OLS equation adequately described the data.

### Consistency of Model 1 With Thermodynamics

Models describing the rate of change of HE per unit of MEI should reflect biology and the laws of thermodynamics; as described by Model 1 (LG1 and BARC data), for  $MEI > \sim 0.325$  Mcal/ $BW^{0.750} \times d^{-1}$ ,  $dHE/dMEI > 1$ ; HE is increasing at a rate greater than MEI. For MEI such that  $RE > 0$  the source of HE is MEI, therefore  $dHE/dMEI$  cannot be greater than 1 if the laws of thermodynamics hold and indicates that Model 1 is a mathematical solution to a mathematical problem. Model 1 describes not only  $HE > MEI$  for  $MEI < ME_m$  but also for  $MEI > 0.490$  Mcal/ $BW^{0.750} \times d^{-1}$ . Such descriptions of responses either require that RE be negative, which is likely only at lesser MEI, or that the first law of thermodynamics not hold (at greater MEI), which is even more unlikely. Attempts to infer responses for predictor variables not represented in the data base (e.g., MEI = 0) may lead one to erroneous conclusions regarding energy transactions. Estimates of  $H_eE$  and therefore  $ME_m$  and  $k_m$  determined using Model 1 may not be equal to the true parameters. Functional forms of variables in Model 1, and any estimate based on the model, are likely to be mathematical artifacts with no basis in either biology or thermodynamics.

### Single-Variable OLS Estimates of $k_g$

The ordinary least squares estimates for Model 2 of  $k_g$  from LG2 was greater ( $P < 0.050$ ) than that for LG1 and BARC (Table 3). Estimates of the vector predicted RE ( $RE_{\text{predicted}}$ ) for LG1 and BARC data, but not LG2, were different from the vector observed RE ( $RE_{\text{observed}}$ ) ( $P < 0.050$ ). Lin's concordance coefficients for the relationships between predicted and observed were 0.879 (LG1), 0.983 (LG2), and 0.939 (BARC). Bootstrapped parameter estimates ( $a$  and  $k_g$ ) for all data sets were different from OLS parameter estimates ( $P < 0.050$ ). As was seen with Model 1, the model was not properly specified for any data set ( $P < 0.050$ ). Therefore, for data scaled by  $BW^{0.750}$ , Model 2 lacks global consistency. Old and Garrett (1987), used Model 2 and reported  $k_g$  to range from 0.27 to 0.33. For ME reported by these investigators (2.72 Mcal/kg)  $k_g$  is calculated (NRC, 1984) as 0.428; once again, solutions are nonunique and estimates may not be equal to the true parameter. Within a data set, Model 2 OLS estimates of  $k_g$  within a data set, for scaled and raw data, were similar only for LG1 data (Table 3). For LG2 and BARC raw data, estimates

**Table 3.** Estimates of energy utilization for Model 2 using data from [Lofgreen and Garrett \(1968\)](#) and [Reynolds et al., \(1991\)](#)<sup>1</sup>

Parameter estimate	Data set		
	LG1 <sup>2</sup>	LG2 <sup>3</sup>	BARC <sup>4</sup>
RE at MEI = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	-0.0387	-0.0498	-0.0374
95% CI about RE at MEI = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	-0.0530 to -0.0244	-0.0561 to -0.0434	-0.0492 to -0.0256
95% prediction interval about RE at MEI = 0 (Mcal/BW <sup>0.750</sup> × d <sup>-1</sup> )	-0.0677 to -0.00977	-0.0615 to -0.0381	-0.0729 to -0.0195
RE at MEI = 0 (Mcal/d)	-2.35	-2.81	-4.20
95% CI about RE at MEI = 0 (Mcal/d)	-3.12 to -1.57	-3.20 to -2.42	-5.05 to -3.36
95% prediction interval about RE at MEI = 0 (Mcal/d)	-4.14 to -0.556	-3.64 to -1.47	-6.38 to -2.03
MEI at RE = 0 (Mcal/ BW <sup>0.750</sup> × d <sup>-1</sup> )	0.114	0.114	0.0972
95% CI about RE = 0 (Mcal/ BW <sup>0.750</sup> × d <sup>-1</sup> )	-0.0074 to 0.0074	-0.00334 to 0.00334	-0.00681 to 0.00681
95% prediction interval about RE = 0 (Mcal/ BW <sup>0.750</sup> × d <sup>-1</sup> )	-0.0263 to 0.0263	-0.0104 to 0.0104	-0.0341 to 0.0341
MEI at RE = 0 (Mcal/d)	7.35	7.20	9.08
95% CI about RE = 0 (Mcal/d)	-0.448 to 0.448	-0.236 to 0.236	-0.411 to 0.411
95% prediction interval about RE = 0 (Mcal/d)	-1.68 to 1.68	-0.776 to 0.776	-2.04 to 2.04
k <sub>g</sub> for data scaled by BW <sup>0.750</sup>	0.339	0.437	0.385
95% CI	0.271 to 0.406	0.408 to 0.465	0.327 to 0.445
k <sub>g</sub> for data unscaled by BW <sup>0.750</sup>	0.319	0.390	0.463
95% CI	0.268 to 0.370	0.366 to 0.414	0.410 to 0.517

<sup>1</sup>RE = a + k<sub>g</sub> × MEI; RE = recovered energy, a = RE at ME intake (MEI) = 0, k<sub>g</sub> = efficiency of ME utilization for gain.

<sup>2</sup>Data from [Lofgreen and Garrett \(1968\)](#) Table 1.

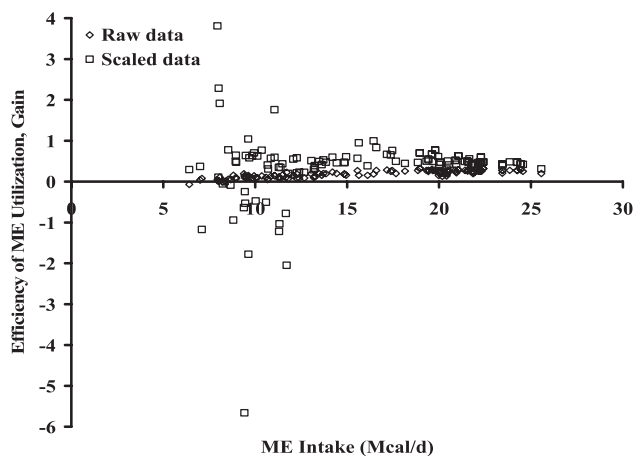
<sup>3</sup>Data from [Lofgreen and Garrett \(1968\)](#) Table 2.

<sup>4</sup>Data courtesy of Christopher K. Reynolds, University of Reading, UK from studies reported in part [Reynolds et al. \(1991\)](#).

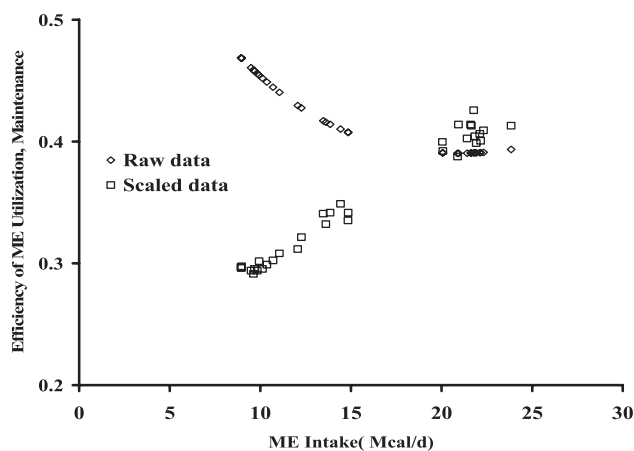
of k<sub>g</sub> were different from each other ( $P < 0.050$ ), and also different from ( $P < 0.050$ ) the estimates for scaled data. As was noted for scaled data, RE<sub>predicted</sub> was not different from RE<sub>observed</sub> only for LG2 data. Bootstrapped parameter estimates for raw data (LG1, LG2, and BARC) were different from OLS estimates. Significant lack-of-fit  $F$  ratios ( $P < 0.050$ ) were found for all data sets, indicating that the model failed to capture variability in RE = f(MEI) in a single-variable OLS framework. As was seen with Model 1 the relationship between either HE or RE and MEI is poorly characterized by a linear, or additive, model. Model 2 (scaled and raw data) lacked external validity ( $P < 0.050$ ), and predictive accuracy was only marginally better for raw data. Metabolizable energy intakes at RE = 0 were not unique for raw LG1, LG2, and BARC data ([Table 3](#)), with broad prediction intervals about RE = 0. Lack of stability in the estimate is evidenced by the magnitude of the prediction intervals and is consistent with model misspecification. Estimates of k<sub>g</sub> were less biased for raw data than for data scaled by BW<sup>0.750</sup>; the relative magnitude of the standard error of k<sub>g</sub> was less for raw compared to scaled data. For LG1, LG2, and BARC data, these reductions were 24.6, 16.5, and 8.8%, respectively. For neither raw data nor data scaled by BW<sup>0.750</sup> were MEI at RE = 0

unique. Prediction intervals at mean RE (standardized regression coefficients) for scaled data (by BW<sup>0.750</sup>) were greater by 20.0 (LG1), 6.70 (LG2), and 25.2% (BARC) when compared to data not scaled by BW<sup>0.750</sup>. Parameter estimates calculated for Model 2, regardless of whether or not data are scaled by BW<sup>0.750</sup>, may not be equal to the true parameters; and performance may be better predicted when input–output data are not scaled by BW<sup>0.750</sup>.

Efficiency of ME utilization for gain may be calculated as RE/(MEI – ME<sub>m</sub>). Parameter estimates of k<sub>g</sub> for each individual (using LG1, LG2 and BARC data), were evaluated by fixing ME<sub>m</sub> as 0.124 Mcal ME/BW<sup>0.750</sup> × d<sup>-1</sup> or as 8.53 Mcal/d. In much the same fashion as nitrogen requirements should be expressed as g/d rather than as percentages, animals do not require energy expressed as a ratio but as Mcal/d. Recovered energy and MEI were either scaled (former estimate) or raw (latter estimate). Estimates of k<sub>g</sub> were different ( $P < 0.050$ ) when data were scaled (0.363; 95% CI = 0.216 to 0.510) or raw ((0.185; 95% CI = 0.169 to 0.200). [Bernier et al. \(1987\)](#) also noted greater variability in the estimates for data scaled by BW<sup>0.750</sup>. Lack of concordance was noted between estimates as  $\rho_c = 0.283$  ([Figs. 2 and 3](#)). Extreme variability in k<sub>g</sub> for scaled data (MEI < 12 Mcal/d) is likely a result



**Figure 2.** Variability in individual estimates of efficiency of ME utilization for gain ( $k_g$ ). Individual efficiency was estimated as  $k_g = RE_i / (ME_i - ME_m)$ ;  $RE_i$  and  $ME_i$  were retained energy and ME intake by the  $i^{\text{th}}$  individual (raw or scaled by  $BW_i^{0.750}$ ,  $BW$  for the  $i^{\text{th}}$  individual) and  $ME_m$  (estimate of heat production = ME intake for the  $i^{\text{th}}$  individual) was calculated as either  $0.124 \text{ Mcal ME} / BW_i^{0.750} \times d^{-1} \times BW_i^{0.750}$  (raw) or  $0.124 \text{ Mcal ME} / BW_i^{0.750} \times d^{-1}$  (scaled).



**Figure 3.** Estimates of efficiency of ME utilization for maintenance ( $k_m$ ). Efficiency was estimated as  $(0.02258 \times 8.613e^{0.02258 ME_i} - 0.0907 \times 5.732e^{-0.0907 ME_i})$  for  $ME_i$  unscaled by  $BW_i^{0.750}$  (raw) or  $(0.00292 \times 89.98e^{0.00292 ME_i} - 23.38 \times 49.86 e^{-23.38 ME_i})$  for  $ME_i$  scaled by  $BW_i^{0.750}$  (scaled).

of lack of concordance of the estimate  $MEI = HE$  with observed when  $MEI \sim HE$ . Scaled estimates of  $k_g$  fall outside the range of values allowed by the first law of thermodynamics. When scaled by  $BW^{0.750}$  ( $RE > 0$ ) the range was  $-5.66$  to  $3.81$ , again, an indication that  $ME_m$ , calculated as  $0.124 \text{ Mcal ME} / BW^{0.750} \times d^{-1}$  is a poor fit to the data. The range in  $k_g$  for raw data ( $RE > 0$ ), was  $0$  to  $0.323$ ; an estimate that, while lacking in stability and less than commonly reported, is consistent with the first law. Estimates of  $k_g$  appear to be biased as neither was the same, although the scaled estimate was more similar to  $k_g$  calculated for Model 2. It is very possible, however, that no model is correctly specified and no estimate of  $k_g$  is equal to the true parameter. This exercise, evaluating predictions of

$k_g$ , provides further evidence that classical linear, constant estimates of ME utilization inadequately describe biological and thermodynamic reality.

As was previously noted, an assumption basic to OLS is that parameter estimates are constant across the range of data. To further evaluate specification of Model 2,  $a$  and  $k_g$  were estimated using BARC data for MEI from  $0.0807$  to  $0.194 \text{ Mcal ME} / BW^{0.750} \times d^{-1}$  and RE was from  $-0.0248$  to  $0.0538 \text{ Mcal} / BW^{0.750} \times d^{-1}$  ( $n = 36$ ). Neither estimator was different from  $0$  ( $P < 0.050$ ) and estimators were different ( $P < 0.050$ ) than those determined for the entire data set ( $n = 59$ ). Metabolizable energy intake at  $RE = 0$  was less ( $0.0617 \text{ Mcal ME} / BW^{0.750} \times d^{-1}$ ) than the minimum observed MEI ( $P < 0.050$ ). This observation suggests that estimates of oxygen consumption may not adequately reflect differences in heat production (Salin et al., 2015) for MEI approximating maintenance. However, when data were not scaled by  $BW^{0.750}$  ( $MEI = 8.66$  to  $17.2 \text{ Mcal/d}$ ,  $RE = -2.57$  to  $4.85 \text{ Mcal/d}$ ), neither  $ME_m$ , a nor  $k_g$  estimated for the subset were different from those determined for the entire data set. This analysis further indicates that the use of scaling by  $BW^{0.750}$  may increase bias in parameter estimates related to energy utilization by growing and finishing beef cattle.

### Efficiencies of Protein and Fat Synthesis Determine $k_g$

Baldwin (1968), Baldwin (1995), and Kennedy and Calvert (2014) estimated the theoretical efficiency of protein synthesis ( $k_p$ ) in ruminants to be from  $0.750$  to  $0.850$  and the efficiency of lipid synthesis ( $k_f$ ) in ruminants to be from  $0.700$  to  $0.750$ . For gain containing  $40\%$  fat, approximately the amount in gain for cattle in LG1 and LG2 data, the maximum theoretical efficiency is  $0.708$  to  $0.765$ , an efficiency of ME utilization for gain much greater than that estimated for any of the data sets evaluated using Model 2. Old and Garrett (1985), employing a model described by Kielanowski (1965), estimated  $k_p$  in Hereford steers to be  $0.0877$  and in Charolais steers as  $0.103$ . The partial efficiency of fat synthesis was reported by Old and Garrett (1985) as  $0.498$  and  $0.524$  for Hereford and Charolais steers, respectively, and  $k_g$  can be calculated from the data in Old and Garrett (1985) as  $0.306$  and  $0.316$  for Hereford and Charolais steers, respectively. Strathe et al. (2010), using a method different from that employed by Old and Garrett (1987) reported  $k_p$ , to be  $0.57$  in pigs, an observation contrasting with that of Geay (1984), who determined  $k_p$  in cattle to be  $0.2$ ; Geay also reported

$k_f = 0.75$ . For gain containing 40% fat and using estimates of  $k_p$  and  $k_f$  reported by Geay (1984),  $k_g$  is 0.518, or approximately 68 to 73% of theoretical maximum. Strathe et al. (2011), using data from lactating dairy cattle in a Bayesian framework, calculated a linear estimate of  $k_g = 0.89$  and a 95% CrI was from 0.85 to 0.95. Although the estimate and 95% CrI are greater than the theoretical maximum it is not uncommon to find reports in the literature in which  $k_f$  are greater than theoretical maxima. Orskov and McDonald (1970) estimated  $k_f = 0.8$ , Bickel and Durrer (1974) reported  $k_f$  to be 1.02 and calculations by Rattray and Joyce (1976) indicated  $k_f$  to be 0.56, 0.95, or 1.28. Again, lack of uniqueness of solution indicates the model structure is wrong and parameter estimates are unlikely to equal the true parameters. Inappropriate magnitude ( $k_f > 1.0$ ) of estimators is further evidence of model misspecification. Models used in the previously cited studies are all of the general OLS structure:  $MEI = \text{estimate of } ME_m + \text{efficiency of synthesis of biomass gain for either protein or fat}$ . Of greater concern, and that should be obvious, parameter estimates  $\geq 1.0$  are inconsistent with the first law of thermodynamics and indicate, at a minimum, inappropriate partitioning (in growing and finishing cattle) of ME for either maintenance or gain. For  $k_f = 1.0$  there is no net synthesis of fat, reactants and products are in equilibrium and for  $k_f > 1.0$  energy is either created or transferred at the expense of the thermal energy of surroundings, again observations in conflict with the first law of thermodynamics. Classical estimates of efficiency of ME utilization, in which efficiencies of processes associated with service and repair functions are greater than those associated with biomass gain, require, incorrectly, that the reactants and products for ATP synthesis lie closer to equilibrium than reactants and products of biomass synthesis. That the efficiency of biomass gain be less thermodynamically favored than ATP synthesis should be obvious; ATP is required for the condensation of monomers, such as acetate, into larger structures, such as storage triglycerides. Taken as a whole, these observations strongly suggest that estimates of the efficiency of ME utilization determined by classical models, in either an OLS or Bayesian framework, may be inconsistent with theoretical and thermodynamically allowed estimates.

### *Sources of Variation in Efficiency*

Given the previously noted similarities (BARC data for greater and lesser forage intakes) in  $k_m$  and

$k_g$  and variability in  $ME_m$  estimated from Models 1 and 2, it is possible that Lofgreen and Garrett (1968) chose variables  $k_m$  and  $k_g$ , with  $k_m > k_g$ , and a fixed  $H_cE$  because it was consistent with dogma regarding energy utilization at the time. Studies represented in LG1 and LG2 may not have been designed to answer the question as to where variability in the efficiency of ME utilization is found by not only evaluating the density of ME, (Mcal/kg), but also quantities of ADFI and MEI. Model 1 analysis for pooled data (LG1 and LG2, not scaled by  $BW^{0.750}$ ) indicate that differences exist ( $P < 0.050$ ) in  $H_cE$  and  $ME_m$  for lesser (6.41 to 13.3 Mcal/d) and greater (13.5 to 25.6 Mcal/d) MEI. Numerical differences were found in  $k_m$ , 0.566 for cattle consuming lesser amounts of ME and 0.653 for cattle consuming greater amounts of ME. Heat energy (Mcal/d) was equally well predicted for either group,  $\rho_c$  was 0.937 and 0.921 for lesser and greater MEI; the regression of **PREDICTED HE** vs. **OBSERVED HE** indicated the same (slope not different from 1, intercept not different from 0). For Model 2, estimates of  $k_g$  did not differ between lesser and greater MEI nor were MEI at RE = 0 different. Recovered energy was poorly estimated;  $\rho_c = 0.766$  or 0.764 for lesser and greater MEI. As a consequence of study design, inappropriate model specification, as noted in the previous paragraph, and variation in the true underlying energetic costs of maintenance, HE may be improperly partitioned between  $ME_m$  and  $H_rE$  in Models 1 and 2. Models 1 and 2 may be adequate empirical descriptors of ME utilization, but are inadequate descriptors of the underlying biochemistry and energy utilization. It cannot be overemphasized that the goal of Lofgreen and Garrett (1968) was to develop a system for improved prediction of performance of growing and finishing cattle using tools available to them, and to nutritionists working to predict cattle performance, not necessarily to predict the efficiency of ME utilization commensurate with biochemistry and the laws of thermodynamics. It seems as though the CNES effectively predicts animal performance in spite of the laws of thermodynamics, not because of them.

### *Equivalence of Predictions of HE + RE With Observed MEI*

As previously noted, the laws of thermodynamics require that  $HE + RE = MEI$ . The rate of change of MEI with respect to MEI ( $dMEI/dMEI$ ) is 1 as is the sum of  $dHE/dMEI$  and  $dRE/dMEI$  (Willcox et al., 1971). If the conditions  $HE_{\text{predicted}} + RE_{\text{predicted}} =$

$MEI_{\text{observed}}$  and  $dHE/dMEI + dRE/dMEI = 1$  are not both satisfied it is possible that parameter estimates  $H_cE$ ,  $ME_m$ ,  $k_m$ , and  $k_g$  calculated using Models 1 and 2 may not represent the true parameters. Failure to approximate either observed MEI or 1 indicates that inappropriate amounts of MEI are accounted for as  $ME_m + H_rE$  or as RE; at  $RE = 0$  ( $ME_m$ ), all  $MEI \rightarrow HE$ . Concordance of predicted MEI (being  $\Sigma HE, RE$ ) with observed MEI for LG1, LG2 and BARC data was evaluated by comparing the areas under the curves (AUC) using the AUC package in R (R Core Team, 2013) for predicted MEI or observed MEI, over the observed ranges of MEI (Table 4). Appropriateness of inference outside the observed data range, from  $MEI = 0$  to observed, was also evaluated by comparing AUC (Table 4). Results are graphically presented in Figs. 4 and 5. Over the observed range of MEI, predicted MEI was similar to observed MEI, the ratios of  $AUC_{\text{predicted}}:AUC_{\text{observed}}$  were  $\sim 1$  (Table 4). For MEI from 0 to the observed range, AUC for predicted MEI was greater than AUC for observed MEI; MEI may not be the sole source of HE as described by Model 1. Although extrapolation to  $MEI = 0$  is required in the CNES and other classically based energy systems, Models 1 and 2 appear to inadequately predict MEI outside the range of observed data (Fig. 4); the pitfalls of extrapolation are well known. Failure of  $dHE/dMEI + dRE/dMEI \sim 1$  over much of the range of MEI

is the result of variability in the estimate of  $dHE/dMEI$  as  $dRE/dMEI$  is static. Rates of change in HE, relative to those in MEI, are poorly characterized by Model 1, therefore, model misspecification is likely (Fig. 5). Observed MEI (Mcal/d) for LG2 data was better characterized as  $\Sigma(HE_{\text{predicted}}, RE_{\text{predicted}})$  in a model for which either response was a bi-exponential function of MEI. Rates of change of HE and RE, with respect to MEI, were also better characterized by the bi-exponential model;  $(\Sigma(dHE/dMEI, dRE/dMEI) \sim 1.0$  across the range of MEI (Table 4). This analysis provides further evidence that, not only do classical linear, constant models fail to describe metabolic processes; Model 1 poorly characterizes the relationship between HE and MEI, possibly due to log transformation of HE.

### Probability Distribution and Variance of Residuals

Runs statistics indicated that residuals, within each data set evaluated using Models 1 and 2, were randomly distributed, with the exception of BARC data (Models 1 and 2,  $P < 0.050$ ) for data scaled by  $BW^{0.750}$ . Failure to meet the assumption that error terms, as represented by the corresponding residuals, are randomly distributed indicates loss of optimal properties of least squares estimators, such as the unbiased nature of estimators. Model 2 residuals for BARC data, scaled by  $BW^{0.750}$ , were skewed; inferences may be biased. Model 2 residuals for

**Table 4.** Concordance of MEI predicted as  $\Sigma(HE, RE)$  with observed  $MEI^{1,2}$

Item	LG1 <sup>a</sup>	LG2 <sup>b</sup>	LG2-1 <sup>c</sup>	BARC <sup>d</sup>
MEI = 0 to minimum $MEI_{\text{observed}}$ AUC <sup>e</sup>	1.45	1.22	0.984	1.43
Minimum $MEI_{\text{observed}}$ to maximum $MEI_{\text{observed}}$ AUC <sup>e</sup>	1.00	0.990	1.00	1.02
MEI = 0 to maximum $MEI_{\text{observed}}$ AUC <sup>e</sup>	1.037	1.039	0.998	1.042
$MEI_{\text{predicted}} = MEI_{\text{observed}}$	1.00	1.00	1.00	1.00
Minimum $MEI_{\text{observed}}$ (Mcal ME/ $BW^{0.750} \times d^{-1}$ )	100	140	---	84
Maximum $MEI_{\text{observed}}$ (Mcal ME/ $BW^{0.750} \times d^{-1}$ )	335	302	---	381
Minimum $MEI_{\text{observed}}$ (Mcal ME/d)	---	---	8.94	---
Maximum $MEI_{\text{observed}}$ (Mcal ME/d)	---	---	23.8	---
Minimum $dRE/dMEI + dHE/dMEI^f$	0.767	0.871	0.998	0.765
Maximum $dRE/dMEI + dHE/dMEI^f$	1.38	1.18	1.01	1.66

<sup>1</sup>HE = heat energy, predicted as  $\log HE = H_cE + b \times MEI$ ;  $H_cE$  = heat energy at ME intake ( $MEI, \text{Mcal ME}/BW^{0.750} \times d^{-1}$ ) = 0 ( $\text{Mcal}/BW^{0.750} \times d^{-1}$ ),  $b$  = parameter estimate (dimensionless); RE = recovered energy ( $\text{Mcal}/BW^{0.750} \times d^{-1}$ ), predicted as  $a + k_g \times MEI$ ;  $a$  = RE at  $MEI = 0$ ,  $k_g$  = efficiency of ME utilization for gain, parameter estimates  $H_cE$ ,  $b$ ,  $a$ , and  $k_g$  are unique to each data set.

<sup>2</sup>HE predicted as  $22.9e^{0.0109MEI} - 20.6e^{0.0212MEI}$ ; RE =  $24.2e^{-0.00429MEI} + 21.7e^{0.0113MEI}$ , HE and RE = Mcal/d, MEI = as Mcal ME/d.

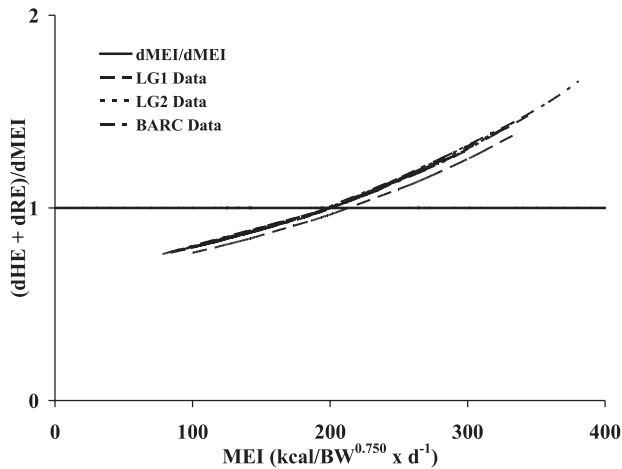
<sup>a,b,c,d</sup>LG1 - data from Lofgreen and Garrett (1968) Table 1, LG2 - data from Lofgreen and Garrett (1968) Table 2, LG2-1- data from Lofgreen and Garrett (1968) Table 2, HE and RE estimated from equations in <sup>2</sup>, BARC - data courtesy of Christopher K. Reynolds, University of Reading, UK, from studies reported in part Reynolds et al. (1991).

<sup>e</sup>AUC = area under the curve, AUC estimated as  $\int (H_cE + b \times MEI + a + k_g \times MEI) dx$  or  $\int (22.9e^{0.0109MEI} - 20.6e^{0.0212MEI} + 24.2e^{-0.00429MEI} + 21.7e^{0.0113MEI})dx$  over the appropriate ranges of MEI shown in Table 4; tabular values for AUC are the ratios of  $MEI_{\text{predicted}}/MEI_{\text{observed}}$ .

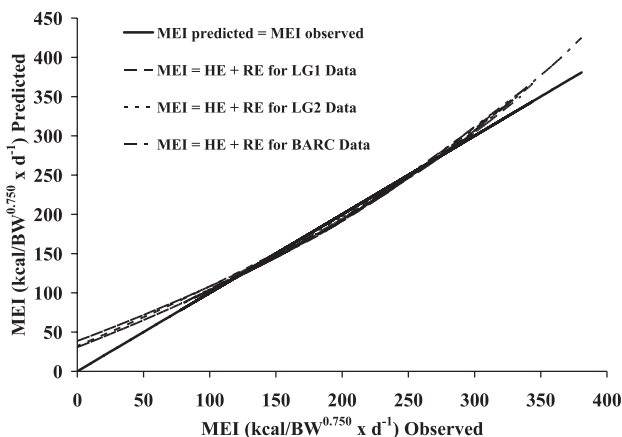
<sup>f</sup> $\Sigma(dRE/dMEI, dHE/dMEI) = 1$ ; failure to approximate 1 indicates failure of prediction equation to describe relationship between predictor and response.

LG2 data (unscaled) and for BARC data, scaled by  $BW^{0.750}$ , were kurtotic; more observations are found at the extreme; predictive accuracy is compromised. Results of the runs statistic, skewness, and kurtosis tests indicate that other models should be evaluated.

When predictor and response variables were scaled by  $BW^{0.750}$  (Model 1) the average value  $[(\text{variance } r_i)/r_i]$  was either less (LG1), not different (LG2) or greater (BARC) when compared to unscaled. For Model 2, scaling by  $BW^{0.750}$  for all data sets, inflated the magnitude of the individual



**Figure 4.** Rate of change of metabolizable energy intake (MEI) with respect to MEI, estimated as the rate of change of heat energy (HE)/dMEI plus the rate of change of recovered energy (RE)/dMEI calculated from data for all three data sets evaluated in the study. The first derivative of the function  $\log HE = H_c E + b MEI$  is  $dHE/dMEI$  and  $dRE/dMEI$  is the slope of the line  $RE = a + k_g MEI$ . Data from Lofgreen and Garrett (1968) are labeled as either LG1 or LG2. Data courtesy of Christopher K. Reynolds, University of Reading, UK are from studies reported in part Reynolds et al., 1991 are labeled BARC.



**Figure 5.** Comparison of observed MEI with MEI calculated as the sum of HE and RE. Heat energy (HE) was estimated as  $HE = H_c E + b \times MEI$ , where  $HE = HE$  at ME intake (MEI) = 0 ( $\text{kcal}/BW^{0.750} \times d^{-1}$ ); recovered energy (RE,  $\text{kcal}/BW^{0.750} \times d^{-1}$ ) =  $a + k_g \times MEI$ , where  $k_g$  = the efficiency of ME utilization for gain,  $a$  and  $b$  are parameter estimates. Data from Lofgreen and Garrett (1968) are labeled as either LG1 or LG2. Data courtesy of Christopher K. Reynolds, University of Reading, UK are from studies reported in part Reynolds et al., 1991 are labeled BARC.

residual variance relative to the residual. This analysis provides further evidence that, for the data and models reported on in this study, scaling by  $BW^{0.750}$  may increase bias in the estimators. Investigators studying data in which observations are scaled by  $BW^{0.750}$  may wish to perform their own evaluations to determine if variances are inflated by the use of ratios.

With the exception of residuals plotted for Model 2, LG2 data (scaled by  $BW^{0.750}$  and unscaled), patterns were noted in all other residual plots; these subjective observations are consistent with analyses indicating overall lack of proper specification for Models 1 and 2. These observations also suggest that, while the structure of Models 1 and 2 require that either HE or RE are  $f(\text{MEI})$  alone, changes in MEI may not be the only factor affecting changes in the observed responses.

### Concomitant Solutions for $ME_m$ , $k_m$ , and $k_g$ in a Bayesian Framework – Model 3

For animals with MEI such that  $RE > 0$ , the differing efficiencies with which ME is utilized for maintenance functions and biomass gain requires that model structure characterize both processes simultaneously; this structure is found in Model 3. A tractable solution to Model 3 (raw LG2 data), in a Bayesian framework, was found and those parameter estimates are shown in Table 5. For LG2 data (raw), the solution to Model 3 was internally valid ( $P < 0.050$ ),  $R^2$  was 0.973 and  $\rho_c$  was 0.986; LG2 data were adequately described by the model. Ninety-five percent CrI for parameter estimates are shown in Table 5. Solutions for LG2 data scaled by

**Table 5.** Parameter estimates for Model 3, raw data<sup>1,2</sup>

Item	Value	95% CrI
$a_1$ (Mcal/d)	8.613	8.417 to 8.808
$k_1$ (Mcal/d) <sup>-1</sup>	0.02258	0.0166 to 0.02851
$a_2$ (Mcal/d)	-5.732	-5.928 to -5.537
$k_2$ (Mcal/d) <sup>-1</sup>	-0.09007	-0.1093 to -0.07085
$k_g$ (no dimension)	0.6756	0.6137 to 0.7372
$k_m^a$ (no dimension)	0.420 <sup>b</sup>	0.390 to 0.469 <sup>c</sup>

<sup>1</sup> $RE = (MEI - (a_1 e^{k_1 MEI} + a_2 e^{k_2 MEI})) \times k_g - RE =$  recovered energy (Mcal/d),  $MEI =$  ME intake (Mcal/d),  $a_1$  and  $a_2 =$  state variables,  $k_1$  and  $k_2 =$  rate constants,  $k_g =$  efficiency of ME utilization for gain,  $k_m =$  efficiency of ME utilization for maintenance.

<sup>2</sup>Data were from Table 2 in Lofgreen and Garrett (1968).

<sup>a</sup> $k_m$  is calculated as the first derivative of  $(a_1 e^{k_1 MEI} + a_2 e^{k_2 MEI})$ .

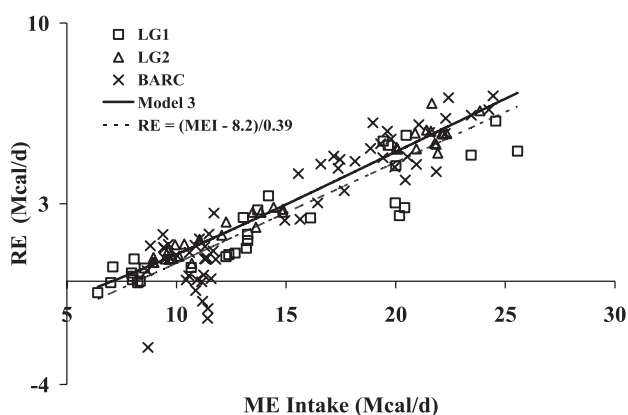
<sup>b</sup>calculated as the average of first derivative of  $(a_1 e^{k_1 MEI} + a_2 e^{k_2 MEI})$ ,  $n = 34$ .

<sup>c</sup> $k_m$  is the range for the first derivative of  $(a_1 e^{k_1 MEI} + a_2 e^{k_2 MEI})$ ,  $n = 34$ .



$BW^{0.750}$  (Table 6) did not converge as well as for raw data, posterior distributions were less informative, and the solution was less than optimal.

The first derivative of the innermost parenthetical value of Model 3 (raw data) is  $k_m$  and parameter estimates for both scaled and unscaled data are shown in Tables 5 and 6. Estimates of  $k_m$  using raw data are within the range of theoretical efficiencies for ATP synthesis from either acetate or stearate. When  $k_m$  was estimated for scaled data, the parameter estimate was less than that for raw data ( $P < 0.050$ ) and at the lesser end of the range of theoretical efficiencies for ATP synthesis from either acetate or stearate. Parameter estimates of



**Figure 6.** Comparison of recovered energy (RE) as  $f(\text{ME intake, MEI})$  using either a nonlinear, Model 3 ( $\text{RE} = \text{MEI} - (8.613e^{0.02258 \text{MEI}} + 5.732e^{-0.0907 \text{MEI}}) \times 0.6756$  or linear [ $\text{RE} = (\text{MEI} - 8.2) \times 0.390$ ] estimate. Recovered energy and MEI shown as Mcal/d for pooled data. Lin's concordance coefficient ( $\rho_c$ ) was not different between predicted RE and observed RE for either nonlinear ( $\rho_c = 0.907$ ) or linear ( $\rho_c = 0.897$ ) model, indicating that either model equally predicted RE. Data from Lofgreen and Garrett (1968) are labeled as either LG1 or LG2. Data courtesy of Christopher K. Reynolds, University of Reading, UK are from studies reported in part by Reynolds et al., 1991 labeled BARC.

**Table 6.** Parameter estimates for Model 3, scaled data<sup>1,2</sup>

Item	Value	95% CrI
$a_1$ (Mcal/ $BW^{0.750} \times d^{-1}$ )	89.98	88.71 to 91.39
$k_1$ (Mcal/ $BW^{0.750} \times d^{-1}$ ) <sup>-1</sup>	0.002292	0.002184 to 0.002386
$a_2$ (Mcal/ $BW^{0.750} \times d^{-1}$ )	-49.86	-51.83 to -47.9
$k_2$ (Mcal/ $BW^{0.750} \times d^{-1}$ ) <sup>-1</sup>	-23.38	-24.24 to -22.44
$k_g$ (no dimension)	0.6582	0.6473 to 0.6822
$k_m^a$ (no dimension)	0.334 <sup>b</sup>	0.279 to 0.403 <sup>c</sup>

<sup>1</sup> $\text{RE} = (\text{MEI} - (a_1 e^{k_1 \text{MEI}} + a_2 e^{k_2 \text{MEI}})) \times k_g - \text{RE} = \text{recovered energy}$  (Mcal/ $BW^{0.750} \times d^{-1}$ ), MEI = ME intake (Mcal/ $BW^{0.750} \times d^{-1}$ ),  $a_1$  and  $a_2$  = state variables,  $k_1$  and  $k_2$  = rate constants,  $k_g$  = efficiency of ME utilization for gain,  $k_m$  = efficiency of ME utilization for maintenance.

<sup>2</sup>Data were from Table 2 in Lofgreen and Garrett (1968).

<sup>a</sup> $k_m$  is calculated as the first derivative of  $(a_1 e^{k_1 \text{MEI}} + a_2 e^{k_2 \text{MEI}})$ .

<sup>b</sup>calculated as the average of first derivative of  $(a_1 e^{k_1 \text{MEI}} + a_2 e^{k_2 \text{MEI}})$ ,  $n = 34$ .

<sup>c</sup> $k_m$  is the range for the first derivative of  $(a_1 e^{k_1 \text{MEI}} + a_2 e^{k_2 \text{MEI}})$ ,  $n = 34$ .

$k_m$ , for raw data, were monotonically negative, whereas  $k_m$  determined for data scaled by  $BW^{0.750}$  were monotonically positive (Fig. 3). Gibbs free energy is greater at lesser concentrations of products and  $\Delta G$  decreases as products accumulate. If, at lesser MEI the concentration of product (ATP) is less, then the estimates of  $k_m$  for raw data may better reflect cell biology than for scaled data. While this idea may be appealing from a teleological standpoint, Newsholme and Start (1976) noted that intracellular concentrations of ATP are relatively stable and differences in observed concentration of ATP are unlikely to cause changes in  $k_m$  of the magnitude noted in this study. Efficiencies of ME utilization for gain were not different between raw and unscaled estimates; 95% CrI for  $k_g$  (raw and scaled) are consistent with theoretical estimates of efficiency of ME utilization for gain in ruminants. Unlike Models 1 and 2, Model 3 simultaneously describes the major uses of ME, and efficiencies, in growing and finishing beef cattle, that is for service and repair functions (maintenance) and gain of biomass; efficiencies of energy utilization thus calculated are consistent with the laws of thermodynamics.

### Comparison of Predictive Accuracy

Estimates of RE (scaled and raw) for LG1 and BARC data, calculated as  $(\text{MEI} - \text{ME}_m) \times k_g$  (LG2 parameter estimates found in Tables 1 and 3) or estimated from Model 3 (LG2 estimates found in Tables 5 and 6) were compared to observed RE (Tables 7 and 8). Predictive accuracy, regardless of how RE was estimated, was marginal at best (Fig. 6). For the OLS function  $\text{RE}_{\text{predicted}} = f(\text{RE}_{\text{observed}})$ , the intercept of the line was often not different from 0, however, variability in the estimates of both intercept and slope, and other indices ( $R^2$  and  $\rho_c$ ) indicated poor fit to the data.

## CONCLUSION

Energetics, at a simplistic level, is accounting; in order to properly “balance the books” all input and outgo must be in the proper “columns.” For growing and finishing beef cattle, metabolizable energy intake is input, recovered energy and heat energy are output:  $\text{RE} = f(\text{MEI})$  and  $\text{HE} = f(\text{MEI})$ . Heat energy is produced by service and repair functions [ $\text{ME}_m$ ; ATP requirements (Baldwin, 1968; Schiemann 1969)] or by product formation ( $\text{H}_r$ ), therefore  $\text{HE} = \text{ME}_m + \text{H}_r$ . Observations by Baldwin (1995), that classically determined

**Table 7.** Evaluation of robustness of prediction of RE as  $(\text{MEI} - \text{ME}_m) \times k_g$  for a static estimate of  $\text{ME}_m$ <sup>1</sup>

Data set	Parameter estimate			
	$R^2$	$\rho_c^a$	Intercept <sup>b</sup> ( $\pm$ 95% CI)	Slope <sup>b</sup> ( $\pm$ 95% CI)
LG1 <sup>c</sup> (RE/BW <sup>0.750</sup> ) <sup>d</sup>	0.784	0.831	4.10 (-3.75 to 11.9)	1.01 (0.810 to 1.21)
LG1 (RE) <sup>e</sup>	0.777	0.837	0.078 (-0.534 to 0.689)	1.05 (0.836 to 1.26)
LG2 <sup>f</sup> (RE/BW <sup>0.750</sup> )	0.968	0.943	-2.84 (-6.09 to 0.412)	0.968 (0.905 to 1.03)
LG2 (RE)	0.972	0.941	-0.302 (-0.532 to -0.071)	0.972 (0.913 to 1.03)
BARC <sup>g</sup> (RE/BW <sup>0.750</sup> )	0.751	0.833	-1.86 (-8.05 to 4.33)	0.852 (0.722 to 0.983)
BARC (RE)	0.841	0.872	0.708(0.406 to 1.01)	0.708 (0.627 to 0.790)

<sup>1</sup>RE = recovered energy, MEI = ME intake,  $\text{ME}_m$  = MEI at RE = 0,  $k_g$  = efficiency of ME utilization for gain.

<sup>a</sup>Lin's concordance coefficient.

<sup>b</sup>Intercept or slope of the function predicted RE = intercept + slope  $\times$  observed RE, RE = recovered energy, either as Mcal/BW<sup>0.750</sup>  $\times$  d<sup>-1</sup> or as Mcal/d.

<sup>c</sup>Data described in Table 1 found in [Lofgreen and Garrett \(1968\)](#).

<sup>d</sup>RE (Mcal/BW<sup>0.750</sup>  $\times$  d<sup>-1</sup>) = [MEI (Mcal ME/ BW<sup>0.750</sup>  $\times$  d<sup>-1</sup>) - 0.124 (Mcal ME/ BW<sup>0.750</sup>  $\times$  d<sup>-1</sup>)]  $\times$  0.437;  $\text{ME}_m$  = 8.2 (Mcal ME/d),  $k_g$  = 0.390.

<sup>e</sup>RE (Mcal/d) = [MEI (Mcal ME/d) - 8.2 (Mcal ME/d)]  $\times$  0.390,  $\text{ME}_m$  = 8.2 (Mcal ME/d),  $k_g$  = 0.390.

<sup>f</sup>Data described in Table 2 found in [Lofgreen and Garrett \(1968\)](#).

<sup>g</sup>Data courtesy of Christopher K. Reynolds, University of Reading, UK from studies reported in part [Reynolds et al., \(1991\)](#).

**Table 8.** Evaluation of robustness of prediction of RE as  $(\text{MEI} - \text{ME}_m) \times k_g$  for a dynamic estimate of  $\text{ME}_m$ 

Data set	Parameter estimate			
	$R^2$	$\rho_c^a$	Intercept <sup>b</sup> ( $\pm$ 95% CI)	Slope <sup>b</sup> ( $\pm$ 95% CI)
LG1 <sup>c</sup> (RE/BW <sup>0.750</sup> ) <sup>d</sup>	0.790	0.819	7.56 (-0.174 to 15.3)	1.01 (0.815 to 1.21)
LG1 (RE) <sup>e</sup>	0.773	0.809	0.444 (-0.180 to 1.07)	1.06 (0.841 to 1.28)
LG2 <sup>f</sup> (RE/BW <sup>0.750</sup> ) <sup>d</sup>	0.968	0.950	1.26 (-2.00 to 4.53)	0.961 (0.898 to 1.02)
LG2 (RE) <sup>d</sup>	0.972	0.941	-0.00240 (-0.238 to 0.233)	0.996 (0.936 to 1.06)
BARC <sup>g</sup> (RE/BW <sup>0.750</sup> ) <sup>d</sup>	0.751	0.833	1.49 (-4.78 to 7.75)	0.852 (0.715 to 0.978)
BARC (RE) <sup>e</sup>	0.842	0.871	1.03 (0.717 to 1.34)	0.726 (0.642 to 0.809)

<sup>1</sup>RE = recovered energy, MEI = ME intake,  $\text{ME}_m$  = MEI at RE = 0,  $k_g$  = efficiency of ME utilization for gain.

<sup>a</sup>Lin's concordance coefficient.

<sup>b</sup>Intercept or slope of the function predicted RE = intercept + slope  $\times$  observed RE, RE = recovered energy, either as Mcal/BW<sup>0.750</sup>  $\times$  d<sup>-1</sup> or as Mcal/d.

<sup>c</sup>Data described in Table 1 found in [Lofgreen and Garrett \(1968\)](#).

<sup>d</sup>RE (Mcal/BW<sup>0.750</sup>  $\times$  d<sup>-1</sup>) = [MEI - (89.98  $\times$  e<sup>0.002292x MEI</sup> - 49.86  $\times$  e<sup>-23.38 x MEI</sup>)]  $\times$  0.6582,  $\text{ME}_m$  = (89.98  $\times$  e<sup>0.002292x MEI</sup> - 49.86  $\times$  e<sup>-23.38 x MEI</sup>) Mcal ME/BW<sup>0.750</sup>  $\times$  d<sup>-1</sup>,  $k_g$  = 0.6582.

<sup>e</sup>RE (Mcal/d) = [MEI - (8.613  $\times$  e<sup>0.02258 x MEI</sup> - 5.732  $\times$  e<sup>-0.09007 x MEI</sup>)]  $\times$  0.6756,  $\text{ME}_m$  = 8.613  $\times$  e<sup>0.02258 x MEI</sup> - 5.732  $\times$  e<sup>-0.09007 x MEI</sup> Mcal ME/d,  $k_g$  = 0.6756.

<sup>f</sup>Data described in Table 2 found in [Lofgreen and Garrett \(1968\)](#).

<sup>g</sup>Data courtesy of Christopher K. Reynolds, University of Reading, UK from studies reported in part [Reynolds et al., 1991](#).

estimates of efficiencies of ME utilization are inconsistent with theoretical estimates, suggest that classical models inappropriately partition HE. Variability in Model 1 parameter estimates, for both OLS and Bayesian frameworks, indicates that H<sub>c</sub>E and  $\text{ME}_m$  as described by [Lofgreen and Garrett \(1968\)](#) and calculated for Model 1 may not be equal to the true parameters, therefore, the model is incorrectly specified. Our analysis also suggests that descriptions of input-output relationships based on Models 1 and 2 fail to conform to the laws of thermodynamics. Classically determined  $k_m$  and  $k_g$  reported in this study indicate an underestimate of MEI used for service and repair functions and an overestimate of MEI used for gain of biomass as

a result of assignments of static values to H<sub>c</sub>E and  $\text{ME}_m$ . Consequently, classically estimated  $k_m$  and  $k_g$  are at odds with the thermodynamic favorability of ATP ( $k_m$ ) or biomass synthesis ( $k_g$ ). The relative magnitudes of classically estimated efficiencies of ME utilization are akin to requiring that cold ice melt and warm water freeze. Ordinary least squares regression models, such as those used by [Lofgreen and Garrett \(1968\)](#), yield parameter estimates for Models 1 and 2 such that  $\Sigma (\text{OBSERVED} - \text{PREDICTED})^2$  is a minimum. It has been assumed that Models 1 and 2 represent the true functional relationship between either HE and MEI or RE and MEI; the only correct assumption may be that  $\Sigma (\text{OBSERVED} - \text{PREDICTED})^2$  is a minimum.

In a Bayesian framework (Model 3) the point at which RE = 0 is dynamic; maintenance is a continuous function of MEI and estimates of  $k_m$  and  $k_g$  are more similar to efficiencies determined from biochemical pathways. The California Net Energy System is still in use because it predicts animal performance well. Unfortunately, many who utilize the CNES, and other empirical descriptors of energy utilization, fail to understand that those systems are merely mathematical solutions to mathematical problems. An improved understanding of biochemical pathways and stoichiometry, readily available computing power, and the inevitable growth of data storage and sharing, provide a compelling basis that constraints imposed by the linear, monotonic empirical approaches used since the middle 20th century be re-evaluated and rejected if inappropriate as descriptors of energy utilization by animals. The use of such tools should encourage those working in animal energetics to collaborate, integrating and expanding biochemical models already available and to develop new models for use in practical feeding systems.

#### AUTHOR DISCLOSURES

The authors declare no conflicts of interest.

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