

Evaluation of Net Energy Expenditures of Dairy Cows According to Body Weight Changes over a Full Lactation

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ABSTRACT

Equations that predict daily dry matter intake (DMI) of a lactating cow could be evaluated by comparing the predicted accumulation of energy in body weight (BW) over the course of lactation with the observed BW evolution. However, to do so requires that first the energy balance calculations from observed DMI are evaluated. The purpose of the work reported here was to determine the degree of deviation of predicted from observed BW, according to net energy for lactation (NE_L) balance calculated from weekly observations of DMI, BW, and fat-corrected milk production in 21 sets of full-lactation data, and to determine an appropriate correction of the NE_L bias for subsequent DMI prediction evaluations. When the National Research Council maintenance equation $0.08 \times \text{BW}(\text{kg})^{0.75}$ was used in energy balance calculation, BW was overpredicted with an increasing difference between the cumulative predicted BW and observed BW as lactation progressed. Placing all the error of BW prediction into maintenance energy expenditures resulted in a best-fit equation of 0.096 ± 0.003 Mcal/kg of BW^{0.75}. A time-dependent equation was also developed, in which weekly maintenance expenditures were determined as the NE_L expenditure to yield a zero NE_L balance and could be described by a second-order polynomial equation related to week of lactation (WOL) where maintenance NE_L = $[-0.0227(\pm 0.0098) \times \text{WOL}^2 + 1.352(\pm 0.456) \times \text{WOL} + 78.09(\pm 4.92)$ Mcal/kg of BW^{0.75}] $\times 10^{-3}$. Average maintenance energy expenditure at the onset of lactation was approximately 0.08 Mcal/kg of BW^{0.75}, and this value increased to a plateau at wk 15 of lactation of approximately 0.098 Mcal/kg of BW^{0.75}. Standard deviations between data sets of weekly maintenance parameter estimates throughout lactation were large but consistent at approximately 25% of the mean. Revision of the maintenance energy expenditure estimate substantially improved BW prediction by the energy balance model. On average, the

0.096 Mcal of NE_L/kg of BW^{0.75} equation resulted in the best BW predictions, although substantial variation existed around this value.

Key words: maintenance energy expenditure, energy balance, dairy cow

INTRODUCTION

With the advent of the dynamic computer model to describe biological systems, there has arisen the potential to predict the response of an animal over time to various interventions. In models of lactation, instantaneous milk production rates by dairy cows are typically calculated from rates of nutrient flow from the diet. In turn, DMI prediction equations typically require daily milk production and BW as inputs. Such equations carry an implicit description of energy balance between intake and use. In a static prediction at one point in time, there is little penalty to being off by a small fraction from the true energy balance. In a dynamic model, however, in which any imbalance between predicted intake and use of energy accumulates in body stores, a small deviation could rapidly escalate errors in BW prediction over simulated time.

In the process of developing approaches to predict daily DMI in a dynamic simulation of dairy cow performance, it is important to first evaluate and correct, if necessary, the energy accumulation in body stores implied from observed DMI and milk production rates. McNamara and Baldwin (2000) found, using a model of the metabolic transactions in the lactating cow (Baldwin, 1995), that in response to dietary changes, body fat accumulation was either over- or underpredicted in simulations of more than a few weeks. They concluded that the model's precision in predicting long-term dynamic changes in energy-utilizing reactions was inadequate. Heuer et al. (2001) also observed, in a model designed to predict herd mean NE_L energy balance for the first 12 wk of lactation (WOL), that the predicted NE_L balance was generally higher than calculated NE_L balance in all weeks of lactation. However, at the individual cow level, they observed that the standard deviation was often larger than the mean difference.

A companion paper (Ellis et al., 2006) describes the performance of selected DMI prediction equations in a

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Table 1. Summary of evaluation data sets

Data set	Source	Treatment	Parity	WOL ¹	n ²
1	Mohrenweiser and Donker, 1967	Diet 1 - Early alfalfa pre, early alfalfa postcalving	1	2 to 39	9
2	Mohrenweiser and Donker, 1967	Diet 2 - Early alfalfa pre, late alfalfa postcalving	1	2 to 39	10
3	Mohrenweiser and Donker, 1967	Diet 3 - Late alfalfa pre, early alfalfa postcalving	1	2 to 40	10
4	Mohrenweiser and Donker, 1967	Diet 4 - Late alfalfa pre, late alfalfa postcalving	1	2 to 40	10
5	Wohlt and Clark, 1978	Diet 1 - no supplemental nitrogen	Mostly >1	1 to 42	10
6	Wohlt and Clark, 1978	Diet 2 - urea	Mostly >1	1 to 42	10
7	Wohlt and Clark, 1978	Diet 3 - soybean meal	Mostly >1	1 to 42	10
8	Wohlt and Clark, 1978	Diet 4 - urea and soybean meal	Mostly >1	1 to 42	10
9	Wohlt and Clark, 1978	Diet 5 - soybean meal (2× inclusion level)	Mostly >1	1 to 42	10
10	DePeters et al., 1985	2× milking, H to M diet at 28 kg/d, M to L diet at 23 kg/d ³	>1	1 to 42	12
11	DePeters et al., 1985	2× milking, H to M diet at 25 kg/d, M to L diet at 20 kg/d ³	1	1 to 42	7
12	DePeters et al., 1985	3× milking, H to M diet at 25 kg/d, M to L diet at 20 kg/d ³	1	1 to 42	8
13	DePeters et al., 1985	3× milking, H to M diet at 28 kg/d, M to L diet at 23 kg/d ³	>1	1 to 42	13
14	Holter and Hayes, 1992	CP balanced using 1 grain	1	2 to 45	14
15	Holter and Hayes, 1992	CP balanced using 2 grains	1	2 to 45	14
16	Holter and Hayes, 1992	CP balanced using 1 grain	>1	2 to 45	22
17	Holter and Hayes, 1992	CP balanced using 2 grains	>1	2 to 45	22
18	Holter et al., 1993	No RUP protein-fat supplement	1	2 to 37	10
19	Holter et al., 1993	RUP protein-fat supplement	1	2 to 37	10
20	Holter et al., 1993	No RUP protein-fat supplement	>1	2 to 37	13
21	Holter et al., 1993	RUP protein-fat supplement	>1	2 to 37	13

¹WOL = Week of lactation; period of time for which data set reported DMI, FCM, and BW.

²Number of animals used in treatment groups.

³Dietary treatment change; H = high energy, M = medium energy, and L = low energy diets, based on daily milk production for each cow.

dynamic model of energy flows in the lactating dairy cow. The test variable used to compare model predictions with observations, and thereby evaluate the DMI prediction equations, is the integrated instantaneous NE_L balance, expressed as weekly BW throughout lactation. Published data on DMI, BW, and milk production over a full lactation were collected for this goal. To use a predicted NE_L balance as the test variable, it was necessary to first evaluate NE_L balances obtained from the observations alone. The purpose of the work reported here was to determine the degree of deviation of predicted from observed BW according to NE_L balance calculated from observations in the collated data sets and to determine an appropriate correction of the bias for subsequent DMI prediction evaluations (Ellis et al., 2006). The bias was placed in maintenance expenditures so that a time-independent, as well as a time-dependent, equation relating maintenance expenditures to WOL could be developed.

MATERIALS AND METHODS

Data Sets

The database used to evaluate predicted BW and determine a new description of maintenance energy expenditures consisted of 777 data points from 21 sets of lactation performance data averaged from groups of 7 to 22 Holstein cows (Table 1). Information about the data sets is summarized in Table 1. Criteria for data

set selection were that weekly BW, DMI, and 4% FCM production for at least 37 WOL were reported and that information was given on parity and diet. Data plots from the publications were scanned into Adobe Photoshop Elements (Adobe Systems, Inc., San Jose, CA), a grid was snapped over the image, and lined up with the x- and y-axes to an appropriate scale. Data points were extracted and recorded to 1 or 2 decimal places for each WOL.

Energy Balance Model

Energy balance at each WOL was calculated from daily NE_L flows in Mcal/d as:

$$\text{NE}_L \text{ Balance} = \text{NE}_L \text{ Intake} \quad [1]$$

$$- \text{NE}_L \text{ for Milk Production} - \text{NE}_L \text{ for Maintenance}$$

The NE_L equivalents of body mass, according to NRC (1988), were assumed so that BW change (ΔBW_i) in kilograms per day was 0.203 times NE_L balance (Mcal/d; equation 1) if the NE_L balance was negative and 0.195 times NE_L balance if positive. The older NRC (1988) factors were used because information on BCS, required for calculating the newer NRC (2001) factors, was not available from the data sets. Assuming a BCS of 3.5, BW change would be 0.196 and 0.171 times NE_L balance for negative and positive balances, respectively, according to NRC (2001). Analysis showed that the

model was relatively insensitive to a 15% change in NE_L equivalents of body mass, and so the single NRC (1988) factors were used.

Predicted BW of cows starting at wk 3 of lactation was obtained from the initial observed BW at wk 2 of lactation adjusted for the predicted BW changes for that week (ΔBW_n). Similarly, the BW of cows at progressive WOL (BW_{n+1}) was obtained from the previous predicted BW (BW_n) adjusted for that week's predicted BW changes (ΔBW_n):

$$BW_{n+1} \equiv BW_n + \Delta BW_n \cdot 7 \quad [2]$$

Maintenance NE_L expenditures were calculated as 0.08 Mcal of NE_L /kg of $BW^{0.75}$ (NRC, 2001) where BW was the predicted, not the observed value, to simulate a dynamic system. The NE_L intake was calculated as observed DMI (kg/d) multiplied by the energy content of the feed, estimated for each WOL by the NRC (2001) computer formulation program, from information on diet composition provided in each publication. Assumptions were that pregnancy commenced at 90 DIM, age at first calving was 24 mo, calving interval was 12 mo, BCS was 3.5, calf birth weight was 45 kg, and no animals were grazing. If lactation number was greater than 1, mature BW was set to the observed value at the onset of lactation. For first-lactation cows, mature BW was calculated as 1.25 times observed BW at the start of lactation (NRC, 2001). Milk production was entered as kg of FCM, 4% milk fat, 3% true protein, and 4.78% lactose.

The NRC (2001) feed library was used, with modifications, when chemical composition of the feed was provided. When diet NE_L values were provided in the publications, the NRC (2001) program was still used to calculate NE_L . This ensured that all diet NE_L values were obtained from the same set of assumptions.

Net energy (NE_L) for milk production was the observed FCM production (kg/d) multiplied by 0.749 Mcal of NE_L /kg (NRC, 2001).

Extra energy expenditures by first-lactation heifers was calculated according to the NRC (2001) for a BCS of 3.5 as 0.0103 Mcal of NE_L /kg of $SBW^{0.75}$, where SBW is shrunk $BW = 0.96 \times BW$.

Statistical Analyses

Mean square prediction error (**MSPE**) for each of the 21 data sets was calculated as:

$$MSPE = \sum_{i=1}^n (O_i - P_i)^2/n \quad [3]$$

where n is the number of observations, O_i is the observed value, and P_i is the predicted value. Square root of the MSPE, expressed as a proportion of the observed mean, gave an estimate of the overall prediction error. The MSPE was decomposed into random error, error due to deviation of the predicted vs. observed regression slope from unity, and error due to overall bias (Bibby and Toutenburg, 1977).

Predictions were also evaluated by examining the slope and intercept of predicted vs. observed BW for the 21 sets of lactation data. Using PROC MEANS in SAS (SAS Institute, 2000), the slopes and intercepts were tested for significant difference from the line of unity (slope of one, intercept of zero). To identify patterns of bias in the predictions, residual BW (predicted - observed) was regressed against WOL and predicted BW, and the average linear and quadratic coefficients of the plots were tested against zero using PROC MEANS in SAS. Mean predicted BW over the full lactation was compared against the observed means by t -test, where $n = 21$.

To account for the bias detected in predicted energy balance, maintenance energy expenditures, in Mcal/kg of $BW^{0.75}$, were estimated for each of the 21 data sets as the value that minimized residual sum of squares (**RSS**) between predicted and observed BW from wk 4 through 37 of lactation. Weekly maintenance energy expenditures were also calculated from the weekly DMI, FCM yield, and BW observations as the value that yielded a NE_L balance of zero; that is, predicted $BW_n =$ observed BW_n .

RESULTS

Evaluation of the Original Energy Balance Model

Simulations with maintenance calculated as 0.08 Mcal of NE_L /kg of $BW^{0.75}$ in the energy balance model showed an overall trend for BW to be overpredicted as lactation progressed (Figure 1). The average intercept of the predicted vs. observed regression line (-884.6 ± 192.6) was significantly different from zero, and the average slope (2.70 ± 0.38) was significantly different from 1 ($P < 0.05$). There was a trend for residual BW to increase with WOL (Figure 1) and with predicted BW, and the plots could be described by significant linear and quadratic equations (linear equation for residual vs. WOL slope = 2.92 ± 0.66 , intercept = -13.74 ± 2.28 and linear equation for residual vs. predicted BW slope = 0.52 ± 0.12 , intercept = -281.86 ± 59).

Predicted BW mean (602.8 ± 2.1 kg) was significantly different from the observed mean (558.2 ± 3.4 kg), and the majority of prediction error was due to regression and bias, whereas only 27% of MSPE was from random sources.

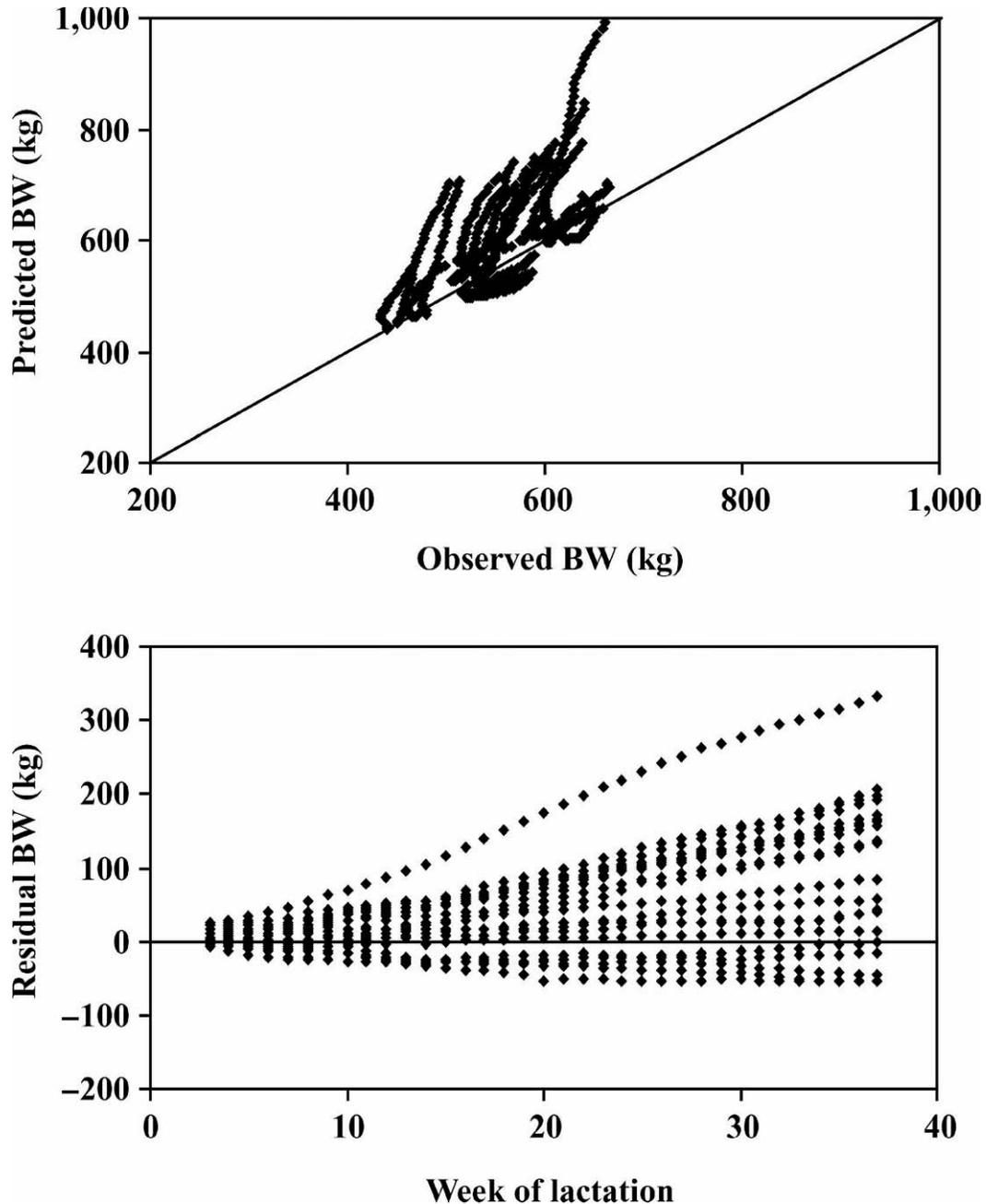


Figure 1. Predicted vs. observed BW (top) and residual (Predicted – Observed) BW vs. week of lactation (bottom) for evaluation of the energy balance model using the original 0.08 Mcal of NE_I/kg of $BW^{0.75}$ maintenance equation.

New Maintenance Descriptions

In an attempt to correct the bias in BW prediction, an optimum estimate of maintenance energy expenditures, as a function of $BW^{0.75}$, was obtained for each of the 21 data sets. The average expenditure was 0.097 ± 0.004 Mcal of NE_I/kg of $BW^{0.75}$ (Table 2). An adjusted mean, eliminating 2 values that were likely sources of

errors (data sets 10 and 19), was 0.096 ± 0.003 Mcal of NE_I/kg of $BW^{0.75}$, a 1% change that reduced SE by 25%. In addition, second-order polynomial equations relating weekly maintenance estimates to WOL were parameterized for each of the 21 data sets (Table 2), and for the average of weekly estimates obtained (Table 2, Figure 2). The average maintenance energy expenditure at the onset of lactation was approximately 0.08 Mcal

Table 2. Individual and averaged time-independent maintenance equations (Mcal of NE_L/kg of BW^{0.75}) and time-dependent maintenance energy expenditure equations

Data set	Time-independent maintenance equation ¹		Time-dependent maintenance equation ²			r ²
	Value	RSS ³	Intercept (10 ⁻³)	Week of lactation (10 ⁻³)	Week of lactation ² (10 ⁻³)	
1	0.114	22,850	52.46	6.774	-0.1313	0.823
2	0.091	1,851	76.10	2.066	-0.0457	0.272
3	0.120	2,554	101.19	2.338	-0.0497	0.455
4	0.097	854	90.60	0.835	-0.0143	0.115
5	0.109	203	109.30	-0.427	0.0025	0.108
6	0.107	1,261	107.41	-1.097	0.0300	0.069
7	0.108	1,451	105.82	-0.614	0.0140	0.010
8	0.102	2,970	105.89	-1.724	0.0472	0.138
9	0.108	906	110.65	-2.249	0.0524	0.155
10	0.135	2,554	127.31	0.595	-0.0237	0.232
11	0.102	5,319	107.57	-0.277	0.0060	0.001
12	0.110	2,437	110.82	-0.136	0.0097	0.098
13	0.111	12,326	84.55	1.809	-0.0244	0.573
14	0.070	2,231	59.12	1.055	-0.0165	0.208
15	0.072	990	70.71	0.063	0.0038	0.171
16	0.083	1,539	67.16	0.461	-0.0048	0.213
17	0.079	12,108	43.59	2.080	-0.0266	0.823
18	0.075	1,436	69.57	0.402	0.0005	0.183
19	0.068	2,909	74.51	-1.332	0.0466	0.231
20	0.086	948	90.45	-1.994	0.0529	0.176
21	0.086	1,019	97.47	-2.733	0.0697	0.116
Average	0.096 (± 0.003) ⁴		78.09 (± 4.92)	1.352 (± 0.456)	-0.0227 (± 0.0098)	0.804

¹The maintenance equation (Mcal of NE_L/kg of BW^{0.75}) that resulted in the least residual sum of squares for that data set for the entire lactation period.

²The quadratic equation that described maintenance energy expenditures (Mcal of NE_L/kg of BW^{0.75}) for that data set for the entire lactation period, determined by fitting an equation to weekly maintenance energy expenditure estimates that resulted in zero difference between predicted and observed BW.

³RSS = Residual sum of squares.

⁴Mean ± SEM, deleting 2 data sets likely contributing error.

of NE_L/kg of BW^{0.75}. This value increased until wk 15 of lactation where it plateaued at approximately 0.098 Mcal of NE_L/kg of BW^{0.75} (Figure 2).

Plots of predicted vs. observed BW and residual BW vs. WOL obtained from simulations with the 2 new descriptions of maintenance expenditures are presented in Figures 3 and 4. The 0.096 time-independent equation and the time-dependent equation corrected the overprediction seen with the original 0.08 factor, but a large degree of variation remains evident.

Root MSPE for the original maintenance factor was 14.5% of the observed mean (Table 3). The 0.096 time-independent maintenance equation reduced root MSPE to 10.9%, and the new average maintenance equation reduced it to 11.2%. As root MSPE decreased, the proportion of MSPE from random sources (error due to disturbances) increased (Table 3). The new estimates reduced error due to mean bias to less than 1% for the 0.096 factor and average equation, where the original factor resulted in 30.2% of MSPE arising from mean bias.

Both new maintenance descriptions improved BW predictions of the energy balance model when compared with the original 0.08 maintenance equation (Table 3). Overall, the new 0.096 time-independent maintenance equation yielded the lowest RSS and MSPE values. Each of the new maintenance prediction scenarios resulted in average predicted BW substantially lower than that for the original 0.08 factor (Table 3) indicating that the BW overprediction was corrected. In predicted vs. observed plots, the regression lines were not significantly different from the line of unity for the 0.096 time-independent equation or the time-dependent maintenance equation (for the 0.096 equation: intercept = -46.1 ± 223.3, slope = 1.14 ± 0.41; for the time-dependent equation: intercept = 367.5 ± 263.9, slope = 0.45 ± 0.47). Plots of residual BW vs. WOL were also not significant; however, plots of residual vs. predicted BW yielded significant regression equations (linear equation for 0.096 maintenance equation slope = 1.09 ± 0.17, intercept = -600.88 ± 100.5; linear equation for time-

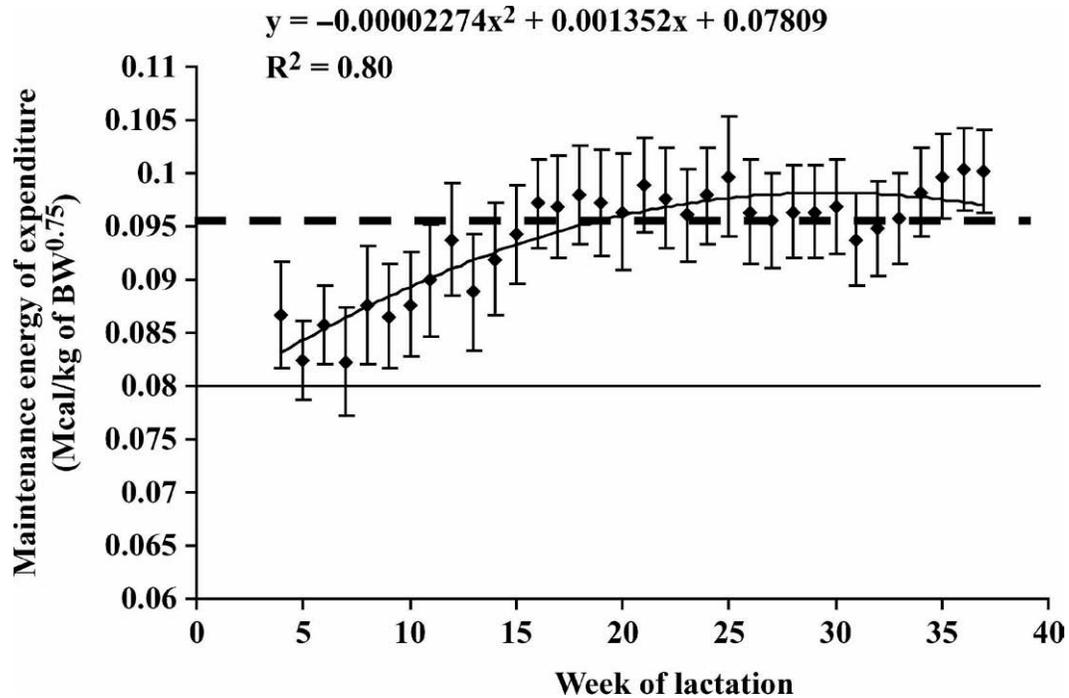


Figure 2. Maintenance energy expenditures (Mcal of NE_L /kg of $BW^{0.75}$) vs. week of lactation where the bottom solid line represents the original $0.08 \times BW^{0.75}$ maintenance equation, the top dashed line represents the least residual sum of squares determined time-independent $0.096 \times BW^{0.75}$ equation, and the fitted line is the time-dependent maintenance energy expenditure equation (\pm SE) determined by averaging weekly estimates that resulted in zero difference between predicted and observed BW.

dependent maintenance equation slope = 0.847 ± 0.178 , intercept = -456.19 ± 98.59).

DISCUSSION

The preceding work was undertaken to evaluate, and correct if necessary, the cumulative energy balance implied by weekly observations of DMI, BW, and FCM production over the course of a full lactation. Equations of the NRC (1988, 2001) were used to make the evaluations, which clearly showed a trend for BW to be over-predicted as lactation progressed (Figure 1). This cumulative error is consistent with errors reported by others (McNamara and Baldwin, 2000; Heuer et al., 2001). To use these energy balance calculations for evaluation of DMI predictions in a dynamic model, as was our intent (Ellis et al., 2006), we were obliged to first attempt to correct the apparent bias. A review of the literature suggested that the NRC (2001) maintenance energy expenditures are underpredicted during lactation by anywhere from 10 to 49% (for examples see Ritzman and Benedict, 1938; Ferrell and Jenkins, 1987; Kebreab et al., 2003). Although maintenance is likely not the only source of error in this energy balance estimation, and whereas a higher maintenance expenditure during lactation is indistinguishable from a lower efficiency of

conversion of dietary ME to NE_L , the bias correction was simplified by putting it all in one place, that being the estimate of maintenance energy expenditures. The value of 0.096 Mcal of NE_L /kg of $BW^{0.75}$, a 20% increase over NRC (2001), substantially improved BW prediction, where BW was predicted dynamically from NE_L balance and then used in calculating maintenance NE_L expenditures. On average, using the new maintenance term equaled approximately an additional 1.84 Mcal/d, or 6.5% of NE_L intake. Although parameters of the predicted BW vs. observed BW and residual BW vs. WOL plots became nonsignificant with modification of the maintenance description, residual BW vs. predicted BW plots were still significant and indicated that the model remains in need of further improvements.

Weighting time-independent and time-dependent maintenance equations by the number of cows per treatment result in a time-independent maintenance equation of 0.94 Mcal of NE_L /kg of $BW^{0.75}$, and a time-dependent equation of: Maintenance $NE_L = [-0.00002014 \times WOL^2 + 0.00122316 \times WOL + 0.07643808]$ Mcal of NE_L /kg of $BW^{0.75}$, in which the same 2 data sets were removed as in the original scenario. Thus, weighting had little effect on the parameter estimates. Although weighting can remove bias in parameter estimates introduced by data sets with a low n, the goal of our

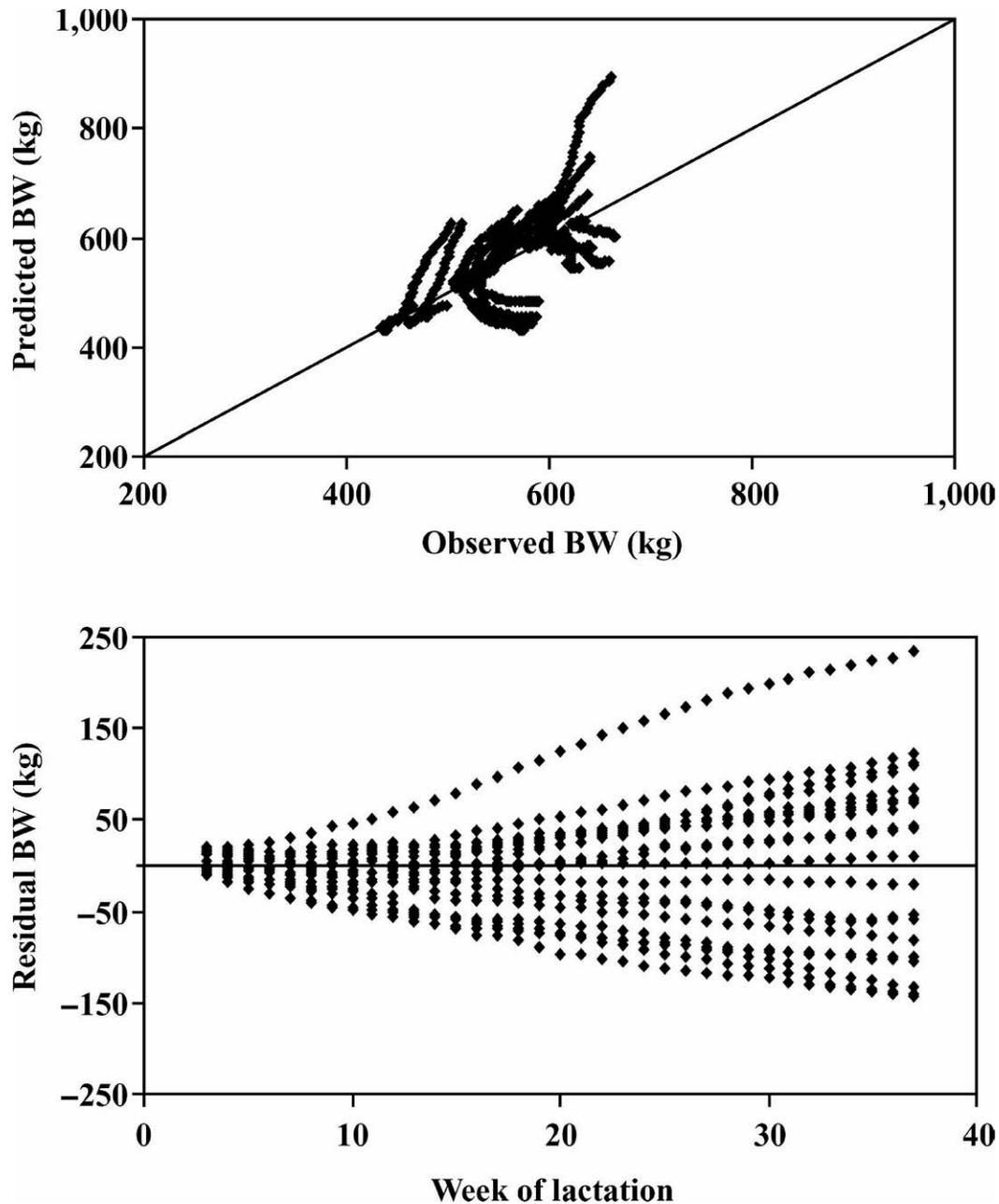


Figure 3. Predicted vs. observed BW (top) and residual (Predicted – Observed) BW vs. week of lactation (bottom) in the model of energy balance using the 0.096 Mcal of NE_l/kg of $BW^{0.75}$ time-independent maintenance equation.

subsequent work (Ellis et al., 2006) was to attempt to correct bias through a biological feedback of energy stores onto DMI predictions instead of a statistical weighting procedure. Using weighted maintenance parameters would result in maintenance expenditures further away from what some individual data sets need to correct the energy balance problem, and this additional error would have to be absorbed by the feedback mechanism. For this reason, although we present the

weighted factors, the unweighted factors were focused on for model development.

Potential Sources of Error

Components of the energy balance model other than the maintenance calculation could have contributed to the error in BW prediction. Milk production, expressed as kilograms of 4% FCM (Gaines, 1928), allows a con-

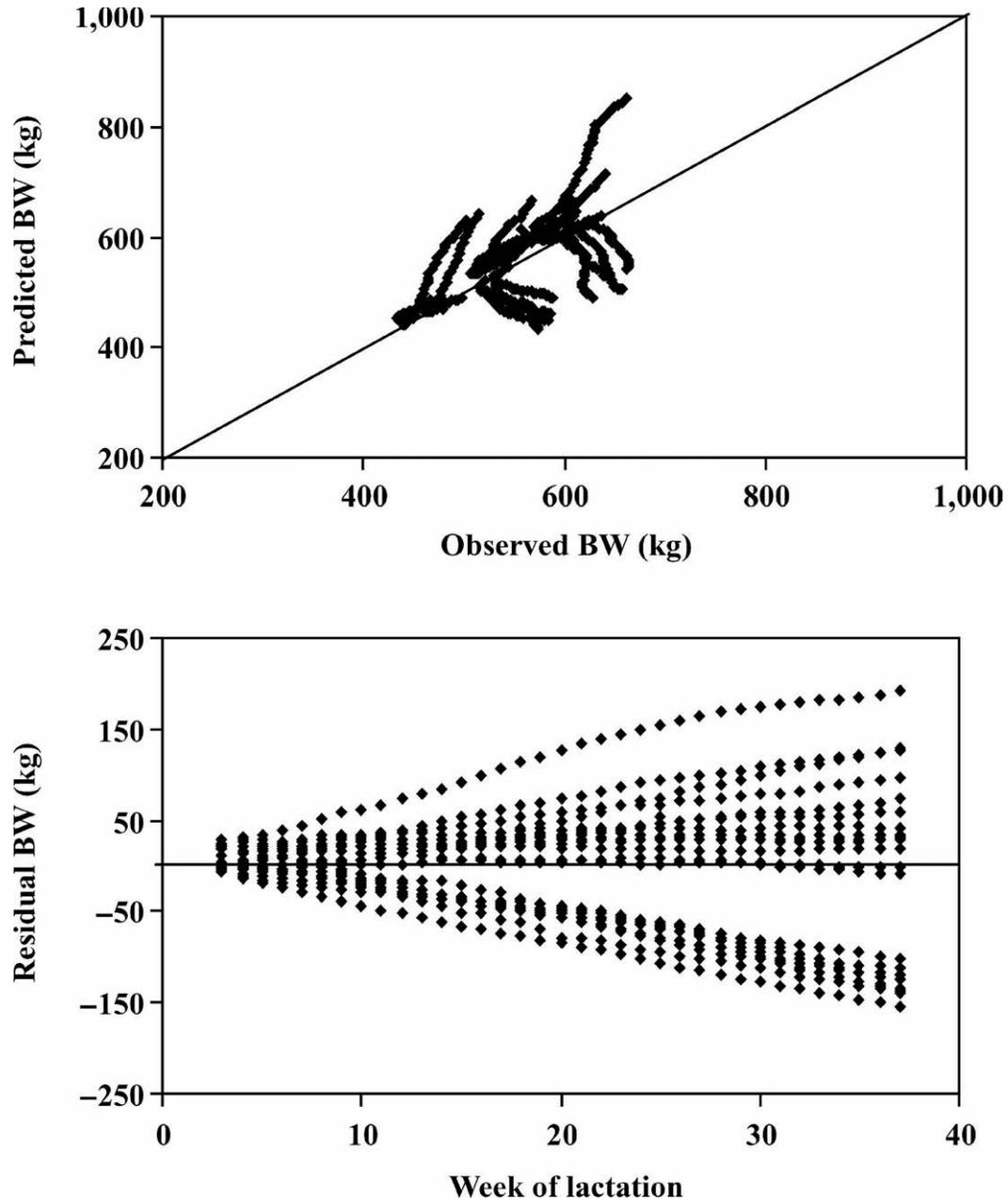


Figure 4. Predicted vs. observed BW (top) and residual (Predicted – Observed) BW vs. week of lactation (bottom) in the model of energy balance using the time-dependent maintenance equation.

stant energy content of 0.749 Mcal of NE_L /kg to be used (NRC, 2001), except when milk fat is less than 3% (NRC, 2001), such as during milk fat depression due to dietary manipulation (Weiss, 2002). In the performance data used for model evaluation here, none of the average milk fat percentages fell below 3%, and milk fat depression was not evident or reported. It is unlikely, then, that using 4% FCM to describe milk production substantially contributed to the error in energy balance seen here.

A second potential source of error is calculation of the energy content of the feed. The NRC (2001) computer model program is commonly used to calculate dietary NE_L in North America, and is an improvement over the NRC (1988) method of determination. In 2 separate evaluations of accuracy, NE_L values for feeds according to NRC (1989) were 5% (Weiss, 1998) and 5 to 7% (Vermorel and Coulon, 1998) too high, whereas with the NRC (2001) method, overprediction of dietary NE_L was decreased to 1.2% (Weiss, 1998). Depending

Table 3. Summary of BW predictions by the energy balance model using all observed values as inputs, and maintenance energy expenditures were described by either the original maintenance equation, the new time-dependent equation, or the time-dependent equation

	Predicted BW ¹		Root MSPE, ² %	MSPE			Residual sum of squares ⁶
	Mean	SEM		ECT, ³ %	ER, ⁴ %	ED, ⁵ %	
Original 0.08 equation ⁷	602.8*	2.1	14.5	30.2	42.9	27.0	4,825,722
Time-independent 0.096 equation ⁸	556.2	3.0	10.9	0.1	49.4	50.6	2,734,479
Time-dependent equation ⁹	559.6	2.7	11.2	0.1	41.4	58.6	2,873,146

¹Average predicted BW over all weeks of lactation (n = 21).

²Root mean square prediction error (MSPE) expressed as a percentage of the observed mean.

³ECT = Error due to bias, as a % of total MSPE.

⁴ER = Error due to regression, as a % of total MSPE.

⁵ED = Error due to disturbance, as a % of total MSPE.

⁶Residual SS = $\Sigma(\text{predicted} - \text{observed})^2$

⁷Maintenance = 0.08 Mcal of NE_L/kg of BW^{0.75}

⁸Maintenance = 0.096 Mcal of NE_L/kg of BW^{0.75}, average least RSS determined maintenance equation for the 21 herd average data sets

⁹Maintenance = $[-0.0227(\pm 0.0098) \times \text{WOL}^2 + 1.352(\pm 0.456) \times \text{WOL} + 78.09(\pm 4.92) \text{ Mcal of NE}_L/\text{kg of BW}^{0.75}] \times 10^{-3}$

*Predicted mean is significantly different from the observed mean (558.2 ± 3.4 ; $P \leq 0.05$).

on the feed used, prediction of dietary energy content with this methodology may partially contribute to poor prediction of BW within an energy balance model. However, the 1.2% overprediction reported by Weiss (1998) is not large enough to account for the degree of BW overprediction evident in this study. Adjustment downwards of dietary NE_L within the model by 1.2% decreased the average predicted BW from 602.7 to 593.9 kg and decreased the total RSS by approximately 15%. Adjusting dietary NE_L accounted for only 8.8 kg (20%) of the average 44.5-kg BW overprediction, leaving 80% of the BW overprediction unaccounted for. Although calculation of dietary NE_L using the NRC (2001) methodology might have contributed to error in predicted BW within the energy model, it was not the major contributing factor. However, until systems that can more accurately represent the true dietary NE_L are available, these limitations must be acknowledged and accepted as likely having a role in contributing to errors in energy balance calculations.

In this study, the energetic cost of pregnancy was not included in the estimation of energy balance. There is usually little or no increase in energy requirements due to pregnancy during lactation, and thus any increases in energy expenditures due to pregnancy would not come into play until after the cessation of lactation (Bauman and Currie, 1980). Because none of the data sets used here extended beyond 37 WOL, excluding pregnancy did not contribute to overprediction of BW. In addition, calf weight should not significantly affect average daily gain of the cow until days pregnant is greater than 190, or approximately 40 WOL (NRC, 2001). Thus, the actual weight of the fetus would not

affect observed BW against which the predicted values, which do not consider fetus weight, were tested.

Another source of error to be considered is that changes in BW may not always reflect changes in retained tissue energy (NRC, 1988). From wk 5 to 12, energy reserves can differ by 40% with no change in BW (NRC, 1988), due to rapid changes in DMI and gut fill. Chilliard et al. (1991) found that a 4-kg increase in gut fill accompanies a 1-kg increase in DMI, whereas more recent studies (Komaragiri and Erdman, 1997; Komaragiri et al., 1998) suggest a 2.5-kg increase per 1-kg increase in DMI. Because tissue mobilization occurs at the same time that DMI is rapidly increasing in early lactation, decreases in BW due to depleting energy stores are masked by a simultaneous increase in gut fill. After peak lactation, DMI and gut fill decrease at the same time as body energy stores begin to increase. Although BW may not always accurately represent changes in body tissue weight, the model predicts similar BW at the end of lactation whether the effect of gut fill is included or not and including this effect does not correct the substantial overprediction of BW. If observed BW is adjusted downwards to account for a 2.5-kg increase in gut fill per 1-kg increase in DMI, the overall mean BW changes by 0.03%.

The NE_L content of BW gain/loss is another potential source of error. The NRC (1988) values were used here because information on BCS was not available, and is required for the NRC (2001) system. The energy content of gain/loss definitely changes across BCS, and the error in using average equations to describe all cows is acknowledged. However, analysis here showed that this model is fairly insensitive to these values. The energy

content of gain would have to be increased by over 200% to correct the discrepancy between predicted and observed BW. Although these factors contribute to overall error, they are likely not the major contributing factor.

Additional maintenance energy expenditures for growing animals were added to the energy balance model for first-lactation data sets only. Unfortunately, not all data sets reported age of the animals used, and all these studies grouped animals in any lactation greater than one together. It is acknowledged that there will be some growth in cows in their second lactation but, determination of which, if any, data sets should be given additional energy expenditures was impossible here. This error is acknowledged, and although it may contribute to some of the error in energy balance calculation, it will remain unaddressed until more descriptive data come available.

The above review suggests that, although errors may exist within components of energy balance calculation other than the maintenance cost, none by itself is substantial enough to account for the degree of BW overprediction reported here. Furthermore, even when adjustments were applied simultaneously to the energy content of feed, gut fill, growth, and the NE_L content of BW gain and loss, the maintenance energy expenditure equation still has to be increased to approximately 0.090 Mcal/kg of $BW^{0.75}$ to correct the remaining BW overprediction. The body of literature suggesting that maintenance energy expenditures during lactation are currently underestimated (for examples, see Yan et al., 1997; Kirkland and Gordon, 2001; Kebreab et al., 2003) supports the idea that the BW overprediction in this model is caused at least partially by underestimation of maintenance energy expenditures.

Correction of the Bias

Maintenance energy expenditure by the lactating dairy cow, defined here as the NE_L equivalent used to maintain the animal, as it is, at zero BW content change, is described by the NRC (2001) as 0.08 Mcal/kg of $BW^{0.75}$, based on measured fasting heat production estimates of 0.073 Mcal/kg of $BW^{0.75}$ for dry nonpregnant dairy cows housed in tie stalls or metabolic chambers (Flatt et al., 1965). A 10% allowance for normal voluntary activity of cows that would be housed in dry lot or freestall systems increased the factor to 0.08 Mcal/kg of $BW^{0.75}$ (NRC, 2001). The dairy estimates agree with beef cattle estimates (NRC, 1996), in which the base maintenance requirement, 0.065 Mcal/kg of $BW^{0.75}$, with a Holstein/Jersey breed adjustment factor of 1.2, results in a maintenance energy requirement of 0.079 Mcal/kg of $BW^{0.75}$.

Several studies have shown that energy expenditures for maintenance are substantially higher than this during lactation. By nonlinear and linear regression analysis of milk energy output on energy intake adjusted to zero energy balance, Kebreab et al. (2003) estimated maintenance energy expenditures to be 16 to 22% higher during lactation than predicted by NRC (2001). Similarly, Moe et al. (1970) reported a 22% increase in maintenance energy expenditures based on multiple regression analysis of energy balance data. Although such estimates were based on extrapolation outside the range of observations to zero energy retention, indirect calorimetry has also yielded estimates of the lactation effect on maintenance energy expenditures as an increase of 49% (Ritzman and Benedict, 1938), 23% (Flatt et al., 1969), 27% (Kirkland and Gordon, 2001), and 29% (Yan, et al., 1997). According to observed changes in BW, maintenance energy expenditures have been estimated to be increased more than 30% (Neville and McCullough, 1969) or 10 to 20% (Ferrell and Jenkins, 1987) during lactation.

Smith and Baldwin (1974) showed that organ weights were higher in lactating compared with nonlactating cows for liver (25%), heart (22%), mammary gland (73%), lungs (22%), rumen (20%), abomasums (35%), intestines (31%), spleen (20%), and adrenals (19%). Assuming no change in energy expended/weight of tissue, a 10% increase in energy expenditures during lactation could be attributed to differences in organ tissue weight alone. According to our estimates, maintenance energy expenditures rose until approximately 15 WOL, where it plateaued at approximately 0.098 Mcal of NE_L /kg of $BW^{0.75}$ (Figure 2). The 0.096 time-independent equation represents the weighted average of this curve. Interestingly, the 0.08 Mcal of NE_L /kg of $BW^{0.75}$ maintenance equation (NRC, 2001) seems to agree with values obtained here in early lactation (Figure 2). It is only as the demands of lactation increase and lactation persists that maintenance energy expenditures rise to a higher value. It appears that the 0.08 maintenance equation still describes well the energy expenditures of a nonlactating dairy cow. Maintenance energy expenditures rise in early lactation because milk production and DMI both peak within the first 15 WOL, placing increased demands on the internal organs to increase in both size and activity. In comparative slaughter measurements, rumen, small intestine, and liver weights of dairy cattle increased as a percentage of empty BW from 2 to 17 WOL, and then decreased by wk 34 (Baldwin et al., 2004). Similarly, weights of ewe liver and rumen reached a maximum at 6 WOL, and small intestines at 4 WOL, and weights declined thereafter (Fell et al., 1972). The increase, plateau, and eventual decline in metabolically active organ size and activity are likely

associated with a similar pattern in maintenance energy expenditures. Although our data showed no decline in maintenance energy expenditures, it is possible, had the data extended further into late lactation, that a decline would be observed. Some individual data sets did show a decline in maintenance energy expenditures after peak lactation, but averaging curves smooths out any rise to peak, peak, or eventual decline observed. More extensive data would be required to determine the exact pattern of maintenance energy expenditure change over the course of lactation.

Increased metabolic activity of organs to support lactation could be considered either as a maintenance cost or an inefficiency of conversion of ME to NE_L . The 2 are actually indistinguishable mathematically and the selection of one over the other remains a matter primarily of philosophical preference. In the NRC (2001) system, an efficiency adjustment to correct the bias we encountered would be accommodated by changing NE_L values of feedstuffs, which is rather more difficult to do than the alternative maintenance adjustment undertaken here.

The variation in energy balance bias represents a problem in the use of one equation to describe all lactating dairy cows. The between-data set variation in maintenance energy expenditures around the updated 0.096 maintenance equation was 25%. The highest maintenance value was 0.135 and the lowest was 0.068 Mcal of NE_L /kg of $BW^{0.75}$. Although this variation likely encompasses multiple sources of error, others have reported similar, if not higher, degrees of variation. Ritzman and Benedict (1938) found between-animal variation in maintenance energy requirements under uniform conditions of up to 50% in Holstein and up to 71% in Jersey cows. Carstens et al. (1989) and Taylor and Young (1968) found that maintenance requirements varied by 20 to 30% due to genetic differences alone, which appeared moderately to highly heritable.

Genetic potential for production, previous plane of nutrition, estimation of dietary energy content, environment, BCS, and physiological status likely contribute cumulatively to a high degree of variation between animals. It was evident from a review of the literature that maintenance is not a constant function of BW (Webster et al., 1982; Ferrell and Jenkins, 1985). The possible roles of several factors contributing to the variation in energy balance bias reported here were examined. The relationship between maintenance energy expenditures and average BW, average DMI, peak FCM yield, total FCM yield, and dietary NE_L content were not significant. In contrast, Ferrell and Jenkins (1987) found that maintenance energy expenditures increased about 9.6 kcal/kg of $BW^{0.75}$ per d for each 1-kg increase in milk yield at peak lactation. Interestingly, they re-

ported that 40% of the variation in maintenance energy expenditures could be explained by variation in milk production potential alone.

It is important to reiterate that the maintenance description developed here is essentially an error term, containing errors associated with the other aspects of energy balance calculations discussed above. It was not the goal of this paper to assign individual correction factors to all of these components, but to provide a feasible solution to the model, agreeable with data in the literature, such that the model could be used for further evaluations of DMI prediction equations.

CONCLUSIONS

Revision of the maintenance energy expenditure estimate substantially improves BW prediction by a dynamic simulation of energy balance. On average, the time-independent 0.096 Mcal of NE_L /kg of $BW^{0.75}$ equation resulted in the best BW predictions, although there was 25% variation around this value, likely encompassing other sources of error.

The 0.096 Mcal of NE_L /kg of $BW^{0.75}$ equation is 20% higher than the original 0.08 Mcal of NE_L /kg of $BW^{0.75}$. This increase is in agreement with estimates of maintenance energy expenditures presented in the reviewed literature, which ranged from 10 to 49%, but averaged from 20 to 30% (for examples see Moe et al., 1970; Yan et al., 1997; Kirkland and Gordon, 2001). This new time-independent equation, as well as a time-dependent quadratic equation relating maintenance expenditures to WOL, are useful in better describing energy balance within a dynamic model, but do little to account for the substantial variation that is evident. It is the goal of the companion paper (Ellis et al., 2006) to address between-data set variation and correction of errors that persist in accumulating over time.

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