Accounting for Energy and Protein Reserve Changes in Predicting Diet-Allowable Milk Production in Cattle

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ABSTRACT

Current ration formulation systems used to formulate diets on farms and to evaluate experimental data estimate metabolizable energy (ME)-allowable and metabolizable protein (MP)-allowable milk production from the intake above animal requirements for maintenance, pregnancy, and growth. The changes in body reserves, measured via the body condition score (BCS), are not accounted for in predicting ME and MP balances. This paper presents 2 empirical models developed to adjust predicted diet-allowable milk production based on changes in BCS. Empirical reserves model 1 was based on the reserves model described by the 2001 National Research Council (NRC) Nutrient Requirements of Dairy Cattle, whereas empirical reserves model 2 was developed based on published data of body weight and composition changes in lactating dairy cows. A database containing 134 individually fed lactating dairy cows from 3 trials was used to evaluate these adjustments in milk prediction based on predicted first-limiting ME or MP by the 2001 Dairy NRC and Cornell Net Carbohydrate and Protein System models. The analysis of first-limiting ME or MP milk production without adjustments for BCS changes indicated that the predictions of both models were consistent (r^2 of the regression between observed and model-predicted values of 0.90 and 0.85), had mean biases different from zero (12.3 and 5.34%), and had moderate but different roots of mean square errors of prediction (5.42 and 4.77 kg/d) for the 2001 NRC model and the Cornell Net Carbohydrate and Protein System model, respectively. The adjustment of first-limiting ME- or MP-allowable milk to BCS changes improved the precision and accuracy of both models. We further investigated 2 methods of adjustment; the first method used only the first and last BCS values, whereas the second method used the mean of weekly BCS values to adjust ME- and MP-allowable milk production. The adjustment to BCS

changes based on first and last BCS values was more accurate than the adjustment to BCS based on the mean of all BCS values, suggesting that adjusting milk production for mean weekly variations in BCS added more variability to model-predicted milk production. We concluded that both models adequately predicted the first-limiting ME- or MP-allowable milk after adjusting for changes in BCS.

Key words: body condition score, fat mobilization, fat repletion, modeling

INTRODUCTION

Computer programs based on the NRC (2001) model formulate rations for lactating dairy cows by computing energy and protein requirements for an inputted milk production and then formulate a diet that will meet requirements for that amount of milk at the DMI predicted from BW and milk. Rations in early lactation are typically deficient in energy and assume the deficiency will be met by mobilization of body reserves. Then in mid- and late lactation, energy intake must exceed requirements for milk production to replenish body reserves before the next lactation. With current and proposed environmental regulations, precision feeding is needed to more accurately formulate diets to avoid under- or overfeeding nutrients (Cerosaletti et al., 2004) while optimizing milk and reproductive performance. Dairy nutrition models are being designed with these objectives (Tylutki and Fox, 2005). Precision ration formulation for dairy cows requires accounting for fluxes in body reserves when formulating diets. In addition, dairy nutrition models with the capability of accounting for body reserves can be used to more accurately evaluate experimental results in which milk response to dietary inputs is the variable of interest. Baldwin et al. (1987b,c) developed a mechanistic model of metabolism and digestion for lactating dairy cows and concluded that models can realistically simulate lactation and the partition of nutrients (Baldwin et al., 1987a).

Body weight changes reflect the use of energy reserves either to supplement ration deficiencies during

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early lactation or to store energy consumed above the requirements (Moe et al., 1972; NRC, 2001). The BW gain and loss after maturity is similar in composition to changes during growth (NRC, 2001) and can be used to predict changes in energy balance over the reproductive cycle (Reynoso-Campos et al., 2004). However, most dairy and beef producers monitor BCS changes in cows to manage energy reserves because frequent measurements of BW are not feasible under practical conditions. The Cornell Net Carbohydrate and Protein System (CNCPS; Fox et al., 2004) and the NRC (2000, 2001) models use the body reserves model as devised by Fox et al. (1999), which was developed from data on the chemical body composition and BCS of 106 mature beef cows of diverse breed types and BW. As applied to dairy cattle, the model was evaluated with the data of Otto et al. (1991) and accounted for 95% of the variation in body fat, with only a -1.6% bias (Fox et al., 1999). The model predicted 80 kg of BW change per BCS compared with 84.6 kg observed in Holstein cows slaughtered over the range of dairy BCS.

For lactating dairy cows, the CNCPS and NRC models estimate energy and protein requirements for maintenance and pregnancy, and the amount remaining above intake is used to estimate ME- and MP-allowable milk production, respectively (Fox et al., 2004). The changes in BCS are not accounted for in predicting ME and MP balances. The objective of this study was to develop and compare 2 empirical models to eliminate biases in energy retention by adjusting the predicted ME- and MP-allowable milk production after consecutive changes in observed BCS have been accounted for.

MATERIALS AND METHODS

Model Development

Two empirical models were developed to estimate milk production based on changes in BCS. Empirical reserves model 1 (**ERM1**) was based on the reserves model described by the NRC (2001), whereas empirical reserves model 2 (**ERM2**) was developed based on literature data on BW changes in lactating dairy cows.

Milk Energy and Body Content of Energy and Protein. For both empirical models, the energy contained in milk production is computed using milk fat and milk true protein contents, as described by the NRC (2001). This energy in milk (**MkE**), as shown in Equation [1], is assumed to be the NE_L :

$$MkE_i = 0.0929 \times MkF_i + 0.0563 \quad [1]$$

$$\times MkTP_i + 0.192$$

where MkE_i is the energy content of milk (Mcal/kg), MkF_i is the milk fat content (g/100 g), $MkTP_i$ is the

milk true protein content (g/100 g), and the subscript i is the i th time period.

The BCS is a 5- (Wildman et al., 1982) or 9-point (Cantrell et al., 1981; Herd and Sprott, 1986) scale system that is highly related to body fat in cows (Houghton et al., 1990; Buskirk et al., 1992; NRC, 2000, 2001). Other scale systems that are used around the world (CSIRO, 1990) can be interconverted. Because the body reserves model used by the NRC (2001) is based on that developed by the NRC (2000), a BCS scale of 1 to 9 is used. Equation [2] is used to convert a BCS scale of 1 to 8 (**BCS**_[1-8]), as used by the Commonwealth Scientific and Industrial Research Organisation (CSIRO, 1990), to a BCS scale of 1 to 5 (**BCS**_[1-5]) and Equation [3] converts **BCS**_[1-5] to a BCS scale of 1 to 9 (**BCS**_[1-9]), and vice versa. As adopted by the NRC (2000, 2001), shrunk BW (**SBW**) is computed from BW as shown in Equation [4] and empty BW (**EBW**) is estimated from SBW as shown in Equation [5], which is used to predict body reserves:

$$BCS_{[1-5],i} = \frac{(BCS_{[1-8],i} - 1) \times 4}{7} + 1 \quad [2]$$

$$BCS_{[1-9],i} = (BCS_{[1-5],i} - 1) \times 2 + 1 \quad [3]$$

where $BCS_{[1-5],i}$ is the BCS on a scale of 1 to 5, $BCS_{[1-8],i}$ is the BCS on a scale of 1 to 8, and $BCS_{[1-9],i}$ is the BCS on a scale of 1 to 9,

$$SBW_i = BW_i \times 0.96 \quad [4]$$

$$EBW_i = SBW_i \times 0.851 \quad [5]$$

where SBW_i is shrunk BW (kg) and EBW_i is empty BW (kg).

Empirical Reserves Model 1. This model is based on the equations published by Fox et al. (1999) in which $BCS_{[1-9]}$ and EBW are used to compute the amount of body fat (**TF**; Equation [6]) and protein (**TP**; Equation [7]):

$$TF_i = (0.037683 \times BCS_{[1-9],i}) \times EBW_i \quad [6]$$

$$TP_i = (0.200886 - 0.0066762 \times BCS_{[1-9],i}) \times EBW_i \quad [7]$$

where EBW_i is empty BW (kg), TF_i is the amount of body fat (kg), $BCS_{[1-9],i}$ is the BCS (on a scale of 1 to 9), and TP_i is the amount of body protein (kg).

For mature lactating cows, a change in BW does not necessarily indicate changes in tissue reserves, and vice versa. Andrew et al. (1994) and Gibb et al. (1992) ana-

lyzed slaughter data of dairy cows and reported as much as 40% variation in energy with no change in BW. This is likely because the gut fill varies from 2.5 (Komaragiri and Erdman, 1997) to 4 kg/kg of increase in DMI (Chilliard et al., 1991), which may offset the weight loss attributable to tissue mobilization by an increase in DMI during early lactation. Because of this disconnection between actual BW and energy reserves, ERM1 uses BCS changes to estimate EBW and energy reserves.

As discussed by Fox et al. (1999), the database used at the NRC (2000) to develop the body reserves model indicated that the mean BW change associated with a BCS change was equivalent to 6.85% of the mean BW. The Commonwealth Scientific and Industrial Research Organisation (1990) uses 8% of the standard reference weight per change in BCS_[1-8], which is equivalent to 7% per change in BCS_[1-9]. Therefore, a weight adjustment factor (**WAF**; Equation [8]) is computed from the BCS. Adjusted EBW values (**aEBW**; Equation [9]) are then computed for all other periods ($i \geq 2$) based on their respective WAF values (Equation [8]), which are a function of the measured BCS for each period:

$$WAF_i = 1 - 0.0685 \times (5 - BCS_{[1-9],i}) \quad [8]$$

$$aEBW_i = \frac{EBW_{i=1}}{WAF_{i=1}} \times WAF_i \quad [9]$$

where BCS_{[1-9],i} is the BCS (on a scale of 1 to 9).

The ($EBW_{i=1}/WAF_{i=1}$) factor in Equation [9] computes the expected BW at BCS 5. The aEBW for each period ($aEBW_i$) is then used to assess the variation in tissue energy, which is added or subtracted from the tissue energy computed using the previous aEBW ($aEBW_{i-1}$) and Equations [6] and [7].

Empirical Reserves Model 2. This model is based on the equations derived by Otto et al. (1991) to compute the proportion of fat (Equation [10]) and protein (Equation [11]) in the 9th to 11th rib section of Holstein cows:

$$EE_{9^{th}-11^{th} Rib} = \frac{(16.44 + 12.65 \times BCS_{1-5}) \times (19.15 + 7.23 \times BCS_{1-5})}{100} \quad [10]$$

$$Protein_{9^{th}-11^{th} Rib} = \frac{(75.59 - 12.19 \times BCS_{1-5}) \times (19.15 + 7.23 \times BCS_{1-5})}{100} \quad [11]$$

where EE is ether extract (%) and BCS_[1-5] is the BCS on a scale of 1 to 5.

Conversion of the fat and protein contents from the 9th to the 11th rib to EBW is performed using the relationship between 9th and 11th rib and carcass com-

position as developed by Hankins and Howe (1946; Equations [12] and [13], respectively) and from the carcass to EBW as derived by Garrett and Hinman (1969; Equations [14] and [15], respectively):

$$EE_{Carcass} = 2.82 + 0.77 \times EE_{9^{th}-11^{th} Rib} \quad [12]$$

$$Protein_{Carcass} = 5.98 + 0.66 \times Protein_{9^{th}-11^{th} Rib} \quad [13]$$

$$EE_{EBW} = 0.9246 \times EE_{Carcass} - 0.647 \quad [14]$$

$$Protein_{EBW} = 0.7772 \times Protein_{Carcass} + 0.713 \quad [15]$$

where EE is ether extract (%) and EBW is empty BW.

Equation [16] was derived by combining Equations [3], [10], [12], and [14], and was solved for fat in the EBW. Similarly, Equation [17] was derived by combining Equations [3], [11], [13], and [15], and was solved for protein in the EBW:

$$TF_i = \frac{(5.65 + 1.61 \times BCS_{1-9,i} + 0.163 \times BCS_{1-9,i}^2) \times EBW_i}{100} \quad [16]$$

$$TP_i = \frac{(13.9 + 0.651 \times BCS_{1-9,i} - 0.113 \times BCS_{1-9,i}^2) \times EBW_i}{100} \quad [17]$$

Like the ERM1, the ERM2 assumes that changes in BW may reflect changes in gut fill and may not represent a true change in tissue. Therefore, BCS changes are used to compute changes in the tissue as a function of EBW. However, unlike the ERM1, the ERM2 relies on a fixed variation of EBW per change in BCS based on the analyses of Otto et al. (1991), who found that each unit of BCS change was associated with a 56-kg change in live BW. When converted to EBW, assuming a gut fill of 15%, this change was 47.7 kg of EBW. Therefore, WAF values are computed for each interval based on the initial EBW and changes in the BCS using Equation [18] and aEBW are computed based on EBW and WAF values, as shown in Equation [19]:

$$WAF_i = 1 - \left(\frac{47.7 \times (BCS_{[1-5],i=1} - BCS_{[1-5],i})}{EBW_{i=1}} \right) \quad [18]$$

$$aEBW_i = EBW_{i=1} \times WAF_i \quad [19]$$

where BCS_{[1-5],i} is the body condition score (on a scale of 1 to 5).

For both models (ERM1 and ERM2), total energy (TE; Equation [20]) is computed from TF and TP multiplied by their respective heat of combustion. For growing animals, the heat of combustion of fat has been assumed to be 9.367 Mcal/kg (Blaxter and Rook, 1953) and protein has varied from 5.554 to 5.686 Mcal/kg (Lofgreen, 1965; Garrett, 1987). For dairy cows, Andrew et al. (1994) derived values of 9.2 and 5.57 Mcal/kg for fat and protein, respectively. The NRC (2000, 2001) has adopted the growing animal values (9.367 and 5.554 Mcal/kg). Because both estimates are nearly identical, the NRC (2000, 2001) values are used in these models:

$$TE_i = 9.367 \times TF_i + 5.554 \times TP_i \quad [20]$$

where TF_i is the amount of body fat (kg), TP_i is the amount of body protein (kg), TE_i is the total energy (Mcal), and the subscript i is the i th period.

Assessing Changes in Body Energy. The TE of the first period, which uses the current EBW of the cow, remains unchanged; however, the TE of subsequent periods is computed with the aEBW and Equation [20]. The variation in TE is computed using Equation [21]:

$$\Delta TE_i = TE_i - TE_{i-1}; i \geq 2 \quad [21]$$

where ΔTE_i is the change in total energy (Mcal), and subscripts i and $i-1$ represent actual and previous TE values, respectively.

When the ΔTE value is negative, there is a mobilization of reserve energy for milk production. The amount of milk production supported from mobilized reserves is added to the diet-allowable milk production. When the ΔTE value is positive, the intake of energy is greater than the energy required for milk production. In this case, part of the available energy is used for reserve deposition rather than milk production; therefore, the amount of energy deposited has to be used to reduce the diet-allowable milk production. The variation in body protein is computed using Equation [22]:

$$\Delta TP_i = TP_i - TP_{i-1} \quad \text{for } i \geq 2 \quad [22]$$

where ΔTP_i is total protein variation (kg), and the subscripts i and $i-1$ represent actual and previous TE values, respectively.

The mobilized ($\Delta TE < 0$ or $\Delta TP < 0$) or deposited ($\Delta TE > 0$ or $\Delta TP > 0$) energy and protein are converted to milk equivalents using efficiencies of energy and protein conversion factors, as described in the next section.

Energy and Protein Efficiencies. The coefficients of energy interconversion used in our model were derived by Moe et al. (1970) using a multiple regression analysis of respiration chamber data from 126 and 224

lactating dairy cows in negative and positive energy balances, respectively. The confidence interval of the coefficients reported by Moe et al. (1970) indicated a statistical difference ($P < 0.05$) between the efficiency of ME to net energy of reserves (NE_R ; 72.6%), ME to NE_L (63.5%), and NE_R to NE_L (84%), suggesting there are significant differences in the metabolism of lactating cows at a positive and negative energy balance that affect the efficient use of energy.

When $\Delta TE < 0$, it indicates a negative energy balance, and energy reserves (NE_R) were used for milk production. An efficiency for NE_R to NE_L of 82% is generally used (Moe, 1981; Fox et al., 1999; NRC, 2001). The Commonwealth Scientific and Industrial Research Organisation (1990) and the Agricultural Research Council (ARC, 1980) assume an efficiency of 84%, which is supported by the study of Vermorel and Bickel (1980). Similarly, Moe et al. (1970) observed an efficiency of 84% for lactating cows in negative energy balance, which was used in these models. Analysis of the variation in the Moe et al. (1970) data indicated that the true efficiency value was between 81.7 and 86%, assuming $\alpha = 5\%$ and a less rigid combination of coefficients; we used the average efficiency of 84% in our model. The milk from mobilized reserves is added to the predicted diet ME-allowable milk using Equation [23]:

$$\text{if } \Delta TE < 0 \text{ then } \Delta Milk_i = \frac{-\Delta TE_i \times 0.84}{MkE_i} \quad [23]$$

$$\text{for } i \geq 2$$

where ΔTE is tissue energy variation (Mcal NE_L /d), $\Delta Milk$ is milk variation (kg/d), and MkE is energy content of the milk (Mcal of NE_L /kg).

A $\Delta TE > 0$ indicates a positive energy balance in which diet energy was used for reserves rather than milk production. Therefore, the first step is to convert the NE_R to ME, the second step is to convert this amount of ME to NE_L , and finally this NE_L is divided by milk energy to compute the amount of milk that was not produced (Equation [24]). Commonly, an efficiency of ME to NE_R of 75% and ME to NE_L of 64.4% are assumed (Moe, 1981; Fox et al., 1999; NRC, 2001). Moe et al. (1970) reported that lactating cows in positive energy balance had an efficiency of 63.5% for ME to NE_L . An analysis of the possible combinations of the confidence intervals of the coefficients reported by Moe et al. (1970) suggested that the true efficiency value was between 61.2 and 65.9%, assuming $\alpha = 5\%$. Moe et al. (1970) reported an efficiency of 72.6% for ME to NE_R for lactating cows in positive energy balance; the confidence interval was 67.3 to 78.7% ($\alpha = 5\%$). Therefore, for $\Delta TE > 0$ (positive energy balance), we assumed 63.5% for

ME to NE_L and 72.6% for ME to NE_R (Moe et al., 1970) for our models. We then calculated the amount of milk from this amount of TE and subtracted it from the predicted diet ME-allowable milk using Equation [24]:

$$\text{if } \Delta TE > 0 \text{ then } \Delta Milk_i = \frac{\Delta TE_i \times 0.635}{MkE_i \times 0.726}, \quad [24]$$

$$i \geq 2$$

where ΔTE is tissue energy variation (Mcal of NE_L /d), $\Delta Milk$ is milk variation (kg/d), and MkE is the energy content of the milk (Mcal of NE_L /kg).

The mobilization of body tissue will also release AA that can be used directly and indirectly for milk production. The indirect form is through the recycled N into the gastrointestinal tract; this form is accounted for by the CNCPS model (Fox et al., 2004). The direct form, which is discussed here, is related to the incorporation of the AA produced from mobilized reserves into milk protein. In lactating sows, daily mobilization of protein was previously shown to be approximately 11 to 63 g and 45 to 195 g for first and third lactations, respectively, with an efficiency of use of 68.9 to 73.4% for milk production. These values are much greater than the values for efficiency of use of feed protein for milk production (42.7 and 46% for the first and third lactations, respectively; Lahrssen, 1988).

Dairy cows can mobilize between 7 and 13 kg of body protein within the first 2 to 4 wk of lactation (Journet et al., 1983). Increasing the quantity of RUP fed prepartum had a positive effect by decreasing the loss of BW and increasing the milk protein content (Van Saun et al., 1993).

Information regarding the efficiency with which these AA are utilized for milk production in cattle is scarce. Not all mobilized AA appear in milk protein, and the AA profile of muscle does not match the milk protein profile; therefore, adequate accounting for this phenomenon is needed (McNamara, 2000). The efficiency of use of mobilized AA for milk production is likely to vary depending on the nutritional status of the animal and the N balance. With N-deficient diets, the efficiency of use of N can be as great as 75% (NRC, 1985). Ruiz et al. (2002) indicated that using an efficiency of MP to net protein for milk production (NP_L) of 75% resulted in no bias in the CNCPS-predicted MP-allowable milk. The Commonwealth Scientific and Industrial Research Organisation (1990) suggests that the mobilized net protein (NP_R) has an efficiency of 80% for NP_L . Therefore, when $\Delta TP < 0$ (mobilization of body protein), we assume an efficiency of NP_R to NP_L of 80% and the amount of milk attributable to protein mobilization (Equation [25]) is added to the MP-allowable milk production:

$$\text{if } \Delta TP < 0 \text{ then } \Delta Milk_i = \frac{-\Delta TP_i \times 0.8}{MkTP_i}, \quad [25]$$

$$i \geq 2$$

where ΔTP is tissue protein variation (g/d), $MkTP_i$ is the milk true protein content (g/100 g), and $\Delta Milk$ is milk variation (kg/d).

This efficiency depends on the profile of the AA of the mobilized protein and on the profile of the milk protein (Newbold, 1994). Ionophores may have an impact on sparing AA from gluconeogenesis (Tedeschi et al., 2003), leading to a greater efficiency of use.

Like energy, a $\Delta TP > 0$ indicates a positive protein balance, in which protein was used for reserves rather than milk production. Therefore, to adjust the diet MP-allowable milk, we convert NP_R to MP, which is converted to NP_L . There is little information on the efficiency of conversion of MP to NP_R and vice versa, likely because of the difficulty in measuring it. We assume an efficiency of 70% for our model. The efficiency of MP to NP_L is assumed to be 64% in the Institut National de la Recherche Agronomique (1989) system, 65% in the beef NRC (2000) system, 67% in the dairy NRC (2001) system, and 68% in the Agricultural and Food Research Council (AFRC, 1992) system. The 65% efficiency was used in this model.

The amount of milk change attributable to deposition of tissue protein is computed as shown in Equation [26], which is used to adjust the diet MP-allowable milk:

$$\text{if } \Delta TP > 0 \text{ then } \Delta Milk_i = \frac{\Delta TP_i \times 0.65}{MkTP_i \times 0.7}, \quad [26]$$

$$i \geq 2$$

where ΔTP is tissue protein variation (g/d), $MkTP_i$ is milk true protein content (g/100 g), and $\Delta Milk$ is milk variation (kg/d).

Adjusting Predicted ME- and MP-Allowable Milk. Figure 1 depicts a flowchart of the calculation for the 2 methods used to adjust the predicted ME- and MP-allowable milk production. In method 1 (mean), the adjusted milk production is computed for each BCS measured for the same lactating cow within a given time period, whereas method 2 (period) computes the adjusted milk production based on the first and last BCS within a given time period.

Model Simulations

A database of 134 individually fed lactating dairy cows from 3 trials was used to evaluate the adjustments for milk prediction based on first-limiting energy (ME)

Figure 1. Flowchart of 2 methods to adjust model-predicted milk yield from ME and MP to changes in BCS. TE is total energy change (Mcal/d); TP is total protein change (g/d); and Milk_{ΔTE} and Milk_{ΔTP} are the variations in model-predicted milk attributable to changes in BCS (kg/d), and are functions of efficiency of use of energy and protein.

or protein (MP). All diets were balanced to meet NRC (2001) recommendations for minerals and vitamins. Trial 1 had 15 multiparous Holstein cows averaging 126 DIM and 560 kg of BW that were fed fresh-cut orchardgrass (*Dactylus glomerata* L.) and a concentrate mix with or without monensin for 3 wk (Ruiz et al., 2001). Trial 2 consisted of 22 multiparous and 16 first-lactation Holstein cows averaging 263 DIM and 614 kg of BW, receiving 3 levels of CP (low, medium, and high) in the TMR for 4 wk (Ruiz et al., 2002). Trial 3 comprised 60 multiparous and 21 primiparous Holstein cows (Stone, 1996). Animals from trial 3 were fed 3 treatments to evaluate soyhulls as forage or concentrate replacement for 14 wk. In general, energy was first limiting in trial 3, whereas protein was first limiting in trials 1 and 2. The database contained adequate

information on feed characteristics, animal description and performance, and environment to predict daily milk production using the NRC (2001) and CNCPS (Fox et al., 2004) models. All predictions were made for each cow weekly. The BCS measurements were taken by the same person within each trial.

Evaluation of the Model Predictions

Assessment of the adequacy of mathematical models is only possible through the use of a combination of several statistical and empirical analyses and proper investigation regarding the purposes of the model initially conceptualized (Tedeschi, 2006). Therefore, several techniques were used to evaluate and compare the models in this study. Briefly, linear regression analysis

observed on model-predicted values was conducted to identify precision and accuracy in the prediction of the rate of milk production. The coefficient of determination (r^2 ; Neter et al., 1996), confidence intervals for the parameters (Mitchell, 1997), and a simultaneous test for the intercept and slope (Dent and Blackie, 1979; Mayer et al., 1994) were used. The deviation plot (model-predicted minus observed values against observed values) were used to study the behavior of model prediction compared with observed values (Mitchell and Sheehy, 1997). All residual analysis for outliers (extreme and influential points), homoscedasticity, and normal distribution assumptions were performed on the residual (regression-predicted minus observed values) against regression-predicted values (Neter et al., 1996).

Additional techniques were also used, as discussed by Tedeschi (2006), including accuracy from the concordance correlation coefficient (CCC by Lin, 1989; C_b by Nickerson, 1997; and A_p by Liao, 2003), mean bias (Cochran and Cox, 1957), and mean square error of prediction (**MSEP**; Bibby and Toutenburg, 1977). The MSEP values were expanded into 3 fractions to represent errors in central tendency, errors attributable to regression, and errors attributable to disturbances (or random errors), that is, unexplained variance that could not be accounted for by the linear regression (Theil, 1961). Equation [27] has the equation modified by Tedeschi (2006):

$$MSEP = (\bar{X} - \bar{Y})^2 + s_X^2 \times (1 - b)^2 + (1 - r^2) \times s_Y^2 \quad [27]$$

where MSEP is the mean square error of prediction, X_i is the i th model-predicted value, Y_i is the i th observed value, s^2 is the variance associated with observed and model-predicted values, and r^2 is the coefficient of determination.

The 3 terms in Equation [27] represent errors in central tendency (mean bias), errors attributable to regression (systematic or slope bias), and errors attributable to disturbances (or random errors), that is, unexplained variance that cannot be accounted for by the linear regression. Each error term is commonly evaluated as a proportion of the total MSEP, thus indicating which terms have a greater influence in the MSEP. Detailed information about all these assessment techniques and the software used to perform the model comparison analyses are discussed in Tedeschi (2006).

The MSEP was used to compare the model accuracy among different combinations of nutritional models (CNCPS vs. NRC), reserves models (ERM1 vs. ERM2), and methods of calculation (mean vs. period) compared with observed values. Equation [28] was used to com-

Figure 2. Prediction of the content of body fat (solid lines) and protein (dotted lines) in the empty BW (EBW) as a function of the BCS, using the empirical reserves model based on NRC (2001; open circles) and a new model (solid circles).

pute the difference between MSEP (Δ MSEP) of any 2 sets of model predictions for each data point, and Equation [29] was used to compute the mean and variance of the Δ MSEP. A t -test was conducted to statistically verify the difference of Δ MSEP from zero. In a practical application, if the standard deviation of Δ MSEP were greater than the Δ MSEP value, it would indicate that the Δ MSEP was not different from zero:

$$\Delta MSEP_i = (Y_i - f(X)_i)^2 - (Y_i - g(X)_i)^2 \quad [28]$$

$$\overline{\Delta MSEP} = \frac{1}{n} \sum_{i=1}^n [\Delta MSEP_i] \quad [29]$$

$$\sigma_{\Delta MSEP}^2 = \frac{1}{n-1} \sum_{i=1}^n [\Delta MSEP_i - \overline{\Delta MSEP}]^2$$

where Δ MSEP is the difference between the 2 sets of model predictions for each data point, $f(X)_i$ are model-predicted values using one set of predicted values and $g(X)_i$ are the model-predicted values using another set of predicted values, Y is the observed milk production, $\overline{\Delta MSEP}$ is the mean of Δ MSEP, and $\sigma_{\Delta MSEP}^2$ is the variance of Δ MSEP.

A meta-analysis was conducted according to Equation [30] (Littell et al., 1999) and indicated no random influence of the trials on the intercept ($P = 0.20$) and slope ($P = 0.36$); therefore, the trials were pooled in the analysis:

Table 1. Calculation of body reserves for an actual cow to demonstrate adjustment of predicted milk production on a weekly or initial and final calculation basis¹

BW	BCS	Mk	Fat	Prot	ME	MP	TF	TP	TE	Δ TE	Δ TP	ME _{adj}	MP _{adj}
(Weekly calculation basis)													
676	4.4	44.7	4.3	3.1	28.3	32.1	162.3	82.2	1,977	0	0	28.3	32.1
669	4.1	51.4	3.6	2.6	35.5	42.9	144.7	81.5	1,808	-169	-0.70	65.7	46.0
640	4.0	53.6	3.4	2.5	39.9	48.2	139.0	81.2	1,753	-55	-0.27	50.1	49.4
640	3.7	56.3	3.1	2.3	45.4	56.5	122.5	80.3	1,593	-160	-0.90	76.8	61.0
626	3.3	52.7	3.2	2.4	38.7	47.3	101.8	78.9	1,392	-202	-1.44	77.5	54.2
643	3.2	50.6	3.2	2.5	41.1	48.1	96.9	78.5	1,343	-48	-0.40	50.3	50.0
619	3.0	49.9	3.1	2.5	45.1	51.6	87.3	77.6	1,249	-94	-0.86	63.4	55.5
626	3.3	50.3	2.9	2.4	48.8	56.7	101.8	78.9	1,392	143	1.26	18.9	49.7
604	3.2	46.5	3.1	2.5	46.7	53.6	96.9	78.5	1,343	-48	-0.40	56.0	55.4
624	3.0	47.3	2.9	2.4	45.4	52.9	87.3	77.6	1,249	-94	-0.86	64.4	57.0
613	3.0	42.4	3.1	2.7	46.3	49.3	87.3	77.6	1,249	0	0.00	46.3	49.3
617	3.1	45.2	2.7	2.4	49.7	56.2	92.0	78.1	1,296	47	0.44	39.5	53.8
609	3.0	39.6	3.0	2.7	47.0	49.6	87.3	77.6	1,249	-47	-0.44	56.1	51.4
602	3.0	41.1	2.7	2.6	50.5	52.8	87.3	77.6	1,249	0	0	50.5	52.8
(Initial and final calculation basis)													
676	4.4	44.7	4.3	3.1	28.3	32.1	162.3	82.2	1,977	0	0	28.3	32.1
602	3.0	41.1	2.7	2.6	50.5	52.8	87.3	77.6	1,249	-728	-4.56	53.4	51.3

¹Calculations were performed for cow #4675 from trial 3. BCS is body condition score (on a scale of 1 to 5); Mk is observed milk (kg/d); Fat is milk fat (%); Prot is milk true protein (%); ME is ME-allowable milk production (kg/d); MP is MP-allowable milk production (kg/d); TF is amount of body fat (kg); TP is amount of body protein (kg); TE is energy from body fat and protein (Mcal); Δ TE is variation in energy content of the body attributable to changes in BCS (Mcal); Δ TP is variation in protein content of the body attributable to changes in BCS (kg); ME_{adj} is ME-allowable milk adjusted for changes in body energy content (kg/d); and MP_{adj} is MP-allowable milk adjusted for changes in body protein content (kg/d).

$$Y_{ij} = a_i + b_i X_{ij} + e_{ij}$$

$$\begin{pmatrix} a_i \\ b_i \end{pmatrix} \sim iid N \left[\begin{pmatrix} \alpha \\ \beta \end{pmatrix}, \Omega \right] \quad [30]$$

$$\Omega = \begin{pmatrix} \sigma_a^2 & \sigma_{ab} \\ \sigma_{ab} & \sigma_b^2 \end{pmatrix}$$

where Y_{ij} is the observed milk production (kg/d); X_{ij} is the model-predicted milk production (kg/d); e_{ij} is the random error, independently, identically, and normally distributed with mean zero and variance σ^2 ; and a and b are fixed variables, with variance-covariance represented by Ω . A variance component structure was used

in this analysis based on the -2 REML log likelihood values.

RESULTS AND DISCUSSION

Figure 2 depicts the comparison of ERM1 and ERM2 to predict empty body TF and TP from BCS (Equations [6] to [7] and [16] to [17], respectively). The prediction of TF was very similar between ERM1 and ERM2. However, the prediction of TP was consistently greater for ERM1, which is implemented in the NRC (2000, 2001) models.

Table 1 demonstrates the sequence of calculation of ME- and MP-allowable milk adjusted for changes in

Table 2. Energy reserves (Mcal) for cows with different shrunk BW (SBW, kg) and BCS for 2 empirical reserves models (ERM1 and ERM2, respectively)¹

BCS	SBW for ERM1					SBW for ERM2				
	400	450	500	550	600	400	450	500	550	600
1 to 2	154 (2.8)	164 (2.9)	173 (3.1)	182 (3.2)	191 (3.4)	164 (4.3)	184 (4.3)	205 (4.3)	225 (4.3)	245 (4.3)
2 to 3	172 (3.1)	182 (3.2)	191 (3.4)	201 (3.6)	211 (3.8)	168 (4.9)	189 (4.9)	210 (4.9)	231 (4.9)	252 (4.9)
3 to 4	190 (3.4)	200 (3.6)	211 (3.8)	222 (4.0)	232 (4.1)	172 (5.4)	193 (5.4)	215 (5.4)	236 (5.4)	258 (5.4)
4 to 5	209 (3.7)	220 (3.9)	231 (4.1)	243 (4.3)	254 (4.5)	175 (5.9)	197 (5.9)	219 (5.9)	241 (5.9)	262 (5.9)
5 to 6	228 (4.1)	240 (4.3)	253 (4.5)	265 (4.7)	277 (4.9)	178 (6.5)	200 (6.5)	222 (6.5)	244 (6.5)	267 (6.5)
6 to 7	249 (4.4)	262 (4.7)	275 (4.9)	288 (5.1)	301 (5.4)	180 (7.0)	203 (7.0)	225 (7.0)	248 (7.0)	270 (7.0)
7 to 8	270 (4.8)	284 (5.1)	298 (5.3)	312 (5.6)	325 (5.8)	182 (7.6)	205 (7.6)	228 (7.6)	251 (7.6)	273 (7.6)
8 to 9	293 (5.2)	307 (5.5)	322 (5.7)	336 (6.0)	351 (6.3)	184 (8.1)	207 (8.1)	230 (8.1)	253 (8.1)	276 (8.1)

¹Within parentheses are megacalories per kilogram of SBW change. The ERM1 assumes a variable value for change in BW per change in BCS, whereas the ERM2 assumes a fixed value of 56 kg of SBW (see text).

Figure 3. Comparison between observed milk (kg/d) and first-limiting ME- or MP-allowable milk using (A) the NRC (2001) and (B) the Cornell Net Carbohydrate and Protein System (Fox et al., 2004) models without BCS adjustment. Symbols designate different trials (Stone, 1996, $n = 81$, $\circ$; Ruiz et al., 2001, $n = 15$, $\times$; Ruiz et al., 2002, $n = 38$, $\square$).

BCS, using a cow from trial 3 that averaged 50 kg/d of milk. The mean of first-limiting diet ME- or MP-allowable milk as predicted by the CNCPS (Fox et al., 2004) using ERM1 was 43.5 kg/d (Table 1), indicating that the model was underpredicting milk production by 6.5 kg/d. When the adjustment for BCS change was performed, the mean first-limiting ME- or MP-allowable milk was 47.4 kg/d for the method 1 calculation (mean across all measurements) and 51.3 kg/d for the

method 2 calculation (first and last measurements; Table 1). This suggests that adjusting for the first and last BCS values (method 2) was more accurate than using the mean of the adjusted ME- or MP-allowable milk values for all BCS changes (method 1), likely because the BCS changes between weeks were highly variable.

The mobilization of protein and its use for milk protein production may explain part of the variation associated with prediction of the dynamics of fat reserves by mathematical models (McNamara, 2000). Unlike fat mobilization, protein mobilization as a proportion of BW change seems to be less variable (Figure 2). The Agricultural and Food Research Council (AFRC, 1992) suggests a fixed contribution of 13.8% of BW change for protein, which is very similar to the values predicted in Figure 2. Metabolizable protein was predicted by both models (NRC and CNCPS) to be the first-limiting factor driving milk production for trials 1 and 2 (Ruiz et al., 2001, 2002), whereas ME was the first-limiting factor for trial 3 (Stone, 1996). Therefore, the MP adjustment (Equations [25] and [26]) was more important in trials 1 and 2 than in trial 3. The Commonwealth Scientific and Industrial Research Organisation (1990) indicates that the mobilized protein could be used in the rumen rather than for milk production (indirect effect).

Table 2 lists the energy content of repletion and depletion of body reserves for changes in the BCS of cows for 5 different SBW. These calculations were made with Equations [6] to [9] for ERM1, Equations [16] to [19] for ERM2, and Equation [20] for both models. The energy content per change in kilogram of SBW (Δ SBW) varied from 4.3 to 8.1 Mcal/ Δ SBW for ERM2 and 2.8 to 6.3 Mcal/ Δ SBW for ERM1. These values are in agreement with several studies (Houghton et al., 1990; Buskirk et al., 1992). Buskirk et al. (1992) reported values ranging from 2.8 to 7.8 Mcal/ Δ SBW. However, for ERM2, within a BCS the megacalories per Δ SBW did not change with SBW, whereas for ERM1 this value changed with SBW. The mean of ERM1 is greater than the value of 3.6 Mcal/ Δ SBW reported by Schwager-Suter et al. (2001b).

The values for energy content of repletion and depletion of body reserves were lower in ERM1 compared with ERM2 for a given BW and BCS status (Table 2). This difference was expected because ERM2 assumes a fixed value of 56 kg of SBW (47.7 kg of EBW) regardless of the BCS of the animal (Equations [18] and [19]), whereas ERM1 assumes a variable value, depending on the BCS of the animal (Equations [8] and [9]). The values for megacalories per Δ SBW obtained for ERM1 (Table 2) were identical to those reported by Fox et al. (1999), but the values for energy of repletion and

Table 3. Evaluation of 2 submodels [empirical reserves model 1 (ERM1) and 2 (ERM2)]¹ and 2 methods (mean or period) for adjusting ME- and MP-allowable milk production²

Item	NRC-predicted milk production					CNCPS-predicted milk production				
	Original	ERM1		ERM2		Original	ERM1		ERM2	
		Mean	Period	Mean	Period		Mean	Period	Mean	Period
Linear regression analysis										
r^2	0.90	0.90	0.92	0.89	0.92	0.85	0.83	0.89	0.82	0.89
$\sqrt{MSE}$	3.59	3.71	3.31	3.79	3.30	4.50	4.76	3.84	4.87	3.87
$P\text{-value}_{(\beta_0=0, \beta_1=1)}$	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.32	<0.01	0.53
Concordance correlation analysis										
C_b	0.95	0.95	0.97	0.95	0.97	0.98	0.97	1.00	0.97	1.00
A_ρ	0.95	0.95	0.96	0.94	0.96	0.98	0.97	1.00	0.97	1.00
Mean bias, %	12.3	12.7	6.21	13.1	7.13	5.34	7.34	−0.45	7.54	0.42
Mean square error of										
prediction (MSEP) $\sqrt{MSEP}$	5.42	5.61	4.69	5.71	4.72	4.77	5.23	3.85	5.35	3.86
Mean bias, %	44.0	43.2	16.8	44.6	21.4	12.2	18.6	0.15	18.5	0.13
Systematic bias, %	12.8	13.8	34.1	12.1	30.3	0.14	0	1.58	0	0.83
Random errors, %	43.2	43.0	49.1	43.3	48.2	87.7	81.5	98.3	81.5	99.0

¹See text for more information on the ERM1 and ERM2 submodels.

²Mean uses the mean of weekly BCS values, and Period uses the first and last BCS values to adjust ME- and MP-allowable milk. National Research Council (NRC)-predicted milk production is from NRC (2001), whereas Cornell Net Carbohydrate and Protein System (CNCPS)-predicted milk production is from Fox et al. (2004). MSE = mean square error; β_0 = intercept of the linear regression; β_1 = slope of the linear regression. C_b = Accuracy (Lin, 1989); A_p = concordance correlation coefficient (Liao, 2003).

depletion per unit of BCS change were different from those developed by Fox et al. (1999) and the NRC (2000).

Figure 3 depicts the relationship between observed milk yield and milk yield predicted by the NRC (2001) and CNCPS (Fox et al., 2004) models without adjustment for changes in BCS. The NRC (2001) model had greater precision (based on the coefficient of determination of the regression between observed and model-predicted values) than the CNCPS model (0.90 vs. 0.85, respectively; Table 3) but had a greater mean bias (12.3 vs. 5.34%, respectively; Table 3). The root of MSEP values of the unadjusted (original) predictions by the CNCPS and NRC models differed (4.77 vs. 5.42, respectively; $P = 0.03$). Within the CNCPS and NRC predictions, the mean method for both ERM1 and ERM2 had similar MSEP ($P > 0.20$) and were lower ($P < 0.01$) than the unadjusted (original) and the period method MSEP values (Table 3). Analysis of the MSEP decomposition indicated that the mean and systematic biases in the NRC (2001) predictions were a greater source of disparity than in the CNCPS prediction and that the random errors were greater in the CNCPS than in the NRC (2001) predictions. These findings suggest that the NRC (2001) predictions tended to be more homogeneous (precise) than those from the CNCPS model but were less accurate, as also indicated by the concordance correlation coefficient analysis (Table 3). We concluded that both models adequately predicted the first-limiting ME- or MP-allowable milk.

Table 3 also shows the outcome of the comparison between ERM1 and ERM2, and methods 1 (mean of the adjustments) and 2 (first and last measurement to adjust milk production to BCS changes) of calculation for both systems (NRC and CNCPS). The adjustment of first-limiting ME- or MP-allowable milk for BCS changes improved the precision and accuracy of both systems, as shown in Table 3. In general, method 2 was more appropriate than method 1 for both ERM1 and ERM2, suggesting that adjusting milk production for weekly variations of BCS added more variability to a measurement (BCS) that is already highly subjective. In agreement with our findings, McNamara (2000) concluded that the use of BCS is quite helpful when applied over a long period of time (>1 mo). The amount of BW or fat change per unit of BCS is highly variable (25 to 50 kg/ Δ BCS; Garnsworthy, 1988; Komaragiri and Erdman, 1997) and depends on several factors (e.g., age, breed, plane of nutrition, parity, etc.). This might explain why a simple adjustment (method 2 of calculation) can be more accurate than sequential adjustments (method 1 of calculation).

Figure 4 shows the relationship of observed milk production and first-limiting ME- or MP-allowable milk adjusted for changes in BCS. In agreement with Table 3, the adjustment shifted the prediction to the right, decreasing the overall underprediction of both models. However, the improvements in model precision and accuracy were small.

Figure 4. Comparison between observed milk (kg/d) and first-limiting ME- or MP-allowable milk using (A) the NRC (2001) and (B) the Cornell Net Carbohydrate and Protein System (Fox et al., 2004) models with BCS adjustment with first and last BCS measurements (method 2) based on equations from Otto et al. (1991; model 2). Symbols designate different trials (Stone, 1996, $n = 81$, $\circ$; Ruiz et al., 2001, $n = 15$, $\times$; and Ruiz et al., 2002, $n = 38$, $\square$).

Despite the good agreement between ERM1 and ERM2, the adjustments proposed by ERM2 do not account for differences between mature small- and large-sized lactating cows. Changes in BW per unit of BCS change have been shown to be highly variable (25 to 50 kg/ Δ BCS) across BCS categories (Garnsworthy, 1988; Komaragiri and Erdman, 1997). We expect that ERM1 is a more robust model than ERM2 for situations in

which the animals are different from the ones used in the study by Otto et al. (1991).

Schwager-Suter et al. (2001a) found that changes in BW were a better indicator of body tissue change than changes in BCS. The ERM2 can be implemented with a variable change in BW rather than a fixed value of 47.7 kg of EBW, as reported by Tennant et al. (2002). However, as we have stated, variation in BW is difficult to assess at the farm level because of changes in gut fill. As our model evaluation indicated, BCS can be used to account for energy mobilization and repletion.

In our model, we assumed fixed values for the fat and protein content of mobilized and replenished tissue. Williams et al. (1989) suggested that the contribution of energy from fat and protein (Equation [20]) be adjusted by stage of lactation. The authors proposed multiplicative factors for fat and protein (1.4 and 0.6, respectively) to account for differences in the amount of fat and protein mobilized during early lactation, as opposed to the composition of gain during late lactation.

More complex models of adipose tissue biochemistry have been discussed by McNamara (2000) and Baldwin (1995, chapters 12 and 16). These models use substrate saturation and enzyme kinetics or mass action to modulate the mechanisms of lipogenesis and lipolysis biochemically. Simpler models that work within the NRC and CNCPS frameworks are needed to account for BCS changes of lactating cows and predict production responses with different feeding systems given an animal's potential performance, energy and protein supply, environmental conditions, and body reserve management strategies. Our results indicate that the model presented can be used to account for changes in BCS in formulating diets on farms and in evaluating differences in milk production with different experimental diets.

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