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# Partitioning of feed intake into maintenance and gain in growing beef cattle: Evaluation of conventional and Bayesian analyses

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**ABSTRACT:** The robustness of efficiency estimates depends on theoretical consistency of models from which those estimates are developed; functional forms of the variables must be globally consistent with theoretical properties regarding feed utilization for maintenance and gain in growing and finishing cattle. Model parameter estimates and their dimensions must be unique or estimates of feed utilization and gain will not reflect reality. A linear equation commonly used to estimate daily DMI by the  $i$ th individual animal (ADFI <sub>$i$</sub> ), based on mean weight and gain during a feeding period, was evaluated to determine if that model was correctly specified and if the vector predicted ADFI differed from the vector observed ADFI. Three independently gathered data sets were evaluated using a multiple linear regression model; variability described by that model failed to capture observed variability in the data (lack of fit,  $P < 0.10$ ), and predicted ADFI differed from observed ( $P < 0.05$ ); for 1 of the 3 data sets, residuals were not normally distributed ( $P < 0.001$ ). Functional forms of

the variables in the first model evaluated, characterizing ADFI required for maintenance ( $b_1 \times BW^{0.75}$ ) and gain ( $b_2 \times ADG$ ), were consistent with neither published empirical nor theoretical relationships among ADFI, BW, and ADG. Parameter estimates determined for that linear model were not BLUE. Better fits among final BW, initial BW, and ADFI were found for a first-order relationship, in which final BW was a function of initial BW and ADFI, as indicated by  $R^2 > 0.90$ . The linear model and, to a lesser degree, the first nonlinear model lacked theoretical and global consistency. A second nonlinear model, which described retained energy as a function of ME intake, best fit the data, and functional forms of variables describing ME intake at maintenance and the efficiency of ME utilization for gain were consistent with theoretical estimates found in the literature. Changes in feed intake and live BW in linear and nonlinear models failed to adequately describe efficiencies of metabolic processes, which are better characterized by changes in retained energy as a function of ME intake in nonlinear models.

**Key words:** beef cattle, efficiency, mathematical modeling, nonunique solutions, residual feed intake

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## INTRODUCTION

Biology and the laws of thermodynamics place limits on the efficiency of ME utilization for either service and repair functions or gain of biomass. If the relationship between predictor and response variables is correctly specified, functional forms of variables will be globally consistent with theoretical estimates. Koch et al. (1963) estimated ADFI and

ADG in cattle as linear functions of the other; sign and magnitude of residuals were indicative of differences in efficiency. Subsequent investigators (Archer et al., 1997) used linear equations different from those reported by Koch et al. (1963). In either case, estimating equations base measurements of efficiency on changes in BW and/or ADFI, the former was considered by Swift (1942) to be without critical scientific value, preferring changes in energy retention.

Koch et al. (1963) and Archer et al. (1997) assumed residuals were indicators of efficiency and treated residuals as parameter estimates, which demands accuracy of prediction. Model specification

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refers to the choice of a model that correctly defines the relationship between predictors and responses. Improper specification results in biased and inconsistent estimators. To assign biological meaning to residuals, the stated goal of the residual feed intake (**RFI**) approach (Kolath et al., 2006), parameter estimates must have biological meaning where biological meaning is dependent on the accurate prediction of the vector ADFI as well as proper model specification. Given that models and studies designed to estimate differences in observed and predicted individual ADFI are part of a genetic selection index (Koch et al., 1963), failure of models to meet all of these criteria will result in improper inference regarding efficiency.

This study was undertaken to evaluate predictive accuracy, theoretical consistency, and stability of parameter estimates for linear and first-order functions describing the relationships between BW change and ADFI.

## MATERIALS AND METHODS

### Data and Analysis

Data were obtained from the author of a study conducted at the University of California, Davis (Cruz et al., 2010); from a study conducted at the Roman L. Hruska U.S. Meat Animal Research Center (**MARC**; courtesy of Harvey Freetly, USDA ARS, Clay Center, NE, personal communication); or gleaned from the literature (Lofgreen and Garrett, 1968).

Cattle in the Cruz et al. (2010) study were Angus–Hereford crossbred steers ( $n = 60$ ) individually fed a diet consisting of (DM basis) 80% cracked corn, 5% alfalfa hay, 5% oat hay, 4% molasses, and 2% fat and the balance (4.8%) consisting of minerals and feed additives. Reported ME of the diet was 2.59 Mcal/kg DM. Initial animal BW (**BW**<sub>0</sub>) was 338 kg, final BW (**BW**<sub>f</sub>) was 423 kg, and ADG was 1.43 kg. Cattle in this study were fed for 60 d.

Cattle in the MARC study were spring-born castrated male calves ( $n = 187$ ) out of crossbred cows bred to crossbred bulls. Steers were weaned into a feedlot at MARC and fed a grower diet before transport (690 km) to Colorado State University (Fort Collins, CO) where they were placed in a GrowSafe (Airdrie, AB, Canada) feeding system for 3 wk before the initiation of the study. Total DMI by each individual during the 70-d feeding period was calculated using the GrowSafe feeding system. Steers had ad libitum access to feed, which consisted of (DM basis) 15.5% alfalfa hay, 73.4% corn, and 6.3% corn silage, with the remainder being a mineral supplement. Metabolizable energy of the diet was reported as 2.91 Mcal/kg DM. Initial BW averaged 432 kg and steers averaged 353 d of age at the beginning of the feeding

period. Steers were weighed on Days 0, 13, 27, 41, 55, and 70 of the feeding period. A quadratic equation ( $BW_f = BW_0 + at + bt^2$ ) was fit to BW versus time for each animal;  $BW_f$  was the solution for the equation at 70 d and initial BW was the intercept. Final BW averaged 545 kg, and ADG averaged 1.61 kg.

The final study evaluated was that of Lofgreen and Garrett (1968) in which 208 British crossbred steers and heifers were fed at 3 discrete levels from retained energy (**RE**) = 0 to ad libitum intake (**AL**). Five diets were fed, and they varied from 2 to 100% concentrate. Mean BW was 280 kg and empty body gain ranged from -0.040 to 1.38 kg/d. In contrast to data from Cruz et al. (2010) and MARC, ADG was nonstochastic; that is, it was controlled by the investigators, as stochastic predictor variables produce biased parameter estimates (Gunst and Mason, 1980).

The equation used to estimate ADFI for an individual in 2 studies was

$$ADFI_i = a + b_1 \times BW_i^{0.75} + b_2 \times ADG_i + r_i [1]$$

in which daily DMI by the  $i$ th individual animal (**ADFI** <sub>$i$</sub> ) is daily DMI (kg DM/d) by the  $i$ th individual, the vector **ADFI** = (ADFI<sub>1</sub>, ADFI<sub>2</sub>, ..., ADFI <sub>$n$</sub> ),  $a$  is the intercept (kg DM/d),  $b_1$  is a coefficient (kg DM/d  $\times$  BW<sup>-0.75</sup>),  $b_2$  is a coefficient (kg DM/d  $\times$  ADG<sup>-1</sup>),  $BW_i^{0.75}$  is the average BW for an individual raised to the 0.75 power, and  $r_i$  is the residual for the  $i$ th observation. Residual feed intake is calculated as observed ADFI <sub>$i$</sub>  minus predicted ADFI <sub>$i$</sub> . Average BW was calculated for the  $i$ th individual so as to be the least squares mean BW ( $\psi$  such that  $\psi$  minimizes  $\Sigma(BW_i - \psi)^2$ , and ADG <sub>$i$</sub>  is BW gain by the  $i$ th individual (kg/d). For Cruz et al. (2010), least squares mean BW was 380 kg; for MARC, least squares mean BW was 488 kg; and for Lofgreen and Garrett (1968), least squares mean BW was 281 kg. Lofgreen and Garrett (1968) did not report ADFI <sub>$i$</sub> , but they did report daily ME intake (**MEI**); MEI for the  $i$ th individual (**MEI** <sub>$i$</sub> , Mcal/d) replaces ADFI <sub>$i$</sub>  in Model [1] for analyses of Lofgreen and Garrett (1968) data. Model [1] was also evaluated without an intercept term. Transformations of  $BW_i$  to either  $BW_i^{0.75}$  or  $BW_i^x$ , in which  $x$  is a scaler, were evaluated to determine if model specification was improved.

According to Wang et al. (2012), the term  $b_1 \times BW^{0.75}$  represents maintenance; the biological relevance of this statement was evaluated by multiplying  $b_1$  by the appropriate ME. The product  $b_1 \times ME$  (Mcal/kg) was compared to published estimates of coefficients of maintenance (Mcal ME/BW<sup>0.75</sup>) for MEI at RE = 0 (Lofgreen and Garrett, 1968; Old and Garrett, 1987). Relevance of  $b_2 \times ADG$  was determined by estimating the efficiency with which ME was used

for energy deposition ( $k_g$ ), where RE was calculated as either  $0.0557 \times BW^{0.75} \times ADG^{1.097}$  (Mcal/d) for Cruz et al. (2010) or  $0.0493 \times BW^{0.75} \times ADG^{1.097}$  for MARC cattle (NRC, 1984). Metabolizable energy intake available for energy deposition, per kilogram ADG, was calculated as  $b_2 \times ADG \times ME$  (Mcal/kg), so therefore,  $RE/[b_2 \times ADG \times ME$  (Mcal/kg)] is the efficiency (NRC, 1981) with which ME is used for energy deposition (the ratio of useful energy delivered by a dynamic system to the energy supplied to it).

Criteria for evaluating parameter estimates for all models included measures of accuracy of prediction. Model validity was examined internally using regressions of predicted ADFI versus observed ADFI and bootstrapping (Efron, 1979) and examined externally using the alternate data set; data from MARC were evaluated using Cruz et al. (2010) parameter estimates and vice versa. Models were considered valid when bootstrapped parameter estimates did not differ from ordinary least squares (OLS) parameter estimates (within a data set) and regressions of predicted ADFI versus observed ADFI yielded slopes that were not different from 1.00 nor were intercepts different from 0, internally and externally. Parameter estimates  $a$ ,  $b_1$ , and  $b_2$  were also obtained from the literature (Basarab et al., 2003; Tedeschi et al., 2006; Mader et al., 2009; Mujibi et al., 2010) for evaluation of Model [1] global consistency.

Parameter estimates and model specification (i.e., parametric stability) were further evaluated by Markov chain Monte Carlo (MCMC) simulation using WinBUGS in R (Lunn et al., 2000; Martin et al., 2011). Informed priors for Cruz et al. (2010) were either  $a = 0$ ,  $b_1 = 0.0506$ , and  $b_2 = 4.47$  or  $a = 0$ ,  $b_1 = 0.0625$ , and  $b_2 = 2.95$ , whereas those for MARC were either  $a = 0$ ,  $b_1 = 0.045$ , and  $b_2 = 4.79$  or  $a = 0$ ,  $b_1 = 0.0557$ , and  $b_2 = 2.83$ . Informed priors for Cruz et al. (2010;  $a = 0$ ,  $b_1 = 0.0506$ , and  $b_2 = 4.47$ ) and MARC ( $a = 0$ ,  $b_1 = 0.045$ , and  $b_2 = 4.79$ ) are consistent with empirical estimates of ME utilization from Lofgreen and Garrett (1968): Maintenance energy intake at RE = 0 Mcal/d ( $ME_m$  or maintenance (NRC, 1981)) was estimated to be  $0.131 \times BW^{0.75}$  Mcal/d and  $k_g = 0.432$ . Informed priors for Cruz et al. (2010;  $a = 0$ ,  $b_1 = 0.0625$ , and  $b_2 = 2.95$ ) and MARC ( $a = 0$ ,  $b_1 = 0.0557$ , and  $b_2 = 2.83$ ) are consistent with theoretical efficiencies of ME utilization for maintenance and gain in growing beef cattle (Baldwin, 1968, 1995; Williams and Jenkins, 2003; Kennedy and Calvert, 2014). For the latter analysis,  $ME_m$  was  $0.163 \times BW^{0.75}$  Mcal/d and  $k_g = 0.650$ . A 100,000 simulation burn-in (presumed convergence of parameter estimates) was followed by 100,000 simulations for each data set, for which means and credible intervals were estimated. In addition to the parameter estimates in Model [1], the power to which BW (informed prior = 1) was raised was

variable in this evaluation rather than the fixed value of 0.75 as found in Model [1]. Bayesian analysis evaluates the probability about parameter estimates with fixed bounds; if the 95% credible interval about 1.0 included 0.75, then the conclusion would be that no difference existed. Transformation of predictor variables is presumed to increase accuracy of prediction; unless accuracy is increased, model simplicity is preferred.

If parameter estimates calculated for RFI studies are unbiased, then  $E(\mathbf{b}) = \boldsymbol{\beta}$  and the expectation is that for many different samples, the averages of observed parameter estimates  $E(\mathbf{b})$  are equal to the true parameter  $\boldsymbol{\beta}$ . Given the stochastic nature of predictor variables BW and ADG (which were observed, not controlled) in RFI studies, multiple evaluations were used to determine if this expectation is correct and the model is generally applicable. In addition to previously mentioned validations, a reference animal was developed from Table 1 data in Lofgreen and Garrett (1968) to test partitioning (presumed maintenance and gain) of  $ADFI_i$  for parameter estimates in the literature (Basarab et al., 2003; Tedeschi et al., 2006; Mader et al., 2009; Mujibi et al., 2010; or calculated by us for this study). The first reference animal (an average of 31 observations) weighed 280 kg and gained 0.521 kg/d (empty body) and RE was 2.15 Mcal/d and MEI was 14.1 Mcal/d. Average daily feed intake was partitioned into an intercept ( $a$ ), that used for maintenance ( $b_1 \times BW^{0.75}$ ) and that used for gain ( $b_2 \times ADG$ ); diet  $NE_g$  (Mcal/kg) was calculated as  $RE/(b_2 \times ADG)$ . Reference animals ( $n = 6$ ) were also developed from Old and Garrett (1987) data to compare predicted versus observed ADFI and efficiencies of ME utilization based on parameter estimates previously cited. In Old and Garrett (1987), Hereford and Charolais steers were fed for AL and also at ADFI to allow gains of 70 and 85% of the rate of steers (of either breed) fed for AL; predictor variables BW and ADG were, therefore, nonstochastic. For the average animal ( $n = 144$ ; 24/treatment), initial empty BW was 237 kg, ADG was 0.820 kg/d (empty body), final weight of the empty body was 419 kg, RE was 4.01 Mcal/d, ADFI was 7.43 kg/d DM, and MEI was 20.2 Mcal/d. Average daily feed intake was partitioned as previously described. General model and individual parameter estimate validity were evaluated comparing predicted and observed ADFI. When the intercept of the OLS regression of predicted versus observed was not different from 0 nor was the slope different from 1.00, the regression was considered to be valid. Estimates of ADFI partitioning (maintenance and gain) and dietary  $NE_g$  were compared to those reported by Old and Garrett (1987). Predicted changes in ADFI with respect to changes in ADG are assumed to be linear in Model [1]; this assumption was evaluated by comparing the first derivative of  $b_2$  with respect to ADG calculated for Model

**Table 1.** Ordinary least squares and Bayesian parameter estimates for Model [1]<sup>1,2</sup>

| Data set <sup>3</sup>      | Parameter estimate   |                       |                       | R <sup>2</sup> | RSS <sup>4</sup> |
|----------------------------|----------------------|-----------------------|-----------------------|----------------|------------------|
|                            | <i>a</i>             | <i>b</i> <sub>1</sub> | <i>b</i> <sub>2</sub> |                |                  |
| Cruz (OLS)                 | 0.443 (−2.46, 3.35)  | 0.063 (0.040, 0.087)  | 2.76 (1.68, 3.83)     | 0.421          | 35.1             |
| Cruz (BSO)                 | 6.10 (5.84, 6.38)    | 0.025 (0.023, 0.028)  | 1.09 (0.954, 1.18)    | 0.083          | 48.3             |
| Cruz (MCMC1)               | 0.00 (−0.196, 0.196) | 0.051 (−0.145, 0.248) | 4.47 (4.27, 4.67)     | 0.500          | 97.5             |
| Cruz (MCMC2)               | 0.00 (−0.197, 0.197) | 0.063 (−0.133, 0.258) | 2.95 (2.75, 3.15)     | 0.440          | 37.7             |
| MARC (OLS)                 | −2.66 (−4.25, −1.08) | 0.098 (0.081, 0.155)  | 1.80 (1.33, 2.27)     | 0.645          | 114              |
| MARC (BSO)                 | 2.91 (2.67, 3.15)    | 0.054 (0.051, 0.056)  | 1.18 (1.12, 1.24)     | 0.326          | 199              |
| MARC (MCMC1)               | 0.00 (−0.196, 0.197) | 0.045 (−0.151, 0.241) | 4.69 (4.59, 4.79)     | 0.555          | 784              |
| MARC (MCMC2)               | 0.00 (−0.196, 0.197) | 0.056 (−0.140, 0.252) | 2.83 (2.63, 3.03)     | 0.601          | 133              |
| Lofgreen and Garrett (OLS) | 3.96 (−9.25, 17.2)   | 0.060 (−0.155, 0.275) | 11.5 (7.92, 15.1)     | 0.854          | 147              |

<sup>1</sup>ADFI =  $a + b_1 \text{BW}^{0.75} + b_2 \text{ADG}$ ; ADFI (kg/d) is predicted by  $\text{BW}^{0.75}$  (kg<sup>0.75</sup>) and ADG (kg BW change/d).

<sup>2</sup>For Lofgreen and Garrett, the model is ME intake =  $a + b_1 \text{BW}^{0.75} + b_2 \text{ADG}$ ; ME intake (Mcal/d) is predicted by  $\text{BW}^{0.75}$  (kg<sup>0.75</sup>) and ADG (kg BW change/d).

<sup>3</sup>Parameter estimates are shown with 95% confidence interval in parentheses for ordinary least squares (OLS) means and bootstrapped for the observations for 1,000 iterations (BSO) and with 95% credible interval for MCMC1 and MCMC2. MCMC1 and MCMC2 = Markov chain Monte Carlo simulations; for MCMC1 and MCMC2, informed priors for  $b_2$  were such that efficiencies of ME utilization for gain were 0.432 and 0.650, respectively. Data for Cruz are from Cruz et al. (2010), those for MARC were obtained from an unpublished study (H. Freely, MARC USDA ARS, Clay Center, NE, personal communication) at the Roman L. Hruska U. S. Meat Animal Research Center (MARC), and data for Lofgreen and Garrett are from Lofgreen and Garrett (1968).

<sup>4</sup>RSS = residual sum of squares.

[1] to estimates found in Lofgreen and Garrett (1968) or found in editions of the National Academy of Sciences NRC publications entitled *Nutrient Requirements of Beef Cattle* (NRC, 1984, 1996, 2000).

Koch et al. (1963) noted that unless biological functions are accurately described, interpretations are likely to be faulty. These investigators further suggested that a quadratic regression equation, which is a linear regression (Gunst and Mason, 1980), would describe relationships “with almost as much precision as more complex mathematical curves” (Koch et al., 1963). A definition of feed efficiency given by these authors was gain in BW (**dBW**) resulting from consumption of a given amount of diet (**dADFI**). If  $\text{dBW}/\text{dADFI}$  is a function of BW, then the solution is the first derivative, which is

$$\text{BW}_{\text{fi}} = \text{BW}_{0i} e^{k \text{ADFI}_{ci}} + r_i, \quad [2]$$

in which  $\text{BW}_{\text{fi}}$  is final BW (kg) for the  $i$ th individual,  $\text{BW}_{0i}$  is the initial animal BW (kg) for the  $i$ th individual,  $k$  is a rate constant ( $\text{ADFI}^{-1}$ ), and  $\text{ADFI}_{ci}$  is cumulative DMI (kg) by the  $i$ th individual. For both Cruz et al. (2010) and MARC data sets, this equation was evaluated to determine if  $\text{BW}_f$  was a first-order function of  $\text{BW}_0$  and cumulative DMI (Lasdon et al., 1978). Rate constants were evaluated using MCMC simulation using WinBUGS in R (Lunn et al., 2000). A 100,000 simulation burn-in (presumed convergence) was followed by a sample of 100,000 simulations for each data set. Differences in initial body composition or in composition of gain would lead to lack of uniqueness of solution for  $k$ . Solutions to Model [2] were therefore calculated on distinct intervals; rate constants were determined (Lasdon et al., 1978) for each individual ( $k_i$ ) in either data set.

An assumption in Model [1] is that maintenance is discrete and may be described as  $b_1 \times \text{BW}^{0.75}$ ; the following model (Baldwin, 1995) was used to evaluate uniqueness of maintenance:

$$\text{RE}_i = \{\text{MEI}_i - [\alpha \times e^{(\kappa \times \text{MEI}_i)}]\} \times k_g + r_i, \quad [3]$$

in which  $\alpha$  is a parameter estimate (Mcal/d),  $\kappa$  is a rate constant [ $(\text{Mcal ME/d})^{-1}$ ], and  $\text{MEI}_i$  is ME intake (Mcal/d) by the  $i$ th individual. Parametric stability for Model [3] was evaluated using MCMC simulation using WinBUGS in R (Lunn et al., 2000). Data from Lofgreen and Garrett (1968) were evaluated using Model [3]. Swift (1942) preferred the use of carbon and nitrogen balance rather than ADG to characterize change in body substance. To test the assumption that  $b_2 \times \text{ADG}$  characterizes change in body substance,  $\text{ADFI}_i$  and  $\text{ADG}_i$  in Model [1] (with and without an intercept) were replaced with  $\text{MEI}_i$  and  $\text{RE}_i$ , respectively. Only data from Lofgreen and Garrett (1968), who reported RE, were used in this assessment. Validity was evaluated internally and externally for linear solutions as previously described; the external validation was data from Table 2 in Lofgreen and Garrett (1968). Bootstrapping was not used to test validity of Model [3].

It is expected that residuals are a sample from the normal density. To determine if they met this expectation, observed samples (Model [1]) were tested in order. Normality was determined using the eponymous test described by Shapiro and Wilk (1965), computed using the algorithm of Royston (1995) in R (R development core team, 2008) or, for the 0-intercept model, the Wald Wolfowitz runs statistic in R (Swed and Eisenhart, 1943). Tests for skewness (D’Agostino,

**Table 2.** Internal and external validation of Model [1] for data of Cruz et al. (2010) and data from Roman L. Hruska U. S. Meat Animal Research Center (MARC)<sup>1</sup>

| Data set | Validation source                    | Parameter estimate <sup>2,3</sup> |                        | $R^2$ | $P^4$              |
|----------|--------------------------------------|-----------------------------------|------------------------|-------|--------------------|
|          |                                      | $a$                               | $b$                    |       |                    |
| Cruz     | Internal                             | 5.69 (4.42 to 6.97)               | 0.421 (0.292 to 0.550) | 0.421 | <0.00 <sup>a</sup> |
| Cruz     | MARC (OLS) <sup>5</sup>              | 3.64 (1.87 to 5.42)               | 0.477 (0.298 to 0.656) | 0.645 | <0.00 <sup>a</sup> |
| Cruz     | Tedeschi et al. (2006)               | 6.27 (5.34 to 7.20)               | 0.438 (0.213 to 0.402) | 0.419 | <0.00 <sup>a</sup> |
| Cruz     | Mader et al. (2009)                  | 3.06 (1.43 to 4.69)               | 0.438 (0.273 to 0.603) | 0.421 | <0.00 <sup>a</sup> |
| Cruz     | Mujibi et al. (2010) 1 <sup>6</sup>  | 4.98 (2.60 to 7.36)               | 0.609 (0.368 to 0.850) | 0.302 | <0.00 <sup>a</sup> |
| Cruz     | Mujibi et al. (2010) 2 <sup>6</sup>  | 4.87 (2.60 to 7.13)               | 0.526 (0.297 to 0.755) | 0.263 | <0.00 <sup>a</sup> |
| Cruz     | Basarab et al. (2003) 1 <sup>6</sup> | 6.85 (4.89 to 8.80)               | 0.529 (0.332 to 0.726) | 0.328 | <0.00 <sup>a</sup> |
| Cruz     | Basarab et al. (2003) 2 <sup>6</sup> | 7.01 (5.81 to 8.60)               | 0.482 (0.321 to 0.644) | 0.378 | <0.00 <sup>a</sup> |
| MARC     | Internal                             | 3.69 (2.96 to 4.42)               | 0.645 (0.575 to 0.715) | 0.645 | <0.00 <sup>a</sup> |
| MARC     | Cruz (OLS)                           | 4.92 (4.14 to 5.69)               | 0.627 (0.553 to 0.700) | 0.603 | <0.00 <sup>a</sup> |
| MARC     | Tedeschi et al. (2006)               | 5.62 (5.04 to 6.21)               | 0.463 (0.408 to 0.519) | 0.593 | <0.00 <sup>a</sup> |
| MARC     | Mader et al. (2009)                  | 3.10 (2.43 to 3.77)               | 0.592 (0.528 to 0.655) | 0.645 | <0.00 <sup>a</sup> |
| MARC     | Mujibi et al. (2010)1 <sup>6</sup>   | 5.20 (4.29 to 6.12)               | 0.811 (0.723 to 0.898) | 0.644 | <0.00 <sup>a</sup> |
| MARC     | Mujibi et al. (2010)2 <sup>6</sup>   | 5.33 (4.55 to 6.12)               | 0.681 (0.606 to 0.756) | 0.635 | <0.00 <sup>a</sup> |
| MARC     | Basarab et al. (2003)1 <sup>6</sup>  | 6.87 (6.06 to 7.68)               | 0.717 (0.640 to 0.794) | 0.645 | <0.00 <sup>a</sup> |
| MARC     | Basarab et al. (2003)2 <sup>6</sup>  | 6.69 (5.92 to 7.47)               | 0.677 (0.603 to 0.751) | 0.638 | <0.00 <sup>a</sup> |

<sup>a</sup>Parameter estimate  $a = 0$  or parameter estimate  $b = 1.00$  ( $P < 0.05$ ).

<sup>1</sup>Observed ADFI =  $a + b(\text{predicted ADFI})$ .

<sup>2</sup>Parameter estimates are shown with 95% confidence interval in parentheses.

<sup>3</sup>Parameter estimates for validation either found in literature or cited in text.

<sup>4</sup> $E(a) = 0$  and  $E(b) = 1$  for a valid model;  $P$  is probability that either  $a$  or  $b \neq 0$ .

<sup>5</sup>OLS = ordinary least squares.

<sup>6</sup>1 or 2: more than one set of parameter estimates in citation.

1970) and kurtosis (Anscombe and Glynn, 1983) of the residuals were computed in the moments utility of R in which the probability distribution of the third (skewness) and fourth (kurtosis) central moments were determined (Komsta and Novometsky, 2007).

## RESULTS AND DISCUSSION

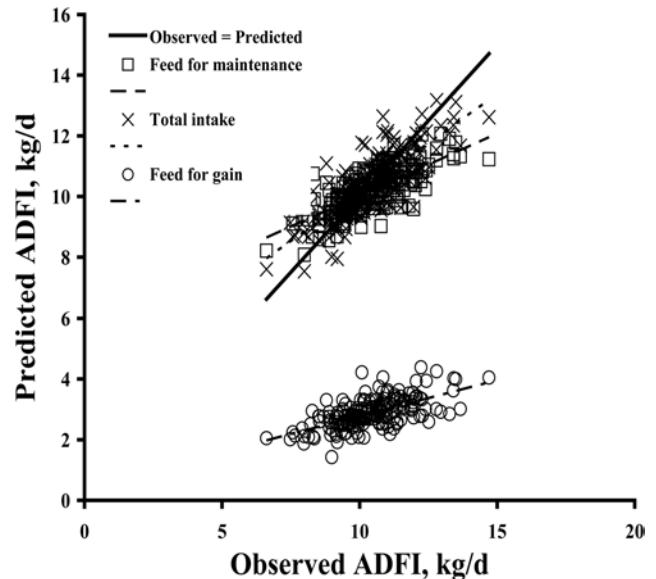
Ordinary least squares, bootstrapped estimators, and MCMC solutions for Model [1] are in Table 1. For data from Cruz et al. (2010), the  $R^2$  for Model [1] is similar to that reported by Tedeschi et al. (2006) and Mao et al. (2013). Basarab et al. (2003) reported an intercept not different from zero, albeit the  $R^2$  was greater. Low  $R^2$  inherently place limits on conclusions that may be drawn from regression analyses (Gunst and Mason, 1980). Therefore, if the goal is to estimate ADFI, conclusions may be of limited value because of the uncertainty of prediction of ADFI. Irreproducibility of intercepts and parameter estimates  $b_1$  and  $b_2$  for Model [1] within and between data sets is an indication that, even if an individual residual was to have predictive value, the model lacks general applicability. However, if the goal is only to determine the role of  $BW^{0.75}$  and ADG on ADFI prediction in a linear model and to ignore other predictors and models, Model [1] may be adequate, but investigators should be aware of these defects in model speci-

fication. Ninety-five percent confidence intervals for bootstrapped parameter estimates obtained from Cruz et al. (2010) were from 4.05 to 9.15 for the intercept, from 0.008 to 0.042 for  $b_1$ , and from 0.183 to 2.00 for  $b_2$ . Analyses of MARC data resulted in 95% confidence intervals for bootstrapped parameter estimates from 1.39 to 4.42 for the intercept, from 0.040 to 0.068 for  $b_1$ , and from 0.776 to 1.59 for  $b_2$ . Parameter estimates  $a$ ,  $b_1$ , and  $b_2$  for Cruz et al. (2010) and MARC were nonunique and confidence intervals were overly broad, both of which are indicators of parametric instability. Ordinary least squares parameter estimates ( $a$ ,  $b_1$ , or  $b_2$ ) were compared to the corresponding bootstrapped and MCMC parameter estimates; when a 95% confidence interval about the OLS parameter estimate did not include the bootstrapped or MCMC estimator, they were considered different ( $P < 0.05$ ). Bootstrapped estimators were different ( $P < 0.05$ ) than OLS estimators; for models with unstable parameter estimates, inferences are biased and predictions are inaccurate. Ordinary least squares and Bayesian parameter estimates differed for Cruz et al. (2010) and for MARC data ( $P < 0.05$ ). Parameter estimates  $a$  and  $b_1$ , for all MCMC estimates, were not different from 0 ( $P < 0.05$ );  $b_2$  was greater than 0 in all cases. Failure of the model to conform with either empirical (MCMC1) or theoretical (MCMC2) estimates of ME utilization is a further indication of the

lack of robust nature of Model [1]; apparent efficiencies determined for Model [1] are those neither observed in classical energy balance experiments nor based on the biochemistry of ME utilization for maintenance or gain. Causes for variability in  $b_1$  will be subsequently discussed. Variability in  $b_2$  is a function of ME density (Mcal/kg), energy content of gain (Mcal/kg), and the efficiency of ME utilization for energy deposition. For the following ranges that may be expected in growing cattle diets and performance—2.4 to 3.2 Mcal/kg for ME, 4.6 to 5.4 Mcal/kg (40 to 50% fat) for RE, and 0.60 to 0.70 for  $k_g$  (Old and Rossow, 2013)—the range of  $b_2$  is from 2.4 to 3.2 kg ADFI/kg ADG. The estimate of  $b_2$  for Cruz et al. (2010) falls within this range, but that for MARC does not; failure to properly partition ADFI into that required for maintenance and that available for gain is associated with model misspecification.

Overly broad confidence intervals for  $a$  and  $b_1$  (Table 1) combined with relative stability, within a data set, of  $b_2$  indicates dependency of  $a$  and  $b_1$ . Eigenvalues for correlation matrices of magnitude and variability of  $b_1$  (Model [1] and 0 intercept) showed that the presence of an intercept increased variability in  $b_1$ ; eigenvalues were 0.031 and 0.002 for Cruz et al. (2010) and MARC, respectively. In the absence of an intercept, eigenvalues for the correlation matrix of [ $b_1$ , variance  $b_1$ ] were 0.100 for Cruz et al. (2010) and 0.104 for MARC. An eigenvalue of 0 is indicative of a perfect correlation; this analysis indicates that the presence of an intercept inflates variances in  $b_1$ , which is further indication of model misspecification. Variability noted in  $a$  and  $b_1$  may be due to the functional form of the variable ( $b_1 \times BW^{0.75}$ ) poorly accounting for changes in maintenance with changes in ADFI (Fig. 1). If this is correct, that changes in ADFI drive changes in maintenance requirements, then model specification should be changed so that ADFI is a predictor variable.

A lack of fit  $F$  statistic ( $P = 0.049$ ) was noted for Model [1] (OLS solution) for Cruz et al. (2010), an indication that variability in the response is not accounted for by the model (i.e., the model is misspecified) and is consistent with unstable parameter estimates. Evaluation of MARC data resulted in similar findings ( $P = 0.07$ ). Correct model specification means that the exact form of the relationship between response and predictor variables is known, whereas a significant  $F$  ratio for model misspecification means that alternative models should be examined (Mason et al., 2003). Significant lack of fit  $F$  ratios for linear models are indicators of nonlinear relationships between predictor and response variables. Inappropriate sign and magnitude of parameter estimates in Table 1 may be due to the existence of collinearities between  $BW^{0.75}$  and ADG for either data set. Serial correlations were minimal; for Cruz et al. (2010),



**Figure 1.** Partitioning of ADFI predicted for Roman L. Hruska U.S. Meat Animal Research Center (MARC) data by Model [1],  $ADFI\ (kg/d) = a + b_1BW^{0.75} + b_2ADG$ , in which  $a$ ,  $b_1$ , and  $b_2$  are parameter estimates,  $BW$  units are kilograms, and  $ADG$  units are kilograms/day. Feed for maintenance ( $kg/d$ ) =  $b_1BW^{0.75}$ . Total intake ( $kg/d$ ) =  $a + b_1BW^{0.75} + b_2ADG$ . Feed for gain ( $kg/d$ ) =  $b_2ADG$ . Feed for maintenance ( $b_1BW^{0.75}$ ) was not different ( $P < 0.05$ ) from observed ADFI. Predicted ADFI does not equal observed ADFI ( $P < 0.05$ ).

$r = -0.319$ , and for MARC,  $r = 0.456$ . Variance inflation factors were likewise minimal ( $< 1.15$ ), and collinearities did not exist between  $BW^{0.75}$  and ADG. Inappropriate sign and magnitude of parameter estimates in the absence of collinearities are indicative of model misspecification. Parameter estimates for regressions of predicted ADFI versus observed ADFI (OLS) using Model [1] are in Table 2. For neither data set was the slope of predicted versus observed 1.00 nor was the intercept 0 ( $P < 0.01$ ), indicating that ADFI predicted by Model [1] did not describe observed ADFI values. The model, calculated for Cruz et al. (2010), could not be internally validated by bootstrapping nor externally with MARC data (i.e., predicted ADFI did not equal observed ADFI [ $P < 0.05$ ]). The same is true for the Model [1] parameter estimates for MARC data, where the model failed both internal and external validation tests. Model [1] failed further testing of validity when predicted ADFI, calculated using 6 sets of parameter estimates from the literature, did not predict observed ADFI for either data from Cruz et al. (2010) or MARC ( $P < 0.05$ ). Inferences drawn from an individual study are likely to be unique to that study, as Model [1] appears to lack global consistency. Estimates of  $b_2$  (1.65 to 2.33) found in published studies cited in Table 2 were outside the previously noted biologically relevant range, an indication of bias in those estimates. Inferences on observed data (Cruz et al. [2010] and MARC) may be conditional due to the stochastic nature of data collection and limited range of

data, in that the data are not representative of all possible predictor variable values. However, parameter estimates  $a$  and  $b_1$  for measured data (Lofgreen and Garrett, 1968) show even greater variability; those data also represent nearly a 4-fold range in MEI compared to 1.66 for Cruz et al. (2010) and 2.22 for MARC data.

The stated goal for calculation of residuals from Model [1] is to rank animals by residuals; the assumption is differences in observed  $ADFI_i$  – predicted  $ADFI_i$  equate to differences in conversion of  $ADFI_i$  to  $BW_i$ . However, differences in ranking by  $ADFI_i$  and  $r_i$  do little to differentiate individuals; ranking by  $ADFI_i$  for Cruz et al. (2010) is correlated with ranking by  $r_i$  ( $r = 0.761$ ) and ranking by  $ADFI_i$  for MARC is correlated with ranking by  $r_i$  ( $r = 0.600$ ). Predicted ADFI does not equal observed ADFI in any of the data sets evaluated using Model [1]; if predicted ADFI = observed ADFI, it is a possibility that rankings by  $ADFI_i$  and  $r_i$  would be even more similar. Were Model [1] valid, the slope of predicted versus observed would not be different from 1 and the intercept not different from 0; the slope of the predicted line would be approximately parallel to that of the observed line. For the case when the slope = 1.00 and the intercept is not different from 0,  $r_i$  are unique and efficiency, as determined by observed  $ADFI_i$  – predicted  $ADFI_i$ , is the same for all animals. Rankings by  $r_i$  in Model [1] may therefore be a statistical artifact merely reflecting the fact that predicted ADFI  $\neq$  observed ADFI.

Zero-intercept model OLS and bootstrapped parameter estimates (Table 3) for Cruz et al. (2010) were not different; the model passed that test of internal validity. For MARC, parameter estimates  $b_1$  for either OLS or bootstrapped solutions were not different, but  $b_2$  was different. Uniqueness of solution for OLS and bootstrapped parameter estimates for Cruz et al. (2010) indicates that a 0-intercept model better describes those data than does Model [1]. The 0-intercept model failed all tests of external validity ( $P < 0.05$ ). Residual sums of squares were the same or greater for 0-intercept models than for intercept models; for Cruz et al. (2010), parameter estimates  $b_1$  and  $b_2$  (0-intercept models) were slightly more stable for the intercept model but were not different. Ninety-five percent confidence intervals for intercept and 0-intercept models were 0.040 to 0.087 and 0.055 to 0.078 for  $b_1$  and 1.68 to 3.83 and 2.17 to 3.58 for  $b_2$ , respectively. Zero-intercept model parameter estimate ( $b_1$ ) variability (MARC data) was less compared to Model [1] and  $b_1$  was different ( $P < 0.05$ );  $b_2$  magnitude and variability were similar for Model [1] and 0-intercept models. For MARC data, the functional relationship between predictor variables was different for intercept compared to 0-intercept models. The term  $b_1 \times BW^{0.75}$  (intercept model) represented more ADFI ( $P < 0.05$ ) than did the same term in the

**Table 3.** Ordinary least squares and bootstrapped parameter estimates for 0-intercept model for data of Cruz et al. (2010), data from Roman L. Hruska U. S. Meat Animal Research Center (MARC) and data of Lofgreen and Garrett (1968)<sup>1,2</sup>

| Data set <sup>3</sup>      | Parameter estimate <sup>4</sup> |                      | $R^2$ | RSS <sup>5</sup> |
|----------------------------|---------------------------------|----------------------|-------|------------------|
|                            | $b_1$                           | $b_2$                |       |                  |
| Cruz (OLS)                 | 0.067 (0.055 to 0.078)          | 2.88 (2.17 to 3.58)  | 0.549 | 35.1             |
| Cruz (BSO)                 | 0.069 (0.056 to 0.081)          | 2.70 (1.90 to 3.50)  | 0.507 | 35.5             |
| MARC (OLS)                 | 0.072 (0.065 to 0.080)          | 1.83 (1.35 to 2.31)  | 0.549 | 120              |
| MARC (BSO)                 | 0.080 (0.073 to 0.086)          | 1.32 (0.907 to 1.34) | 0.507 | 123              |
| Lofgreen and Garrett (OLS) | 0.124 (0.103 to 0.146)          | 10.7 (8.48 to 12.8)  | 0.842 | 148              |
| Lofgreen and Garrett (BSO) | 0.168 (0.143 to 0.195)          | 4.89 (2.60 to 7.18)  | 0.509 | 290              |

<sup>1</sup> $ADFI = a + b_1 BW^{0.75} + b_2 ADG$ ; ADFI (kg/d) is predicted by  $BW^{0.75}$  ( $kg^{0.75}$ ) and ADG (kg BW change/d).

<sup>2</sup>For Lofgreen and Garrett, the model is ME intake =  $a + b_1 BW^{0.75} + b_2 ADG$ ; ME intake (Mcal/d) is predicted by  $BW^{0.75}$  ( $kg^{0.75}$ ) and ADG (kg BW change/d).

<sup>3</sup>OLS = ordinary least squares; BSO = bootstrapped from the observations for 1,000 iterations.

<sup>4</sup>Parameter estimates are shown with 95% confidence interval in parentheses.

<sup>5</sup>RSS = residual sum of squares.

0-intercept model and ( $b_1 \times BW^{0.75} + b_2 \times ADG$ ) represented  $1.26 \times ADFI$  for the intercept model whereas the same term in the 0-intercept model represented  $1.01 \times ADFI$ . Inflated variances when comparing Model [1] to the 0-intercept model are an indication that the intercept is misspecified. Both Koch et al. (1963) and Archer et al. (1997) assumed that unexplained variability in responses (residuals) was due to differences in greater or less efficiency of utilization of ADFI for maintenance and gain. When, as indicated by our analysis, predicted ADFI does not equal observed ADFI, model misspecification of the type found in Model [1] is as much a source of variation as are individual animal responses. Variation in  $ADFI_i$  must be consistent with animal biology; the additive constant  $a$  in Model [1] has no biological equivalent, as indicated by increased parametric stability for the 0-intercept model, nor does it contribute to variation in predicted  $ADFI_i$ . Variances (Model [1]) for predicted ADFI and predicted  $[ADFI - a]$  (OLS solutions) were equal, yet in the case of MARC and Lofgreen and Garrett (1968) data, predicted ADFI were 34.4 and 39.0% greater, respectively, than  $[ADFI - a]$ . This is explained, in part, by the fact that animals in the MARC data produce 2.66 kg of ADFI before consumption begins ( $a = -2.66$  kg ADFI) and cattle described by Lofgreen and Garrett (1968) data have consumed 3.96 kg of ADFI before they have eaten anything. If Model [1] were correctly specified,  $[ADFI - a]$  for Model [1] would equal  $[ADFI]$  for the 0-intercept model; because,



for Cruz et al. (2010),  $a$  is not different from 0 (Model [1]), only MARC data were evaluated. Slopes of the lines for predicted ADFI versus observed ADFI were not the same ( $P < 0.05$ ) between Model [1] and the 0-intercept model, indicating deviation from a linear response, indicating that the additive constant  $a$  does not function as a true constant. Relative parametric stability (OLS solution) between Cruz et al. (2010) Model [1] and 0-intercept models may be explained by the lesser magnitude of the additive constant. Conclusions drawn regarding differences in  $ADFI_i$  vary depending on model selection (intercept versus 0-intercept); lack of uniqueness of solution indicates that either one or both of the models are incorrectly specified. As such, residuals as indices of efficiency, calculated using Model [1], may reflect the deterministic nature more so than the stochastic characteristics of residuals. Because the deterministic (predictive) function of OLS equations should reside solely in predictor variables, such function in residuals is indicative of model misspecification.

Dry matter intakes, within a study, were overestimated at lesser intakes and underestimated at greater intakes for OLS solutions to Cruz et al. (2010) and MARC data for both intercept and 0-intercept models. Cruz et al. (2011) reported a similar finding, albeit for pen-fed cattle. When comparing steers (Cruz et al. [2010] and MARC) whose  $ADFI_i$  (observed) was less than average with those with observed  $ADFI_i$  greater than average, residuals differed from 0 ( $P < 0.001$ ). For cattle in the Cruz study, for those consuming the least  $ADFI_i$  ( $n = 6$ ), the residual was  $-1.03$  kg/d (SEM = 0.373), and for those consuming the most  $ADFI_i$  ( $n = 6$ ), the residual was  $0.948$  kg/d (SEM = 0.449). For MARC data, residuals were  $-0.882$  kg/d (SEM = 0.159) for least  $ADFI_i$  ( $n = 18$ ) and  $0.829$  kg/d (SEM = 0.183) for greatest  $ADFI_i$  ( $n = 18$ ). Consistent with the lack of model validity (intercept and slope of predicted versus observed not equal to 0 or 1, respectively), significant Model [1] residual bias was noted for Cruz et al. (2010; 0.645), MARC (0.355), and Lofgreen and Garrett (1968; 0.145) data (for all,  $P < 0.05$ ).

Irreproducibility and the existence of an intercept term are troubling from a mathematical and biological standpoint. A negative intercept, which was reported by Mader et al. (2009) and Mujibi et al. (2010) and also found for MARC data (OLS solution), means that steers with neither body mass nor gain produce ADFI until a given mass or rate of gain is obtained. A positive intercept, found for bootstrapped estimates (Cruz et al. [2010] and MARC data) and found in the literature (Basarab et al., 2003), means that cattle with neither mass nor gain consume ADFI. Biologically, the intercept ( $a$  in Model [1]) should be 0 and excluded from that model and, therefore,  $b_1 \times BW^{0.75}$  may represent

maintenance (RE = 0) or, in Model [1], ADG = 0. Zero-intercept models require that the response be 0 when the predictors are likewise 0, which is certainly the case in the biological system described by Model [1]. As previously discussed, for Model [1] and the 0-intercept form to be correctly specified,  $(a + b_1 \times BW^{0.75} + b_2 \times ADG) - (b_1 \times BW^{0.75} + b_2 \times ADG)$  would not be different from  $a$ . The expectation for a 0-intercept RFI model is that  $b_1 \times BW^{0.75}$  represents ADFI at maintenance and that  $b_2 \times ADG$  represents the amount of ADFI required per unit gain and that those are the only 2 terms required in the equation. This interpretation is consistent with the fate of ME in growing cattle, where ME consumed at  $RE \leq 0$  is used almost exclusively as fuel for oxidative mitochondrial metabolism and MEI for  $RE > 0$  is used exclusively for synthesis of animal biomass. Although addition of an intercept term may increase goodness of fit, the functional relationship between  $b_1 \times BW^{0.75}$  and  $b_2 \times ADG$  is altered by such an inclusion as was seen for MARC and Lofgreen and Garrett (1968) data. Koch et al. (1963) noted that the intercept may represent maintenance; it does not appear to do so in Model [1]. In addition, given the nature of ME utilization as a function of energy balance in growing cattle, it is impossible to partition an intercept into either maintenance or gain.

Maintenance is defined as RE = 0 (NRC, 1981); it is a transient and dynamic state unlikely to be observed in growing and finishing beef cattle. Cattle in a positive energy balance do not “flip a switch” and move from “maintenance mode” to “gain mode” when daily MEI  $> ME_m$  as suggested by the structure of Model [1]. Discrete estimates of ME required for maintenance and for gain, such as found in Model [1] and NRC (1984), do not adequately reflect the concomitant biological processes underlying what is called maintenance and gain. Model [1] represents the relationship between input and output as 2 straight lines, whereas Lofgreen and Garrett (1968) showed that, over the range of MEI, the data are better fit to a curve. However, models found in NRC (1984) are generally linear. Analytical tools available to Lofgreen and Garrett (1968) were a Marchant rotary calculator (W. N. Garrett, University of California, Davis, Emeritus Professor of Animal Science, personal communication) and OLS solutions. Use of more complex models may have changed interpretation of the data, but use of linear models to describe nonlinear systems continues to this day. As noted by Baldwin (1995), curvilinearity in the relationship strongly suggests that the milieu of biochemical processes contributing to heat production and RE vary over the continuum of MEI. Representation of these processes in Model [1] as discrete linear functions fails to capture variability in the system, accounting, in part, for pronounced lack of uniqueness and variability in  $a$  and  $b_1$  seen in Table 1.

Metabolizable energy intake at  $ADG = 0$  (i.e., presumed maintenance) for OLS solutions of Cruz et al. (2010) was  $0.164 \times BW^{0.75}$  and for MARC data, it was  $0.286 \times BW^{0.75}$ . For the same type of data, Lofgreen and Garrett (1968) reported a discrete estimate of  $0.131 \times BW^{0.75}$ . Noblet et al. (2013) found that, for animals fed near AL,  $d(\text{fasting heat production})/dMEI$  was 0.13 in turkeys, 0.14 in pigs, and 0.23 in calves, whereas Labussière et al. (2011) demonstrated that increased energy intake increased maintenance energy requirements in both pigs and calves. These latter data indicate that, unlike the assumption of a fixed maintenance in Model [1] and Lofgreen and Garrett (1968) and NRC (1984), maintenance is variable. Basarab et al. (2003) noted increased maintenance requirements and body fat for steers with greater residuals (presumed less efficient) compared to those presumed to be more efficient. The functional form of the variable  $b_1 \times BW^{0.75}$  accounted for 41.0 to 67.4% of  $ADFI_i$  for cattle in Cruz et al. (2010) and 76.3 to 131% of  $ADFI_i$  for cattle in MARC data, and these were different ( $P < 0.05$ ). Feed intake partitioned by Model [1] into  $b_1 \times BW^{0.75}$  for MARC data accounted for an average 98% of  $ADFI$ ; the range was from 76.4 to 131% of  $ADFI_i$  (Fig. 1) and was not different from  $ADFI$  ( $P < 0.05$ ). The latter observation, that cattle required more  $ADFI$  for maintenance than was consumed, is consistent with lack of model specification; the model should not be used with that data set. When ranges of confidence or credible intervals determined by a given model include estimates outside the realm of possibility, such as seen here, serious consideration must be given to exploration of alternative models. Irreproducibility of parameter estimates between data sets and the variable nature of maintenance indicate that the functional form of  $BW^{0.75}$  in Model [1] may lack biological relevance.

For cattle in Cruz et al. (2010), RE was calculated to be 4.96 Mcal/kg ADG ( $0.0557 \times BW^{0.75} \times ADG^{1.097}$  Mcal/d) and  $b_2$  was 2.76 kg ADFI/kg ADG. Cattle in the Cruz et al. (2010) study required an ME input of 7.15 Mcal/kg ADG (2.76 kg ADFI/kg ADG  $\times$  2.59 Mcal/kg ADFI) for the previously calculated output (RE) of 4.96 Mcal/kg ADG, yielding an efficiency of 0.694. This estimate, although at the upper end of the expected range (Old and Rossow, 2014), is biologically relevant (Baldwin, 1968; Kennedy and Calvert, 2014). For MARC cattle, RE was calculated to be 5.37 Mcal/kg ADG and  $b_2$  was 1.80 kg ADFI/kg ADG. Calculations using appropriate values for the MARC data ( $0.0493 \times BW^{0.75} \times ADG^{1.097}$ ) for an RE = 5.37 Mcal/kg ADG,  $b_2 = 1.80$  kg ADFI/kg ADG, and ME = 2.91 Mcal/kg DM indicate that RE is greater than ME available for gain ( $k_g = 1.03$ ). Such efficiency is a violation of the First Law of Thermodynamics, further demonstrating

poor model specification. The OLS solution to Cruz et al. (2010) indicates that, for the average animal, ME was used as fuel for functions comprising maintenance and biomass synthesis (gain) consistent with theoretical estimates of efficiency (Baldwin, 1968; Noblet et al., 2013). The same cannot be said of the solutions to MARC data, because  $b_1 \times BW^{0.75}$  represents 98% of  $ADFI$  and is unlikely to represent maintenance, as all animals, including growing cattle, must use ME consistent with the laws of thermodynamics. Unfortunately, the literature lacks any such assessments as to the consistency of Model [1] parameter estimates with theoretical considerations. Kolath et al. (2006) did examine mitochondrial function in low (presumed efficient) and high (presumed inefficient) RFI cattle and reported no differences. Given that the metabolic fuel supplied by ME in growing animals is used for oxidative mitochondrial metabolism (ATP synthesis for ATP used in service and repair functions) more than for biomass gain, the observation by Kolath et al. (2006) fails to show differences in maintenance. It is possible that differences in mitochondrial efficiency exist but are masked by the failure of Model [1] to accurately partition  $ADFI$  into  $b_1 \times BW^{0.75}$  and  $b_2 \times ADG$ .

Correct model specification is basic to fitting of data if model outputs are to have probative value; it is also a tenet of modeling that the simplest model adequately describing the data is the model of choice (Baldwin, 1995). Assumed in Model [1] is that transformation of measured BW ( $BW^{1.00}$ ) to  $BW^{0.75}$  improves model fit. Our OLS analyses indicate that for Cruz et al. (2010)  $R^2$  for the partial regressions,  $ADFI = f(BW^{0.75})$  or  $ADFI = f(BW^{1.00})$  were identical (0.158). For MARC data, the results were similar;  $R^2$  for the partial regression between  $ADFI$  and  $BW^{1.00}$  was 0.535; for  $ADFI$  and  $BW^{0.75}$ ,  $R^2 = 0.534$ . Transformation of  $BW^{1.00}$  to  $BW^{0.75}$  did not change the relationship between  $ADFI$  and BW. For Model [1], residual sum of squares for an OLS solution was minimized for Cruz et al. (2010) when BW was raised to the 1.30 power (35.0 versus 35.1) and was 35.0 when the exponent was 1.00. A similar reduction in residual sum of squares was noted for MARC data when the exponent was 1.41 and when the exponent was 1.00. Mean square (residual) is a measure of variability. When BW was not scaled by the power of 0.75 (power = 1.00), mean square (residual) was less (0.604 versus 0.605) for data from Cruz et al. (2010). Mean square (residual) for MARC was also less when BW was not scaled; it was 0.616 versus 0.618. Scaling mean live weight by 0.75 did not improve model fit and, as such, is unnecessary. Bernier et al. (1987) evaluated a model similar to Model [1] and noted that coefficients of determination increased when data were not scaled by  $BW^{0.75}$ . Atchley et al. (1976) and Dinkel et

al. (1965) have suggested that the use of ratios, such as scaling by  $BW^{0.75}$ , be avoided as it may lead to biased estimators. Others, such as Kielanowski (1965), have described models similar in form to Model [1] with all predictor and response variables scaled by  $BW^{0.75}$ . In Model [1], transformation is best done to linearize non-linear predictor variables. Markov chain Monte Carlo simulations were used to evaluate the power to which  $BW$  should be raised in Model [1]. Informed priors for parameter estimates  $a$ ,  $b_1$ , and  $b_2$  were equal to OLS solutions for Cruz et al. (2010) and MARC, respectively; the prior for the scaler was 0. Bayesian solutions (biologically relevant) were intractable, indicating that the model is overparameterized. Kleiber (1961) and Brody (1945) describe the relationship between fasting heat production and  $BW$  across species, and for the allometric equation used by those investigators, the exponent of  $BW$  is approximately 0.75. Labussière et al. (2011) reported the exponent to be 0.60 in cattle. Although the exponent is not unique, it is generally acknowledged that the exponents of  $BW$  for equations relating maintenance requirements to  $BW$  are less than unity. Given the relationship between surface area and volume and the laws of physics, if heat production was proportional to  $BW^{1.00}$ , it would be difficult for larger animals to dissipate heat. For our study, exponents of  $BW$  greater than unity suggest that the term  $b_1 \times BW^{0.75}$  may be as descriptive of ADFI required for gain as of that required for maintenance. As has been shown by a number of investigators,  $BW$  is the primary determinant of energy content of gain (Reid et al., 1968; Preston, 1971; Jesse et al., 1976; Old and Garrett, 1987). Given that the transformations of  $BW$  from  $BW^{1.0}$  to  $BW^{0.75}$  has no effect on residual sum of squares calculated for Model [1], the power to which  $BW$  is raised is best left as unity.

Similar to the Bayesian analysis for Cruz et al. (2010) and MARC data, when data from Lofgreen and Garrett (1968) were fitted to Model [1] (Table 1),  $a$  was 3.95 and was not different from 0 (95% confidence interval -9.23 to 17.1),  $b_1$  (0.060) was not different from 0 (95% confidence interval -0.154 to 0.275), and  $b_2$  (11.5) was positive (95% confidence interval 7.92 to 15.1). Variability noted for previously discussed posterior distributions of parameter estimates  $a$  and  $b_1$  is similar to the OLS distribution found here and is consistent with incorrect specification. Inappropriate magnitude and inflated variance of parameter estimate  $b_1$  are indicators of collinearity between  $BW^{0.75}$  and ADG. Average daily gain and  $BW^{0.75}$  were correlated ( $r = 0.836$ ); simple correlations greater than 0.70 are indicators of collinearity and reason to either change model specification or use a biased regression method, such as ridge regression. The variance inflation factor was 3.32; had there been no correlation between predictor variables, the variance would have

been reduced by a factor of 1.82. The model was not internally valid ( $P < 0.05$ ), yet  $R^2 = 0.855$ .

Unlike stochastic predictor variables reported in the vast majority of RFI studies, predictor variables in the Lofgreen and Garrett (1968) study were nonstochastic, which is consistent with the requirements of classical regression theory. Use of stochastic predictor variables may cause forfeiture of some of the optimal properties of least squares estimators, such as unbiasedness and consistency. However, increasing the range of MEI measured in studies of this type increases the likelihood of collinearity between  $BW^{0.75}$  and ADG. Because Model [1] appears to be misspecified, a solution to the issue of collinearities and lack of range of MEI would be to change the structure of Model [1] so that the predictor variable is ADFI (MEI) and ADG (RE) is the response (Koong, 1977; Baldwin, 1995).

The term  $b_1 \times BW^{0.75}$  represented from -86.1 to 153% of MEI, estimates indicating an infeasible solution. To reiterate: When confidence and credible intervals include solutions that are either biologically or thermodynamically infeasible, the model is misspecified. The statement by Wang et al. (2012) that Model [1] term  $b_1 \times BW^{0.75}$  represents maintenance is not borne out by this analysis. Estimated  $k_g$  (RE > 0) was 0.341 (95% confidence interval 0.298 to 0.384); a similar value (0.32) was reported for Hereford cattle by Old and Garrett (1987), who used an approach to estimate efficiencies similar to that found in the NRC (1984). Functional form of the variable  $b_1 \times BW^{0.75}$  was different for an intercept compared to a 0-intercept model; MEI for maintenance (0 intercept),  $0.124 \times BW^{0.75}$ , was not different than the value reported by Lofgreen and Garrett (1968) and  $k_g$  (0.368) was similar to that reported by Old and Garrett (1987). Parameter estimates  $b_1$  and  $b_2$  were more stable for the 0-intercept model, in that variability about the parameter estimates was lessened when compared to Model [1] and functional forms of variables in the model were similar to empirical estimates found in the literature. These observations further indicate that an intercept model fails to adequately characterize utilization of properties of ADFI. Adding terms to Model [1] solely to increase  $R^2$  (Basarab et al., 2003) appears to increase the possibility that functional forms of variables lose biological significance. As was found for all other evaluations, the 0-intercept model for Lofgreen and Garrett (1968; Table 3) was not internally valid ( $P < 0.05$ ), although the intercept (observed versus predicted) was not different from 0 and a 95% confidence about the slope was from 0.724 to 0.995. Bootstrapped parameter estimate  $b_1$  for Lofgreen and Garrett (1968) was different from the OLS estimate; the model was internally invalid. As Model [1] is typically not subjected to lack of fit and validity tests in the litera-

ture, similar reports are not available. The application of linear regression methodologies, such as Model [1], demands that a linear relationship exist between predictor and response variables; one seldom is informed if such a relationship does indeed exist. Additionally, tests of predictive accuracy must be performed to clearly demonstrate that the predicted response is not different from the observed (Gunst and Mason, 1980).

The combination of nonstochastic predictor variables for animals fed from RE = 0 to AL and a 0-intercept model yields parameter estimates not different from empirical observations for data from Lofgreen and Garrett (1968). Differences noted in the relative parametric stability of  $b_1$ , for the 0-intercept model and Model [1], are explained in part by variability in maintenance over the range of MEI. As previously mentioned, the additive constant  $a$  appears to function more as an error term than a true intercept. However, greater concordance with empirical estimates does not indicate biological meaning (Baldwin, 1995) nor does it indicate goodness of model fit as the 0-intercept model was internally invalid ( $P < 0.05$ ). Metabolizable energy intake presumed to be required for maintenance ( $0.124 \times BW^{0.75}$ ) is less than the theoretical average ( $0.156 \times BW^{0.75}$ ) determined by Old and Rossow (2013), and efficiency of ME utilization for gain ( $k_g = 0.341$ ) is approximately half the maximum theoretical estimate of 0.727 (Kennedy and Calvert, 2014). Residual plots of  $r_i$  versus predicted  $ADFI_i$  for Cruz et al. (2010) and MARC (both Model [1] and 0-intercept model) or Model [1] for Lofgreen and Garrett (1968) indicated the  $r_i$  were uncorrelated with predicted  $ADFI_i$ . The same plot, using the 0-intercept model for data from Lofgreen and Garrett (1968), showed a curvilinear trend consistent with the inability of the 0-intercept model to account for increasing maintenance costs as MEI increases. When the data range is no longer limited, unlike Cruz et al. (2010) and MARC, or the additive constant no longer functions as a de facto error term, the need for transformation of predictor variables, or change in model structure, is apparent. Because of the limited data range in most studies of this type and presence of the intercept in Model [1], inferences are conditional and may be unique to a study.

To further evaluate the biological relevance of the relationship  $b_2 \times ADG$ , we calculated the first derivative of Model [1] with respect to ADG. That it is a constant,  $b_2$ , is inconsistent with Lofgreen and Garrett (1968) and various editions of the National Academy of Sciences NRC publications (NRC, 1984, 1996, 2000). From the equation of Lofgreen and Garrett (1968),  $RE = (52.72 \times ADG + 6.84 \times ADG^2) \times BW^{0.75}$ , one may calculate the first derivative with respect to ADG as  $52.72 + 13.68 \times ADG$  and for the NRC (1984) as  $1.097 ADG$ . For the integral  $\int b_2 dADG$ , which rep-

resents the change in ADFI with respect to change in BW in Model [1], the area under the curve is  $b_2 ADG$ . Describing the area under the curve as  $b_2 ADG$  requires that RE (Mcal/kg gain) be constant, inconsistent with reports in the literature (Lofgreen and Garrett, 1968; Old and Garrett, 1987). The function that represents the change in ADFI with respect to change in ADG, as described by Lofgreen and Garrett (1968) is

$$\int (52.72 + 13.68 \times ADG) dADG,$$

and the area under the curve is  $[(52.72 + 13.68 \times ADG)^2]/2 \times 13.68$ . For the NRC (1984) equation, area under the curve is  $(ADG^{2.097})/2.097$ . Therefore, a linear relationship between ADFI and ADG, such as that described by Model [1], estimates ADFI as being less than that actually required for gain. Tedeschi et al. (2006) noted that such a relationship will result in cattle with lesser RFI being leaner than cattle with greater RFI. Because  $b_2$  is linear in each  $ADG_i$  in Model [1], deviation from linearity in the biological relationship between ADFI and ADG indicates that the parameter estimate determined for the term  $b_2$  in Model [1] is not BLUE. That the functional form  $b_2 \times ADG$  does not conform to empirical and theoretical properties of the energy content of weight gain in growing cattle is consistent with an overall lack of biological relevance of model terms. Attempts to assign biological meaning to terms inconsistent with biology may result in faulty conclusions regarding efficiency.

Estimates of ADFI for our Lofgreen and Garrett (1968) reference animal (Table 4) indicate a lack of uniqueness of solution and general applicability of Model [1]. Nearly all ADFI (88.2%) was accounted for, among studies, by  $b_1 \times BW^{0.75}$  (presumed maintenance) and only 14.8% by  $b_2 \times ADG$ . Lofgreen and Garrett (1968) reported  $ME_m = 0.131 \times BW^{0.75}$  or 8.97 Mcal/d ( $BW^{0.75} = 68.4$ ). For the reference animal, total MEI is 14.1 Mcal/d; that required for maintenance is 63.6% of the total (8.97/14.1) whereas that available for gain is 36.4%. However, given the variability in the percentage of ADFI required for presumed maintenance in Model [1] (20.4 to 144%), a 95% confidence interval about the mean (61.8 to 115%) included 63.6. Of total Model [1] predicted ADFI, the average available for gain was 14.8% (range, 6.78 to 23.1%), which differed ( $P < 0.001$ ) from the 36.4% calculated for the reference animal. Of 10 estimates of  $NE_g$  (diet), only the estimate calculated for Cruz et al. (2010) was biologically feasible ( $NE_g = 1.49$  Mcal/kg diet). Because of inappropriate partitioning of ADFI into that for maintenance and gain, the remaining estimates of  $k_g$  were outside the realm of either biological or thermodynamic possibilities, consistent with the previously noted inappropriate functional form of the variable  $b_2 \times$

**Table 4.** Lofgreen and Garrett (1968) reference animal evaluation of parameter estimates for Model [1]<sup>1</sup>

| Equation source <sup>2</sup>         | Predicted ADFI | Parameter estimate |                             |                             | NE <sub>g</sub> (diet) <sup>4</sup> |
|--------------------------------------|----------------|--------------------|-----------------------------|-----------------------------|-------------------------------------|
|                                      |                | a <sup>3</sup>     | b <sub>1</sub> <sup>3</sup> | b <sub>2</sub> <sup>3</sup> |                                     |
| Tedeschi et al. (2006)               | 6.59           | 2.47 (0.375)       | 3.01 (0.457)                | 1.11 (0.168)                | 1.94                                |
| Mader et al. (2009)                  | 4.29           | -2.73 (-0.637)     | 6.16 (1.44)                 | 0.860 (0.201)               | 2.49                                |
| Mujibi et al. (2010) 1 <sup>5</sup>  | 6.82           | -3.14 (-0.460)     | 8.89 (1.30)                 | 1.07 (0.157)                | 2.01                                |
| Mujibi et al. (2010) 2 <sup>5</sup>  | 6.68           | -2.25 (-0.337)     | 8.21 (1.23)                 | 0.719 (0.108)               | 2.98                                |
| Basarab et al. (2003) 1 <sup>5</sup> | 8.31           | -0.140 (-0.017)    | 7.39 (0.889)                | 1.06 (0.127)                | 2.03                                |
| Basarab et al. (2003) 2 <sup>5</sup> | 8.08           | 0.770 (0.095)      | 6.09 (0.754)                | 1.21 (0.150)                | 1.77                                |
| MARC OLS <sup>6</sup>                | 4.98           | -2.66 (-0.534)     | 6.70 (1.35)                 | 0.938 (0.188)               | 2.29                                |
| MARC BSO <sup>7</sup>                | 7.22           | 2.91 (0.403)       | 3.69 (0.512)                | 0.615 (0.085)               | 3.49                                |
| Cruz et al. (2010) OLS               | 6.19           | 0.443 (0.072)      | 4.31 (0.696)                | 1.44 (0.233)                | 1.49                                |
| Cruz et al. (2010) BSO               | 8.38           | 6.10 (0.728)       | 1.71 (0.204)                | 0.568 (0.068)               | 3.78                                |

<sup>1</sup>ADFI =  $a + b_1 \text{BW}^{0.75} + b_2 \text{ADG}$ ; ADFI (kg/d) is predicted by  $\text{BW}^{0.75}$  (kg<sup>0.75</sup>) and ADG (kg BW change/d). For the reference animal,  $\text{BW}^{0.75} = 68.4$ ,  $\text{ADG} = 0.521$  (kg empty body), and retained energy (RE) was 2.15 Mcal/d.

<sup>2</sup>Either found in literature cited or those for MARC were obtained from an unpublished study (H. Freedly, MARC USDAARS, Clay Center, NE, personal communication) at the Roman L. Hruska U. S. Meat Animal Research Center (MARC)

<sup>3</sup>Values in column represent response (ADFI, kg/d) as predicted by the intercept,  $b_1 \text{BW}^{0.75}$  or  $b_2 \text{ADG}$ , for reference animal. Parenthetical values are response/total ADFI.

<sup>4</sup>NE<sub>g</sub> (diet; Mcal/kg) calculated as RE (2.15 Mcal/d) divided by  $b_2$ .

<sup>5</sup>1 or 2: more than one set of parameter estimates in citation.

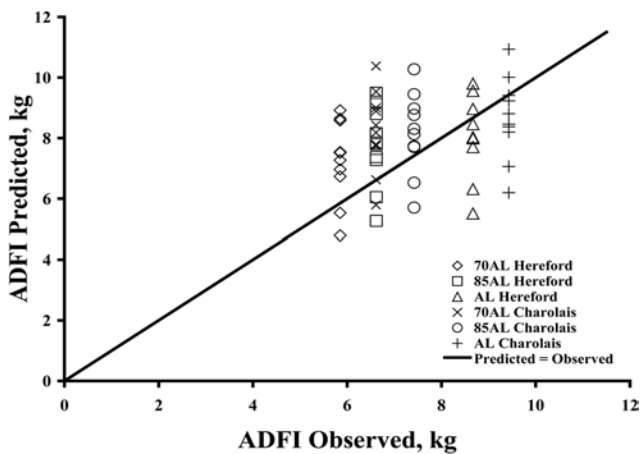
<sup>6</sup>OLS = ordinary least squares.

<sup>7</sup>BSO = bootstrapped from the observations for 1,000 iterations.

ADG. This observation further indicates that Model [1] and its parameter estimates fail to correctly estimate and biologically partition ADFI and efficiencies of ME utilization for maintenance and gain. Estimates of ADFI for the Old and Garrett (1987) reference animals indicated that, similar to Cruz et al. (2010) and MARC data, ADFI was overestimated at lesser intakes and underestimated at greater intakes (Fig. 2) and were not unique. Confidence intervals (95%) about the averages of ADFI, ME<sub>m</sub>, and NE<sub>g</sub> (diet) for 10 RFI estimates did not include values reported by Old and Garrett (1987) with the exception of ADFI for AL Hereford steers. When comparing ADFI predicted by each Model [1] equation to those values observed, we found no intercept equal to 0 ( $P < 0.05$ ). Only the slopes for parameter estimates of Tedeschi et al. (2006), the OLS solution for Cruz et al. (2010), and the bootstrapped parameter estimates obtained for Cruz et al. (2010) were not equal to 0 and none were equal to 1.00 ( $P < 0.05$ ). Maintenance (Mcal ME/d), calculated as  $b_1 \times \text{BW}^{0.75} \times \text{ME}$ , was greater ( $P < 0.01$ ) than ME<sub>m</sub> reported by Old and Garrett (1987), with the exception of Cruz et al. (2010; bootstrapped estimators), which was less ( $P < 0.01$ ), and Tedeschi et al. (2006), which was not different. Estimates of NE<sub>g</sub> were from 1.46 to 4.83 Mcal/kg DM (diet) and were greater ( $P < 0.001$ ) than observed NE<sub>g</sub> values of from 0.780 to 1.18 Mcal/kg DM reported by Old and Garrett (1987). Overestimates of NE<sub>g</sub> (as Mcal/kg DM) means that ADFI available for BW gain, calculated from Model [1], underestimates actual ADFI used for that purpose, thereby further supporting the observation that the relationship between ADG and ADFI is

not adequately described by Model [1]. Old and Garrett (1987) describe ME<sub>m</sub> as a discrete value; of total MEI, that required for maintenance was 47.6% and available for gain was 52.4%. Partitioning of MEI into that used for maintenance and that available for gain by Model [1] is not consistent with partitioning observed in classical energy balance studies reported by Lofgreen and Garrett (1968) and Old and Garrett (1987). Differences in ADFI<sub>i</sub> described by Model [1] fail to conform with well-founded estimates; conclusions regarding differences in animal performance may be an artifact of the statistical properties of the model rather than real, such as differences in efficiencies of ME utilization. For studies reported by Mader et al. (2009) and Mujibi et al. (2010) 1 and 2 and data for MARC, partitioning of ADFI into that used for maintenance exceeded 100% of ADFI, clearly demonstrating inconsistency and bias in estimators.

Durunna et al. (2011) reported that 58% of steers changed RFI ranking from one feed period to the next, and Durunna et al. (2012) reported a similar percentage for heifers (51%). Odds such as these are not greatly dissimilar from that which one might find in completely random events; inferences appear to be greatly conditioned by the observations. That rankings determined by Model [1] are inconsistent over time for the same group of cattle is not surprising based on the lack of correspondence of well-founded theoretical estimates with functional forms of variables in Model [1]. Indeed, when functional forms of predictor variables are incorrectly specified, estimators are biased and so conventional inference procedures will be invalid. When models are incorrectly specified,



**Figure 2.** Predicted ADFI (kg/d) versus observed ADFI (kg/d) for multiple Model [1] parameter estimates; 70AL and 85AL steers of either breed were fed to gain at 70 and 85% of the rate of steers of the same breed fed for ad libitum intake (AL). Data are from Old and Garrett (1987). Parameter estimates were reported by Basarab et al. (2003), Tedeschi et al. (2006), Mader et al. (2009), and Mujibi et al. (2010) or calculated for this study.

predicted ADFI  $\neq$  observed ADFI, magnitude of residuals may be increased due to accumulation of systemwide error in residuals. The only circumstance where residuals may be treated as data is for testing of serial correlation among residuals as suggested by Freckleton (2002).

Model [2] parameter estimates (i.e., rate constants  $k$ ) for the Cruz et al. (2010) and MARC data were 0.000363 (95% credible interval 0.000218 to 0.000500) and 0.000306 (95% credible interval 0.000254 to 0.000357), respectively. Posterior distributions were uninformative and chain convergence was poor when using informed priors. With uninformed priors, chain ( $n = 4$ ) convergence was quite good but required a biologically infeasible solution. Similar to what was noted with Model [1], variability in the relationship between BW change and feed intake was poorly described by Model [2]. As indicated from greater  $R^2$ , which were 0.904 (Cruz et al., 2010) and 0.901 (MARC), this model fit the data better than did Model [1], even though the information contained in the first-order equation is the same as in the RFI equation, that is,  $BW_0$ ,  $BW_{f_i}$  and ADFI. For neither data set (MCMC solution) were slopes (predicted versus observed) equal to 1 or intercepts equal to 0 ( $P < 0.05$ ); increasing  $R^2$  is not a guarantee of predictive success. Changes in  $BW_i$  with respect to changes in ADFI (first derivative of Model [2]) for individuals were not correlated with residuals calculated for either Cruz et al. (2010) or MARC data; correlations were 0.070 and  $-0.037$ , respectively. Residuals determined for an individual ( $r_i$ ) were poorly correlated ( $r = -0.296$ ) with individual rate constants ( $k_i$ ) for Cruz et al. (2010) and poorly correlated as well ( $r = -0.412$ ) with  $k_i$  calculated for MARC data, although the signs of the relationships are indicative of appropriate correlations of

$r_i$  with changes in ADFI $_i$  and BW $_i$ . Rankings by either  $k_i$  or residuals were different ( $P < 0.05$ ). As  $k_i$  increase, ADFI required per unit of BW gain decreases; therefore, it appears that residuals calculated from Model [1] are poorly correlated with unit BW gain per unit ADFI consumed. For Cruz et al. (2010), minimum and maximum  $k_i$  were 0.000218 and 0.000667, respectively. Parameter estimate  $k_i$  range for MARC was from 0.000199 to 0.000505. Although Model [2] clearly lacks adequate predictive accuracy, parameter estimates ( $k$ ) are more stable, in that they are similar in magnitude and sign between studies, than those for Model [1], thereby indicating improved model specification. The importance of initial state in the prediction of outcome is clearly demonstrated in Model [2], a factor ignored in Model [1]. Galyean et al. (2011) noted the importance of including initial state in prediction of performance and ADFI for feedlot cattle. Unlike the first-order Model [2], those investigators developed OLS models for predicting input–output relationships; inclusion of initial state improved predictive accuracy. For this study, predicted  $BW_{f_i}$  calculated using  $k_i$ , is the same as observed; that is, the slope of the regression (predicted versus observed) equals 1.00 and the intercept equals 0.00. Individual rate constants calculated for Model [2], unlike residuals, are deterministic and, as such, are more reliable estimators of individual animal performance. Failure of Bayesian analysis to converge to a biologically feasible solution ( $k$ ) for Model [2] demonstrates excessive variability in  $k$ . However, for some  $BW_{0_i}$ ,  $BW_{f_i}$ , and ADFI $_{ci}$ , unique solutions to Model [2] may exist for more than an individual. Identification of animals on unique integral curves and characterization of properties likely to contribute to that uniqueness, such as composition of changes in BW and mitochondrial efficiency, may allow for a mechanistic evaluation of differences in input–output relationships. Reduced variability in the items of interest ( $k_i$  versus  $a$ ,  $b_1$ ,  $b_2$ , and residuals) and similar magnitude for  $k_i$  across studies makes it more likely that the first-order model better predicts real differences in input–output relationships compared to Model [1]. However, in either case, indices are merely those of variability and fail to explain mechanisms.

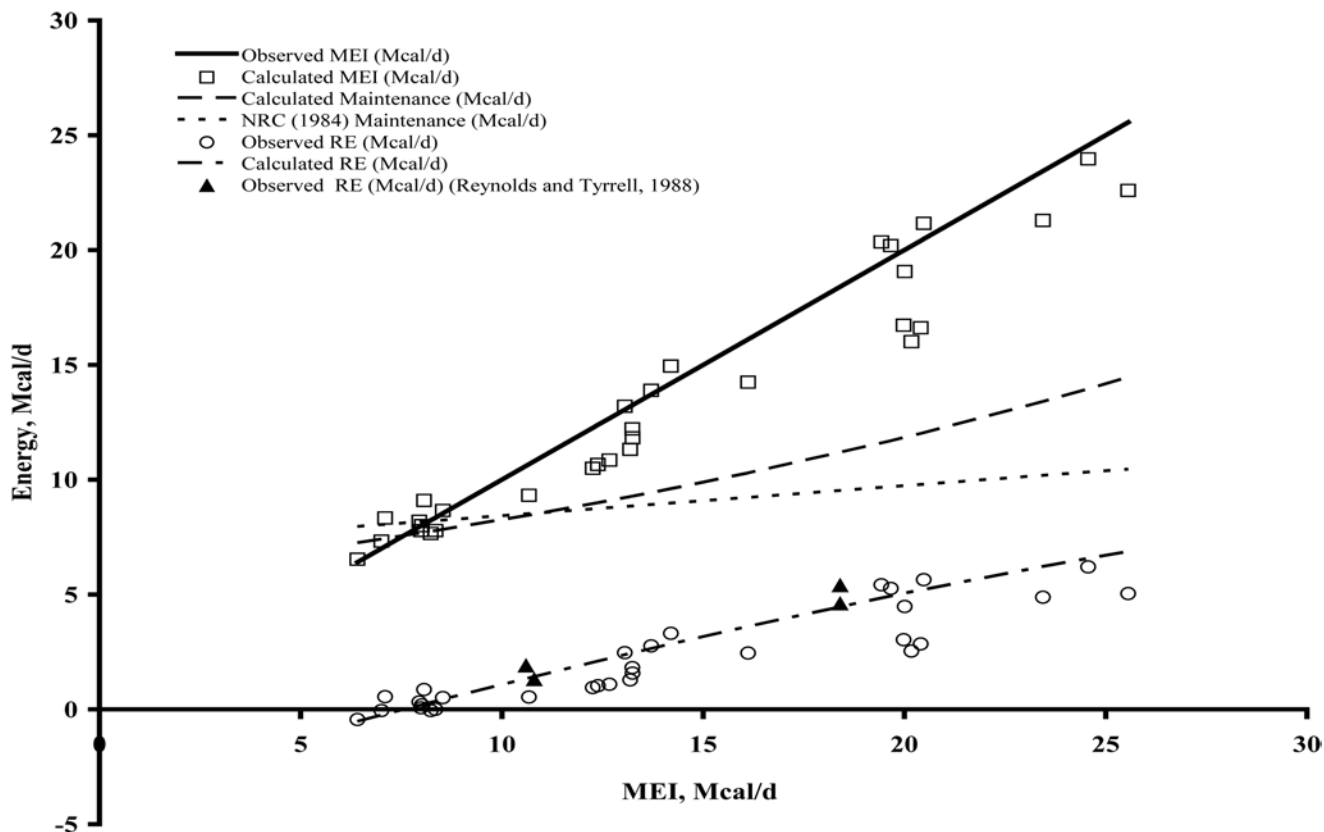
The solution to Model [3] ( $R^2 = 0.837$ ) was tractable and indicated that  $ME_m$  was variable (Fig. 3) across the range of MEI, unlike the discrete estimate of  $b_1 \times BW^{0.75}$  found in Model [1]. All parameter estimates were different from 0 ( $P < 0.05$ ). For MEI from 0.100 to  $0.335 \times BW^{0.75}$  Mcal/d, the range in  $ME_m$  was from 0.101 to  $0.241 \times BW^{0.75}$  Mcal/d and  $k_g$  (0.619; 95% credible interval 0.591 to 0.646) is consistent with theoretical estimates (Baldwin, 1995; Kennedy and Calvert, 2014). In Model [3], intakes of ME were not scaled by  $BW^{0.75}$  but are shown as such for comparison. Model [3] was

internally and externally valid. Functional forms of the variables in Model [3] appear to be correctly specified as parameter estimates demonstrate desired properties over the ranges evaluated. Uniqueness of dimension for state variables RE and MEI are more reflective of ME utilization by growing beef cattle than the mélange of dimensions found in Model [1] and, as such, contribute to improved accuracy of prediction. As previously noted, failure of Model [1] to accurately partition ADFI into that required for maintenance and that available for gain is due to the variable nature of maintenance rather than the discrete estimates found in Model [1]. Metabolizable energy intake by cattle in Cruz et al. (2010) ranged from 0.244 to 0.401 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup> (average = 0.298 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup>), Model [1] estimated maintenance was 0.164 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup>, Model [3] estimated maintenance averaged 0.170, and the range in ME<sub>m</sub> was from 0.139 to 0.230 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup>. Metabolizable energy intakes by cattle in MARC were similar: the range was from 0.218 to 0.373 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup> (average = 0.291 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup>), Model [1] estimated maintenance was 0.286 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup>, Model [3] estimated ME<sub>m</sub> averaged 0.166, and the range was from 0.126 to 0.235 Mcal ME/BW<sup>0.75</sup> × d<sup>-1</sup>. It is apparent from the structure and predictive success of Model [3] that ME<sub>m</sub> is directly affected by MEI. A report by Reynolds and Tyrrell (1988) supports this concept. These investigators studied whole body and tissue O<sub>2</sub> uptake in growing beef heifers fed 2 levels of forage (25 or 75%) and 2 levels of MEI (low and high). Oxygen uptake by the liver and portal drained viscera accounted for from 42 to 52% of whole body O<sub>2</sub> use and differences in O<sub>2</sub> uptake accounted for 70% of the difference in whole body heat production between the 2 diets. Uptake of O<sub>2</sub> by the portal drained viscera increased 50% for cattle fed at the high level of intake compared to the low level; O<sub>2</sub> uptake by the portal drained viscera was 23% greater for high-forage diets compared with low-forage diets. Retained energy (Mcal/d) was similar at the same MEI and *k<sub>g</sub>* was not different. Dry matter intakes, at the same MEI, were less for cattle fed the low-forage diet. Differences in heat production were due to differences in DMI, gut fill, and gut mass (Ferrell et al., 1986), which contributed to a greater cost of maintenance. Model [3] predicted RE for cattle fed high-forage diets (Reynolds and Tyrrell, 1988) were 1.3 (lesser DMI) and 4.6 Mcal/d (greater DMI), whereas observed RE were 1.4 (lesser DMI) and 4.5 Mcal/d (greater DMI). For cattle fed low-forage diets, Model [3] predicted RE were 1.3 (lesser DMI) and 4.5 Mcal/d (greater DMI), whereas observed RE were 1.9 (lesser DMI) and 5.4 Mcal/d (greater DMI). Data from Reynolds and Tyrrell (1988) are shown as filled triangles in Fig. 3. Comparisons show an overestimate of maintenance for the low-forage group. Given the

range of MEI and RE for the 100% forage group from Lofgreen and Garrett (1968) data, which was greater than for other groups in the database from which Model [3] was developed, it is expected that estimates of maintenance vary in the manner described here. These observations lend credence to the idea that the predominant factor affecting maintenance in growing cattle is intake, of either DM or ME. Differences in MEI affect differences in ME<sub>m</sub> in Model [3] thereby explaining the more robust nature of Model [3] when compared to Model [1] and static estimates of maintenance found in that model.

When MEI<sub>*i*</sub> and RE<sub>*i*</sub> replaced ADFI<sub>*i*</sub> and ADG<sub>*i*</sub> in Model [1] and the 0-intercept model, results regarding prediction and parametric stability were similar to those seen for Model [1]. For neither model were parameter estimates *a* and *b*<sub>1</sub> different from 0 (*P* < 0.05); the model was internally invalid as the slopes of the regressions of observed versus predicted ADFI were not 1 nor were the intercepts 0 (*P* < 0.05) and bootstrapped parameter estimates were different from OLS parameter estimates (*P* < 0.05). None of the linear models evaluated appear to approximate the true structure characterizing input (ADG or RE)–output (ADFI or MEI) relationships in growing cattle, primarily as a result of the failure to capture variability in ME<sub>m</sub>. Kleiber (1936) stated that total energetic efficiency is a suitable index for “selecting good utilizers of feed” and that energetic efficiency could be determined by measuring energy content of product, including changes in body substance. As indicated by improved predictive success for Model [3], proper model specification may require MEI or ADFI be predictors of responses such as RE or ADG (Koong, 1977; Baldwin, 1995) rather than responses themselves; model specification is as important as measurements taken in determination of efficiency of feed utilization.

For Cruz et al. (2010), residuals calculated for Model [1] were leptokurtic. For a leptokurtic density, values are more clustered about the peak; the kurtosis estimate was 6.19, which is significantly greater than the expected value of 3.00 (*P* < 0.001). This observation indicates that conclusions regarding selection indices, based on residuals, for Cruz et al. (2010) may be inappropriate unless data are transformed or model specification changed. We failed to find any evaluation of residual normality in the RFI literature; normality in *r<sub>i</sub>* distribution cannot be assumed and lack of normality in *r<sub>i</sub>* will bias inferences regarding ADFI<sub>*i*</sub>. In contrast, Model [1] residuals for the MARC and Lofgreen and Garrett (1968) data appeared to be normally distributed, confirming that data transformation was not required for analysis of that data set. Serial correlation in *r<sub>i</sub>* was noted for all 0-intercept models (*P* < 0.02); underestimates of ADFI<sub>*i*</sub> with increasing ADFI<sub>*i*</sub> for the 0-intercept model is yet one more indicator that the additive



**Figure 3.** Predicted outcome from Model [3],  $RE = (MEI - \alpha e^{kMEI}) \times k_g$ , in which RE = retained energy (Mcal/d), MEI = ME intake (Mcal/d), and  $k_g$  is the efficiency of ME utilization for gain. Calculated MEI =  $\alpha e^{kMEI} + \text{observed RE}/k_g$ . Calculated maintenance =  $\alpha e^{kMEI}$ . NRC (1984) maintenance =  $0.131BW^{0.75}$  (Mcal ME/d). Calculated RE is as shown previously. Observed RE (Reynolds and Tyrrell, 1988) may be found in that reference.

constant acts as an error term. Distribution of individual rate constants ( $k_i$ ) was normal and suggests that transformation of data is not required.

### Conclusions

Our data analysis indicates that Model [1] used to estimate ADFI lacks parametric stability, that the model is incorrectly specified, and that the relationship among initial and final BW, ADFI, and ADG is better described by first-order equations as parameter estimates thus calculated are more stable. Parameter estimates calculated for Model [1] lack uniqueness, theoretical consistency, and stability, which are requisites for general applicability and also indicators of bias in parameter estimates. Assumptions that  $b_1 \times BW^{0.75}$  and  $b_2 \times ADG$  represent ADFI required for maintenance and for gain, respectively, appear to have no basis in biology. Functional forms of the variables are often inconsistent with theoretical and empirical relationships among BW, ADG, and ADFI. It is assumed in Model [1] that residuals are deterministic when in fact residuals contain both stochastic and deterministic elements, even if the model is correctly specified. Furthermore, because the sum of residuals within a random sample is necessarily 0, residuals, unlike errors,

are necessarily not independent. Therefore, use of residuals as predictive tools requires, at a minimum, that classical linear model assumptions of correct model specification, nonstochastic predictor variables, mean of zero for error terms, which are normal, uncorrelated, and with constant variance, be fulfilled. For the data and solutions examined, it appears that Model [1] does not accurately predict ADFI. Indeed, the basic design of the studies evaluated (Cruz et al., 2010; MARC) is such that predictor variables are merely observed and not controlled, which is a violation of a key assumption basic to linear regression analysis. Although the commonly used GrowSafe system allows measurement of ADFI, it does not allow for control of individual BW or ADG, thereby making BW and ADG stochastic variables. Classical regression theory assumes that predictor variables are nonstochastic; when, as is the case with Model [1], predictor variables are random and  $b \neq \beta$ , parameter estimates are biased. Lack of fulfillment of classical linear model assumptions makes it even less likely that residuals can be assumed to be a set of independent Gaussian deviates. Taking the RFI argument to its extreme, for an  $R^2$  of 1.00, all animals must be equally efficient, although it actually means that all of the variation in response is explained by variation in predictors. Were predicted ADFI equal to



observed ADFI, the line representing predicted ADFI versus observed ADFI might be considered a boundary but only for prediction of differences in ADFI<sub>i</sub>. The RFI approach lacks a mechanism describing how and why differences exist across the range of intakes, gain, and composition of gain.

Use of Model [1] as a system for evaluating differences in observed ADFI<sub>i</sub> – predicted ADFI<sub>i</sub> is attractive from the standpoint that required animal observations are relatively easy and inexpensive. However, inputs to the model are inadequate to properly describe utilization of ME by growing animals and its ultimate animal disposition. Functional forms of the variables in Model [1] (i.e.,  $b_1 \times BW^{0.75}$  and  $b_2 \times ADG$ ) are neither mechanistic nor dynamic, merely simple empirical approximations of metabolic functions, which may not have biological meaning. Previous analysis of linear equations used to describe energy input–output relationships in growing and finishing beef cattle (Old and Rossow, 2013) indicate that some of them have empirical validity, but the linear model examined in our study lacked parametric stability thereby invalidating conventional inference procedures and use of residuals as independent variables. Parameter estimates, calculated for first-order models, in contrast, were more stable. Major flaws in Model [1] are the inability to describe variability in ME<sub>m</sub> over the range of MEI and provide a biological mechanism as to why differences in ADFI<sub>i</sub> exist. Variation in Model [3] is explained by variation in ME<sub>m</sub> as f(MEI) and efficiency of ME utilization for gain. Consistent with the statement by Swift (1942) and the First Law of Thermodynamics, feeding studies used to evaluate offspring for efficiency should not be based on weight change but rather on energy input–output relationships.

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