Evaluation of Models for Balancing the Protein Requirements of Dairy Cows

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ABSTRACT

Most diets for dairy cattle in the US are formulated using the mathematical model developed by the National Research Council (NRC). This model is simpler than more mechanistic models and is largely empirical. Based on the research reviewed in this paper, the simpler empirical approach is recommended for routine diet formulation at the present time. Under typical conditions using feed tables for most feed descriptions, the NRC model was more accurate than the Cornell Net Carbohydrate and Protein System, and, in its present form, the model developed by Baldwin et al. (4) is too difficult to run routinely in the field. However, the more mechanistic approaches are recommended to investigate diet and animal interactions under nonstandard environmental conditions, animals, or feeds. Because the NRC model does not address many of the potential limitations of some diets or management conditions, more complex models are needed to identify why some herds appear to underperform. Mechanistic models can be used to study or explain nutritional or physiological concepts and to develop and test research hypotheses. Ultimately, it is the fundamental research in nutrition modeling that enables advances in routine diet formulation procedures. Nonetheless, models used routinely to balance diets need to be as simple and as accurate as possible.
(**Key words**: diet formulation, computer modeling, protein requirements, amino acid requirements)

Abbreviation key: **ADG** = average daily gain, **CNCPS** = Cornell Net Carbohydrate and Protein System, **RMSPE** = root mean square prediction error for the models.

INTRODUCTION

The objective of this paper is to compare and evaluate some of the different mathematical approaches used to determine protein requirements for lactating dairy cows. In the US, most diets for dairy cows are formulated using software based on the mathematical equations published by the NRC (16). The only major objective of this mathematical model is to determine accurately animal nutrient requirements and feed availabilities so as to formulate optimal diets. However, there are a number of reasons to incorporate mechanistic concepts into mathematical models of dairy cow nutrition and physiology (2). Mechanistic models are based on cause and effect relationships instead of simple empirical associations and therefore, are useful to incorporate data and concepts from fundamental research. In addition, such models can be used to test research theories and to focus the development of prediction equations. The practice of developing a mechanistic model can help document the science behind the predictions and point to deficiencies in fundamental knowledge. Mechanistic models can potentially improve the accuracy and precision of predictions by allowing simultaneous consideration of multiple effects, although the same result can also be achieved by adding terms to empirical models.

Although mechanistic models have several advantages over their empirical counterparts, there also are some limitations. Model complexity may increase as mechanisms are included, resulting in an increased risk of misuse and a potential for users to lose sight of the most important issues. Furthermore, more complex models may require more time and money to specify the required variables. Mechanistic models may be less accurate than empirical ones although not necessarily so. Rather than predict a response based on previous observations of treatments, mechanistic models predict responses based on knowledge of causative relationships. However, these relationships may not be properly represented, and the required measurements for making the predictions may be less reliable than those required of empirical models. Building mechanistic models that do not predict accurately helps identify the limits of current knowledge; however, implementation of such models in the field can be detrimental. With both

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mechanistic and empirical models, careful evaluation is necessary to advance the understanding and application of nutrition.

ALTERNATIVE MODELS

Although many mechanistic and empirical models are available, this paper focuses on three popular examples in the US. The Cornell Net Carbohydrate and Protein System (**CNCPS**) (11, 17, 19, 21) is being developed into farm-friendly software by Cornell University (Ithaca, NY), University of Pennsylvania (Kennet Square), and the Miner Agricultural Research Institute (Chazy, NJ). The version of the model used in these evaluations was adapted by the University of Pennsylvania from the original equations in Cornell's Version 2 (w. Chalupa, 1996, personal correspondence). Currently, consultants are provided with Version 3, a modified set of equations (D. Fox, 1997, personal correspondence), which could not be tested because the software is baled to prevent modification of the model, and this version is in active development and changes frequently. The CNCPS includes some physical mechanisms of feed digestion such as the impact of digesta passage on digestibility.

Another important model, named Molly (Version 9), has been developed by Baldwin et al. (3, 4). Molly is considerably more mechanistic than the NRC and CNCPS models and includes both chemical and physical concepts. This model has been useful for understanding and demonstrating how biological processes interact in a dairy cow. Molly is discussed briefly because of its importance to improving the understanding of nutrition, but a more thorough evaluation of mechanistic models has been described previously (2, 5).

The protein components of each of these models were compared with the NRC protein model (16). The spreadsheets we developed to represent the NRC equations were verified against the NRC tables (16). The NRC tables are for cows beyond second parity. The energy requirements predicted by the equations are higher than those reported in the tables by 20 or 10% for first and second parities, respectively.

Protein digestion and metabolism are represented differently in each of the three models. At the heart of the models is the understanding that feed CP is digested first by ruminal microbes, and some of this protein is deaminated to ammonia. The ammonia may be absorbed into the animal, transported to the liver, detoxified to urea, and excreted via the kidney. Alternatively, ammonia may be used in the rumen to support microbial growth, and blood urea can also be absorbed back into the rumen and used for microbial growth. Both the undegraded feed protein and the microbial protein pass from the rumen to the abomasum and small intestine where they are digested as the true protein source for the animal. The cow requires that amino acids or peptides be absorbed from the small intestine to meet needs for maintenance, growth, and lactation. There also is an optimal amount of degradable protein that should be available in the rumen to support microbial growth while the rest passes through undegraded and can be used directly by the cow.

The main objective of the NRC model is to predict the requirements for protein, carbohydrate, and minerals as accurately and efficiently as possible. The protein requirements are divided into two fractions: RUP and RDP. The NRC assumes that the ruminal degradation of protein depends primarily on the characteristics of the feed, and the model does not consider interactions with the cow or microbial population. Therefore, feed tables provide estimates of the CP fraction that is likely to be degraded in the rumen, and the available RDP is equal to the sum for all feeds of the degraded fraction times CP intake. The RDP requirement is based on meeting the needs of the microbial population, which is in turn estimated from NE_L. The assumption is that the more energy a cow consumes, the more the microbial population has to use for growth. Although the NRC tables of nutrient requirements are derived completely from the cow description, the NE_L estimate is based on the amount of energy required by the cow rather than the energy available from feeds. The RUP requirement is the difference between the requirement for absorbed protein and that supplied from microbial synthesis.

The CNCPS was developed to help users understand ruminal kinetics rather than simply to predict animal requirements, and the CNCPS model can adjust for factors that influence predictions in addition to those considered by the NRC model. Each feed in the ration is divided into five CP fractions, and each fraction for each feed is defined by a feed dictionary to degrade in the rumen at a different rate. However, the passage rate for each CP fraction within a feed is assumed to be the same—which is not likely to be true. Protein degradation of each fraction is estimated indirectly from passage and digestion rates. The CP degraded in the rumen is estimated as the degradation rate divided by the sum of the degradation and passage rates. In this way, feed protein degradation depends not only on the intrinsic nature of the feed but also on factors that affect passage rate, including animal description (i.e., DMI) and diet composition (i.e., effective fiber). The available RDP is calculated as the sum for all feeds and all CP fractions of the fraction degraded times the CP intake. The RDP requirement is a function of microbial CP synthesis in both the CNCPS and NRC models, but microbial growth is estimated from ruminally fermentable energy in the CNCPS and from NE_L requirements in the NRC model. Peptides and feed AA can be used to meet some of the requirements for ruminally available N. The postruminal requirements for protein are divided into the requirements for both metabolizable protein and for each essential amino acid. For common feeds, the CP fractions can be derived from a feed dictionary that is part of the CNCPS, or laboratory procedures may be used to measure fraction sizes of feeds. However, the rates of degradation and passage of each fraction from each feed are not easily analyzed, and there is little documentation of how values in feed dictionaries were determined.

Molly represents metabolism and digestion more mechanistically than the NRC or CNCPS models, and Molly is a dynamic model rather than a static one. Like the CNCPS, the protein is divided into solubility fractions. However, unlike the CNCPS, analogous fractions in different feeds are assumed to degrade at the same rates. For example, the soluble protein of soybean meal is assumed to degrade at the same rate as the soluble protein from corn gluten feed, and the reason feeds differ in RDP is because they differ in the amounts of the different fractions. The degradation rates for each protein fraction are a function of the level of microbial activity and the concentration of the fractions in the rumen according to Michaelis-Menten kinetics. In this way, protein degradation can be shown to be inhibited by factors that affect microbial activity or by feeding patterns.

MODEL EVALUATION

The goal of model evaluation is to determine the robustness, accuracy, and precision of model predictions and to identify weak points needing further research and for which recommendations should be made carefully or not made at all (7). The evaluation methodology must be highly organized and rigorously structured to ensure that all situations are properly represented. The results of the evaluation should be documented and should assist users with understanding the limitations and strengths of the system. It is often beneficial for the evaluation not to be coordinated by the same person who coordinates the development of the model, but the developers should continue to be participants in the evaluation to explain proper model use and assumptions.

The accuracy and precision of models are determined by comparing predictions to observed data. The data that are used must reflect the model objectives; if the model is to be used in the field, the data should be derived from animals under the conditions for which the model is recommended. In evaluation of extension applications, the evaluation data set must be independent of the development data set. For example, the same data cannot be used both for model development and for model evaluation, and single studies cannot be split to form the two data sets. The analysis should represent all possible situations for which the model might be recommended (e.g., production levels, types of feeds). The potential situations must be identified, appropriate data must be derived, and special attention must be paid to evaluation at the data boundaries (where extrapolation is likely to be used to derive predictions).

Model evaluation should include a rigorous statistical component. In the early stages of model development, a null hypothesis is that the model cannot predict actual field results. Any positive relationship between observations and predictions would warrant rejection of this hypothesis and a favorable appraisal of the model. Further advances in modeling research require a more critical examination of the model. A second null hypothesis would be that the model predicts observed results consistently. A rejection of this second hypothesis would indicate potential biases in the model. Finally, models that differ in complexity should be compared with each other to ensure that the higher complexity is needed. The null hypothesis tested in this case would be that the model prediction error of one model does not differ from that of the other. Failure to reject this hypothesis would warrant using the more convenient model for the conditions to be tested.

Usually models that are relevant to feeding cattle are evaluated by regression of observed versus predicted responses. However, the information provided by such an analysis is ambiguous and lacks sensitivity (15). Alternatively, a measure of how well predictions fit observed data can be calculated as the root mean square prediction error (**RMSPE**) (6):

$$\text{RMSPE} = \sqrt{\left[\frac{\Sigma(\text{predicted} - \text{observed})^2}{\text{number of observations}}\right]}.$$

This term is the square root of the estimate of variance of observed values about the predicted values (Figures 1 and 2). The RMSPE is the average vertical distance of each point to the line, Y = 0.

The RMSPE can be decomposed in many different ways to identify systematic problems with models (6). In the present study, the RMSPE was initially decomposed into two terms: the mean bias and the

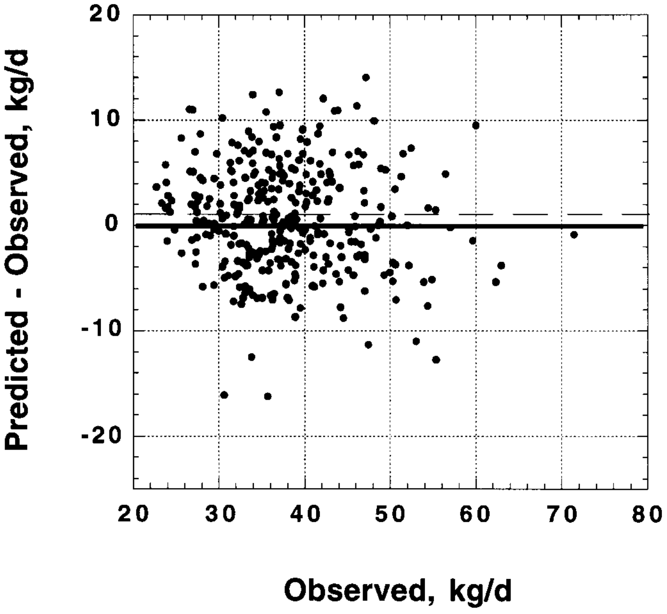

Figure 1. The allowable minus observed milk production (limited by energy or absorbed protein) predicted by the NRC model (16) versus observed milk production. Solid line represents no bias or error. Dashed line represents the mean bias. Data shown are means from 9 to 17 wk of observations on individual cows (Purina Mills, Inc., St. Louis, MO).

residual error. The mean bias represents the average inaccuracy of model predictions across all data.

$$\text{Mean bias} = \frac{\Sigma(\text{predicted} - \text{observed})}{\text{number of observations}}.$$

In Figure 1 and 2, the mean bias is represented as the average of all values on the Y-axis. The residual error was defined as the remaining error in model prediction after accounting for the mean bias. It is also referred to as prediction error excluding mean bias.

$$\text{Residual error} = \sqrt{}\,[\text{RMSPE}^2 - (\text{mean bias})^2].$$

In Figures 1 and 2, the residual error is the average distance of each point to the horizontal line representing the mean bias.

Regression of the residuals (predicted minus observed) against the predicted values can be used to identify whether or not the magnitude of the bias increases or decreases with the magnitude of the predicted values (6). Linear bias and disturbance from the regression line initially were pooled in the present study for calculation of residual error, but subsequently various forms of systematic bias (e.g., linear, treatment effects) were further subdivided to decompose the residual error (8).

INTESTINAL FLOW PREDICTION

A study that was conducted at the University of Pennsylvania has been presented previously (13, 14). Twenty different treatments means from five studies were compared with the predicted duodenal flows using Molly (3, 4) and CNCPS (11, 17, 19, 21). In each case, forages were analyzed for CP and NDF on a DM basis, and these values were used in the models. The feed dictionary from the CNCPS was augmented with literature data to specify the driving variables for Molly. Recently, we added a comparison with the dairy NRC (16), and the results are shown in Table 1. The NRC model overpredicted microbial protein (14%) and underpredicted total protein (10%) flowing to the small intestine compared with reported values. The CNCPS overpredicted microbial protein (35%) and total protein (7%), and Molly underpredicted microbial protein (6.5%) and total protein (21.6%). The CNCPS was more accurate (lower RMSPE) than the NRC model and Molly for total and feed protein flow predictions but was less accurate for prediction of microbial protein flow (Table 1).

Flows to the small intestine only represent the availability of nutrients and not the requirements for

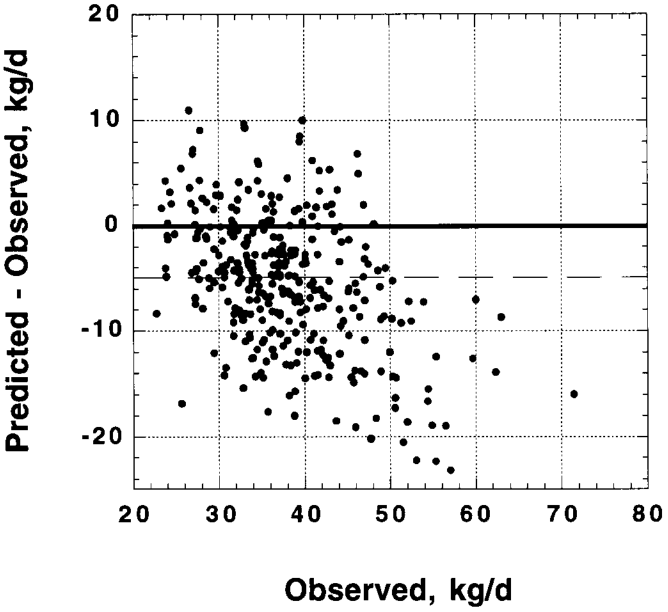

Figure 2. The allowable minus observed milk production (limited by energy, metabolizable protein, Met, or Lys) predicted by the Cornell Net Carbohydrate and Protein System (11, 17, 19, 21) versus observed milk production. Solid line represents no bias or error. Dashed line represents the mean bias. Data shown are means from 9 to 17 wk of observations on individual cows (Purina Mills, Inc., St. Louis, MO).

maintenance, milk production, and growth. If the requirements were accurately determined for these animals used in the duodenal flow studies, the CNCPS would have underfed RUP, and the NRC model and Molly would have overfed protein. However, the requirements may not be predicted equally by the different models, and predictions may not be accurate. A bias in predicting nutrient availability might be countered by an opposing bias in predicting the nutrient requirement. Therefore, analysis of duodenal flow data may not be the best way to judge how a diet formulated using a model will meet the requirements for dairy cows. More recent studies were conducted to compare predictions made using the dairy NRC and CNCPS models using production data.

TABLE 1. Prediction of duodenal CP flow to the small intestine compared with reported means (n = 20) (14).

		Predicted[1]		
	Observed	NRC	CNCPS	Molly
	(kg/d)			
Total NACP[2]				
Mean	3.9	3.51	4.17	3.06
Mean bias[3]	. . .	−0.39	0.27	−0.84
SD or RMSPE[4]	0.24	0.65	0.46	0.90
Feed NACP				
Mean	2.02	1.37	1.62	1.30
Mean bias	. . .	−0.65	−0.40	−0.72
SD or RMSPE	0.30	0.69	0.46	0.75
Microbial CP				
Mean	1.88	2.14	2.55	1.76
Mean bias	. . .	0.26	0.67	−0.12
SD or RMSPE	0.28	0.54	0.77	0.96

[1] NRC = NRC model (16); CNCPS = Cornell Net Carbohydrate and Protein System [Version 2; (11, 19, 21)]; Molly = Molly Version 10 (3, 4).

[2] Nonammonia CP.

[3] Mean predicted minus mean observed.

[4] Standard deviation of observed or root mean square prediction error of model (RMSPE).

TABLE 2. Description of data for comparison of observed versus allowable milk production.[1]

Item	$\overline{X}$	SD[2]
Diets, no.	33	. . .
Cows, no.	333	. . .
Weekly observations, no.	4394	. . .
DIM, d	68.86	30.40
ADG,[3] kg/d	0.024	1.04
BW, kg	560	56
Milk production, kg/d	37.48	8.36
Milk fat, %	3.17	0.60
Milk protein, %	2.87	0.28
DMI, kg	21.27	4.23

[1] Data from Purina Mill, Inc., St. Louis, MO.

[2] Standard deviation across weekly observations.

[3] ADG = Average daily gain; BW was measured twice daily, and changes were smoothed by fitting a fourth-order polynomial across stage of lactation.

A PRODUCTION STUDY

Cows and Diets

A comparison of the models was conducted using data provided from Purina Mills, Inc. (St. Louis, MO) on 333 cows at early and peak production (Table 2) consuming 33 different diets (Table 3). The diets used similar protein sources. Each of the cows was fed the diet in early to midlactation for 9- to 17-wk periods, and daily observations were averaged by week for a total of 4394 weekly observations. Many of the diets included added fat, which is a common practice currently for high producing cows, but was not as common when data were derived to develop the models. The BW measurements were taken twice daily after milking and changes were smoothed by fitting a fourth-order polynomial across the observation period. This procedure reduced the error associated with BW measurements because of gut fill but allowed for both increases and decreases that are expected in early and peak lactation. The average daily gain (**ADG**) was derived from the smoothed BW estimates. Most of the diets included both corn silage and alfalfa hay but differed in the provision of total energy and ruminally fermentable energy (Table 3).

A comparison of how much metabolizable energy and protein each model recommended is shown in Table 4. On average, CNCPS recommended feeding 200 g less RDP (ammonia, amino acids, and peptides) and 310 g more RUP digestible in the lower tract than did the NRC model. Both models predicted adequate or excessive RDP because urea was usually included (Table 3), but the CNCPS predicted a slight deficiency of digestible RUP, and the NRC model predicted an excess of digestible RUP. For this data set, the predictions of availabilities of energy and protein for both models were highly correlated with each other, but predictions of protein requirements were not (Table 4). This difference in predicted requirements could largely be attributed to the prediction of microbial CP. The NRC model predicts microbial CP from predicted NE_L requirement, and the CNCPS predicts microbial CP from predicted availability of rumen fermentable energy. Many of the diets used in this comparison were high in added fat. The fat would increase the prediction of microbial CP for the NRC model because it would increase NE_L, but fat would not increase microbial CP for the CNCPS because it would not affect fermentable energy. The higher estimate of microbial CP with the NRC model than with the CNCPS would in turn increase the estimate for required RDP and decrease the estimate for required digestible RUP. Another difference between the models is that the CNCPS predicted that 460 g/d more absorbed protein were required than was predicted by the NRC model (Table 4). This difference is partly explained by the fact that some of the absorbed CP is assumed to be microbial nucleic acid N in the CNCPS and is not used to help meet the requirement for metabolizable protein.

The frequency at which the models predicted one or more nutrients limited milk production is shown in Table 5. The NRC model predicted that the diets exceeded requirements for energy and protein 58% of the time. When the diets were predicted to be deficient, energy was usually the most limited nutrient. In contrast, the CNCPS predicted that the diets exceeded energy, protein, Met, Lys, and Ile requirements for 26% of the observations, and Met was predicted to be the first-limiting nutrient 42% of the time. Metabolizable protein, independent of Met, Lys, and Ile, was predicted to be first-limiting 23% of the time, Ile limitation was predicted 5% of the time, and Lys was never predicted to be first-limiting.

The predicted DMI was more similar to observed DMI for the NRC model than for the CNCPS (Table

TABLE 3. Experimental diets for comparison of observed versus allowable milk production.[1]

Cows	Alfalfa hay	Corn silage	Corn grain	Molasses cane	Soybean hulls	Soybean meal	Tallow	Urea	Wheat middlings	Other	Minerals and vitamins
(no.)						(% of DM)					
13	27.5	27.5	6.7	0.7	19.7	9.0	1.1	0.5	5.8	0.0	1.5
14	27.5	27.5	6.7	0.7	19.7	10.8	5.0	0.5	0.0	0.0	1.6
14	27.5	27.5	20.9	0.8	0.0	9.3	1.1	0.5	9.0	1.7[2]	1.6
13	27.5	27.5	21.0	0.8	0.0	11.4	5.0	0.5	3.0	1.7[2]	1.7
12	50.0	0.0	24.3	0.8	12.5	4.7	1.1	0.6	3.5	0.0	2.5
12	50.0	0.0	24.3	0.8	12.5	4.7	4.5	0.6	0.0	0.0	2.5
14	0.0	60.0	4.6	0.8	7.8	18.1	1.1	0.5	3.5	0.0	3.4
13	0.0	60.0	4.6	0.8	7.9	18.1	4.5	0.5	0.0	0.0	3.5
12	25.0	25.0	19.5	0.8	15.2	10.8	0.0	0.6	0.0	0.0	3.2
10	25.0	25.0	14.6	0.8	15.2	10.8	4.9	0.6	0.0	0.0	3.2
12	25.0	25.0	14.4	0.8	15.2	10.8	5.0	0.6	0.0	0.0	3.2
4	25.0	25.0	10.5	0.8	13.5	9.3	2.1	0.6	10.4	0.0	2.8
5	25.0	25.0	10.5	0.8	13.6	0.0	2.1	0.6	14.3	5.1[3]	3.0
4	25.0	25.0	10.5	0.8	14.4	11.4	5.8	0.6	3.6	0.0	3.0
5	25.0	25.0	10.6	0.8	13.6	0.0	5.8	0.5	9.2	6.3[3]	3.2
8	25.0	25.0	13.5	0.0	14.9	13.7	0.0	0.5	5.2	0.0	2.2
5	25.0	25.0	13.5	0.0	14.9	13.7	5.0	0.5	0.0	0.0	2.3
7	25.0	25.0	13.5	0.0	14.9	13.7	5.0	0.5	0.0	0.0	2.3
8	25.0	25.0	13.5	0.0	14.9	13.7	5.0	0.5	0.0	0.0	2.3
6	25.0	25.0	13.5	0.0	14.9	13.7	5.0	0.5	0.0	0.0	2.3
2	50.0	0.0	20.5	0.0	21.0	5.4	0.5	0.6	0.0	0.0	2.0
4	50.0	0.0	19.2	0.0	19.6	9.2	0.5	0.0	0.0	0.0	1.5
8	25.0	25.0	20.2	0.0	14.9	12.5	0.0	0.5	0.0	0.0	2.0
11	25.0	25.0	16.4	0.0	14.9	13.3	2.9	0.5	0.0	0.0	2.0
7	25.0	25.0	15.2	0.0	15.6	14.8	1.5	0.5	0.0	0.0	2.3
11	15.0	30.0	14.6	0.0	16.4	15.5	4.7	0.5	0.0	0.0	3.2
11	10.0	30.0	13.4	0.0	18.8	16.6	4.8	0.5	0.0	2.5[4]	3.3
11	5.0	30.0	12.2	0.0	21.3	17.6	4.9	0.5	0.0	5.0[4]	3.5
13	0.0	30.0	11.0	0.0	23.8	18.7	4.9	0.5	0.0	7.5[4]	3.6
12	25.0	25.0	20.2	0.0	14.9	12.5	0.0	0.5	0.0	0.0	2.0
12	25.0	25.0	16.4	0.0	14.9	13.3	2.9	0.5	0.0	0.0	2.0
19	25.0	25.0	20.2	0.0	14.9	12.5	0.0	0.5	0.0	0.0	2.0
20	25.0	25.0	16.3	0.0	14.9	13.2	3.0	0.5	0.0	0.0	2.0

[1] Data from Purina Mills, Inc. (St. Louis, MO).

[2] Rice hulls.

[3] Corn gluten meal and blood meal (1:1, wt/wt).

[4] Cottonseed hulls.

TABLE 4. Comparison of predicted composition and availability of the diet calculated using feed dictionaries and observed DMI.[1,2]

	NRC		CNCPS		Comparison	
	$\overline{X}$	SD	$\overline{X}$	SD	Difference[3]	Correlation[4]
Metabolizable energy, Mcal/d						
Available	61.73	11.69	60.48	11.01	1.25	0.98
Required	59.54	10.18	54.88	9.73	4.66	1.00
Balance	2.19	9.71	5.60	8.97	–3.41	0.96
RDP, kg/d						
Available	2.71	0.52	2.69	0.46	0.01	1.00
Required	2.15	0.41	1.93	0.32	0.22	0.54
Balance	0.56	0.44	0.76	0.19	–0.20	0.42
Digestible RUP, kg/d						
Available	1.06	0.22	1.05	0.28	0.01	0.99
Required	0.82	0.20	1.12	0.53	–0.30	–0.21
Balance	0.24	0.24	–0.07	0.49	0.31	–0.20
Absorbed protein, kg/d						
Available	2.57	0.45	2.72	0.55	–0.15	0.83
Required	2.33	0.38	2.79	0.67	–0.46	0.60
Balance	0.24	0.24	–0.07	0.49	0.31	–0.20

[1] Calculated for 4394 weekly observations of 333 cows on 33 diets (Purina Mills, Inc., St. Louis, MO).

[2] NRC = NRC model (16); CNCPS = Cornell Net Carbohydrate and Protein System (Version 2; (11, 17, 19, 21)]; Molly = Molly Version 10 (3, 4).

[3] NRC model prediction minus CNCPS model prediction.

[4] The correlation coefficient of one model's prediction with the other.

6). Previous research (18) has shown that the accuracy of DMI predictions is highly dependent on the data set used. Accurate DMI predictions are important for accurate diet formulation, particularly when feeding groups of cows. Although many producers estimate group DMI from herd observations, often no observational data are available for individual cow DMI, and the higher producing cows in a group typically consume more DM than do the lower producers. Therefore, the concentration of nutrients in the diet that is required to feed the higher producing cows in the group is determined more accurately from the predicted DMI (which includes cow to cow differences) than from the average DMI for a diverse group of animals.

Production Versus Allowable Milk

Diet formulation models typically use current or target milk production as a driving variable and estimate the amount of protein and energy to feed for that level of production. If these equations are rearranged, the dietary parameters (how much protein and energy fed) can be used to predict the allowable milk production. For example, protein allowable milk is an estimate of the amount of milk production (kilograms per day) that the model predicts can be produced. It has analogous units to energy allowable milk (kilograms per day), and the lower of the two estimates would be considered the first-limiting nutrient for milk production, assuming that all other nutrients are available to meet requirements.

If the allowable milk is 40 kg/d but the actual yield is 45 kg/d, the model would recommend feeding for 5 kg more milk production than was observed. This result indicates a model bias: the model suggests that observed production levels were not feasible. Conversely, if the allowable milk production is higher than the actual production, the model predicts that the herd was fed more than enough for the level of production. This difference does not necessarily mean that the model is biased. Something other than the

TABLE 5. Predicted first limiting nutrients for the NRC model or the CNCPS as a percentage of 4394 weekly observations.[1]

First-limiting nutrient	NRC	CNCPS
	(% of observations)	
None	57.9	26.0
Metabolizable energy	34.6	4.1
Metabolizable protein	7.5	23.3
Met	. . .	41.9
Lys	. . .	0.0
Ile	. . .	4.8

[1] NRC = NRC model (16); CNCPS = Cornell Net Carbohydrate and Protein System [Version 2; (11, 17, 19, 21)].

TABLE 6. Predicted DMI for the NRC model and the CNCPS compared with observed DMI.[1]

	Mean	Mean bias[2]	Residual error[3]	RMSPE[4]
	(kg/d)			
Observed	21.58 (SD = 4.08)	. . .	. . .	. . .
NRC	21.52	–0.06	2.88	2.88
CNCPS	19.97	–1.60	3.30	3.67

[1]NRC = NRC model (16); CNCPS = Cornell Net Carbohydrate and Protein System [Version 2; (11, 19, 21)].

[2]Mean predicted minus mean observed.

[3]Model prediction error excluding that due to the mean bias.

[4]Root mean square prediction error of model.

specific nutrient supply may have limited production. However, if there was a response in production to increased supply of the nutrient, then there would be evidence that the model was incorrect.

Allowable milk production for the predicted protein or amino acid supply was determined for the diets using the CNCPS or NRC models and their feed dictionaries. The DM, NDF, and CP composition of the forages were adjusted according to laboratory results. The DMI levels were set to the observed values, and energy requirements included energy for observed gains or losses. The allowable milk production was calculated by rearranging equations to predict the milk production that is feasible at the observed fat and protein percentages from the diets consumed. This calculation assumed that either energy or metabolizable protein limited production. The production that was allowable from either first-limiting nutrient was taken as the lower of the two. The CNCPS also predicts requirements for Met, Lys, and Ile, and these were also included in allowable milk predictions.

Although the average milk production for the data set provided by Purina Mills was 37.63 kg/d, enough metabolizable energy was predicted for 40.95 and 43.40 kg/d according to the NRC and CNCPS models, respectively (Table 7). The prediction of the amount of milk production that is feasible from the energy supplied in a diet is referred to as the energy-allowable milk production, which differs in different models. The difference between allowable and observed production is the mean bias (Table 7). For these data, the model predicted greater bias and similar residual error in energy-allowable milk for the CNCPS than for the NRC model. The energy requirement appeared to be lower for the CNCPS than the NRC model (Table 4). Unlike the NRC model, CNCPS does not account for increased maintenance energy requirements in first and second parities.

The NRC model predicted the average protein-allowable milk production to be 5.34 kg/d higher than

TABLE 7. Allowable milk production for the NRC model and the CNCPS compared with observed milk production.[1,2]

	Mean	Mean bias[3]	Residual error[4]	RMSPE[5]
	(kg/d)			
Observed	37.63[6]			
NRC Allowable				
Metabolizable energy (ME)	40.95	3.31	9.16	9.74
Metabolizable protein (MP)	42.97	5.34	5.33	7.54
ME or MP	38.71	1.08	7.08	7.16
CNCPS Allowable				
ME	43.40	5.77	9.11	10.78
MP	36.09	–1.54	11.27	11.37
ME or MP	35.04	–2.59	9.99	10.32
ME or MP or Met	32.64	–5.00	8.87	10.18
ME or MP or Met or Lys	32.64	–5.00	8.87	10.18
ME or MP or Met or Lys or Ile	32.37	–5.26	8.54	10.03

[1]Allowable milk is the milk production rate that the models predict is feasible given the availability of the limiting nutrients indicated. When more than one nutrient is considered at a time, the lower of the allowable milk values is used for each observation.

[2]NRC = NRC model (16); CNCPS = Cornell Net Carbohydrate and Protein System [Version 2; 11, 17, 19, 21)].

[3]Mean predicted minus mean observed.

[4]Model prediction error excluding that due to the mean bias.

[5]Root mean square prediction error of model.

[6]Standard deviation of 8.30.

the observed production (Table 7, mean bias). The model suggested that, on average, more than enough protein would have been consumed for the level of production observed, and the excess N would have been excreted. The lower observed production may have resulted simply from feeding more protein than recommended by the model. In contrast, the protein-allowable milk predicted by CNCPS was lower than that observed by 1.54 kg/d. This difference indicates a significant bias for recommending more protein than needed for the observed production. The residual errors of protein-allowable milk predictions were 5.33 and 11.27 kg/d, respectively, for the NRC model and CNCPS. A lower residual error indicates a more accurate prediction of observed data after adjusting for the mean bias.

The estimates of bias that were associated with the models may be overestimated when positive or underestimated when negative. When allowable milk production is greater than the observed milk production, the difference may result from some factor other than protein (e.g., energy or management) limiting production. Therefore, the estimates of bias are overestimated. The positive bias associated with the NRC model does not necessarily indicate a problem with the model (it may actually be lower than estimated), but the negative bias associated with the CNCPS is likely to be an underestimate (the true value may be more negative). Because the same observations were used for both models, feeding more protein than needed biases the predictions of the bias estimates equally in kilograms of milk per day for both models. Furthermore, the true model prediction error is likely to be lower than estimated for both models because some of the higher predictions may have resulted from overfeeding protein.

The prediction of allowable milk considering both energy and protein as limiting nutrients would logically seem to be more accurate and precise than consideration of each nutrient independently. The lower of the two values for energy or protein allowable milk would be considered the allowable milk production for both nutrients combined. In this way, energy allowable milk would be calculated for the low energy diets, and protein allowable milk would be calculated for the low protein diets. However, improving the model prediction by including both nutrients requires being able to predict which nutrient actually does limit production; for the current data, this prediction often appeared to be inadequate. With the NRC model, residual error was higher when energy and protein limitation were considered together than when protein limitation was considered alone, and, for the CNCPS, the residual error was higher when energy and protein were considered together than when energy limitation was considered alone (Table 7).

Several studies have shown a response to infusion of Met or Lys into the small intestine (20) or supplementation with ruminally protected amino acids (1) of diets that appeared to be limited in these amino acids. However, to benefit consistently from balancing for amino acids, models must be available that can predict the occurrence and extent of the limitation more than they increase error. For the CNCPS, also considering Met or Ile deficiency improved the precision (reduced residual error) of the model (Table 7), which shows that these diets may have benefited from balancing for these AA. This observation does not necessarily indicate that specific AA were deficient because alleviating some factor associated with the predicted deficiency would have had the same result. Considering a potential Lys deficiency had no effect on allowable milk because the model never predicted Lys to be first limiting. The residual error from using the CNCPS and balancing for protein, energy, and the first three amino acids was still greater than the residual error from using the NRC model and balancing for energy and protein. This result suggests that a hybrid model would have predicted protein requirements more consistently for this data set.

Although the CNCPS balanced for individual amino acids instead of absorbed protein, the NRC model appeared to predict RUP requirements more accurately and precisely than the CNCPS. In general, the CNCPS appeared to be biased toward overfeeding Met. However, if cows are fed for the average protein requirement predicted by an unbiased model, there would be a 50% chance of underfeeding and a 50% chance of overfeeding protein to any individual. Although feed protein is less valuable than the potential loss of milk protein from underfeeding, the models should be used with safety factors. Ideally, these safety factors would be higher for less precise models to reduce the level of risk from underfeeding protein.

It should be emphasized that the respective feed dictionary values were used to evaluate each of the models (except laboratory analyses for DM, CP, and NDF of forages); therefore, the conclusions pertain to how the models perform when used with their dictionaries. The feed dictionaries are a part of the model that can be overridden with laboratory analyses and doing so may improve the performance of one or both models. Although forages are highly variable in composition and the models are sensitive to changing the

TABLE 8. Systematic bias of the NRC model and the CNCPS as analyzed by regression of allowable minus observed milk production (kilograms per day) versus different variables.[1]

	NRC		CNCPS	
Independent variable	Slope[2]	r^2	Slope[2]	r^2
DIM, d	0.12	0.22	0.04	0.02
Average daily gain, kg/d	0.90	0.01	–5.45	0.24
Body weight, kg	0.02	0.03	–0.02	0.03
Milk yield, kg/d	–0.07	0.007	–0.40	0.15
DMI, kg/d	1.07	0.38	0.28	0.02
Diet CP, % of DM	–2.11	0.03	–1.72	0.01
Diet fat, % of DM	0.24	0.003	–1.49	0.09
Diet NDF, % of DM	0.20	0.006	0.12	0.001
Diet nonfiber carbohydrate, % of DM	–0.18	0.006	0.43	0.03

[1]NRC = NRC model (16); CNCPS = Cornell Net Carbohydrate and Protein System (Version 2; (11, 17, 19, 21)].

[2]All slopes were significantly different from 0 ($P < 0.01$), indicating bias.

feed composition inputs, no study to date has shown that the model predictions actually improve because of inclusion of more detailed composition. The models are calibrated to their respective feed dictionaries so that entering values that are thought to be more accurate could actually increase error and bias.

Systematic Biases

Further analysis of the allowable milk predictions relative to the observed production was carried out by regression of the difference between allowable and observed values for milk production against different variables. A significant slope for the resulting line indicates systematic bias in the model, and the r^2 represents the fraction of the error excluding mean bias that can be explained by the slope bias (6, 8).

Typically, the first residual analysis is regression of predicted minus observed against predicted response. In contrast, predicted minus observed versus observed response often demonstrates a positive slope bias that results from deriving the prediction, Y, from regression against the independent variable X (8). However, when allowable milk predictions are analyzed, it is appropriate to regress predicted minus observed against observed production (shown in Figures 1 and 2). The models were originally designed not to predict allowable milk but rather to predict the nutrient requirements to attain the desired rate of milk production. The equations were then rearranged to predict allowable milk production. Therefore, regression of predicted minus observed against predicted milk production would result in positive slope bias (which was observed in practice).

The most important biases noted for the NRC prediction of allowable milk were for DMI and DIM (Table 8; r^2 = 0.38 and 0.22, respectively). The slope bias per kilogram of DMI was 1.07 kg of milk/d. As DMI increased, the predicted milk production increased because of the additional nutrients provided, but actual milk production did not increase as much as predicted (Figure 3). Cows with high DMI were likely to have been fed excess protein, but this issue is not necessarily a problem with the model prediction of requirements. The significant bias could be an artifact of the data set. The slope bias per DIM was 0.12 kg of milk/d. The DIM was correlated with observed DMI (data not shown; r^2 = 0.35), and most of the variation explained by DIM (85%, determined from multiple regression not shown) could be explained by the effect of DMI.

Table 8 shows that the most important (highest r^2) biases for the CNCPS were for ADG (slope = –5.45), milk production (slope = –0.40), and dietary fat percentage (slope = –1.5). The inclusion of all three variables in a multiple regression analysis explained 48% of the variation, and the effect of each variable was largely independent (data from multiple regression not shown). The allowable milk prediction decreased relative to observed production when ADG increased (Figure 4). One explanation for this effect is that the energy that is required for gain (or obtained from losses) may have been underestimated. When the gains were high, there may have been an unpredicted milk production loss that would have been especially poorly accounted for by protein allowable milk predictions.

As the fat percentage in the diet increases, the protein allowable milk production would decrease because, unlike with the NRC model, fat is subtracted from the energy for microbial protein synthesis. At the same time, if the diets were limited more in energy than was predicted, the higher fat percentage would enable increased production, which would not be accounted for by protein allowable milk (or overall allowable milk when protein is usually limited). The CNCPS may overcorrect for the loss in microbial growth from fat addition. Previous researchers (9, 10) have discussed that dietary lipids can increase microbial efficiency in utilizing fermentable energy and result in just as much microbial protein as diets without added fat.

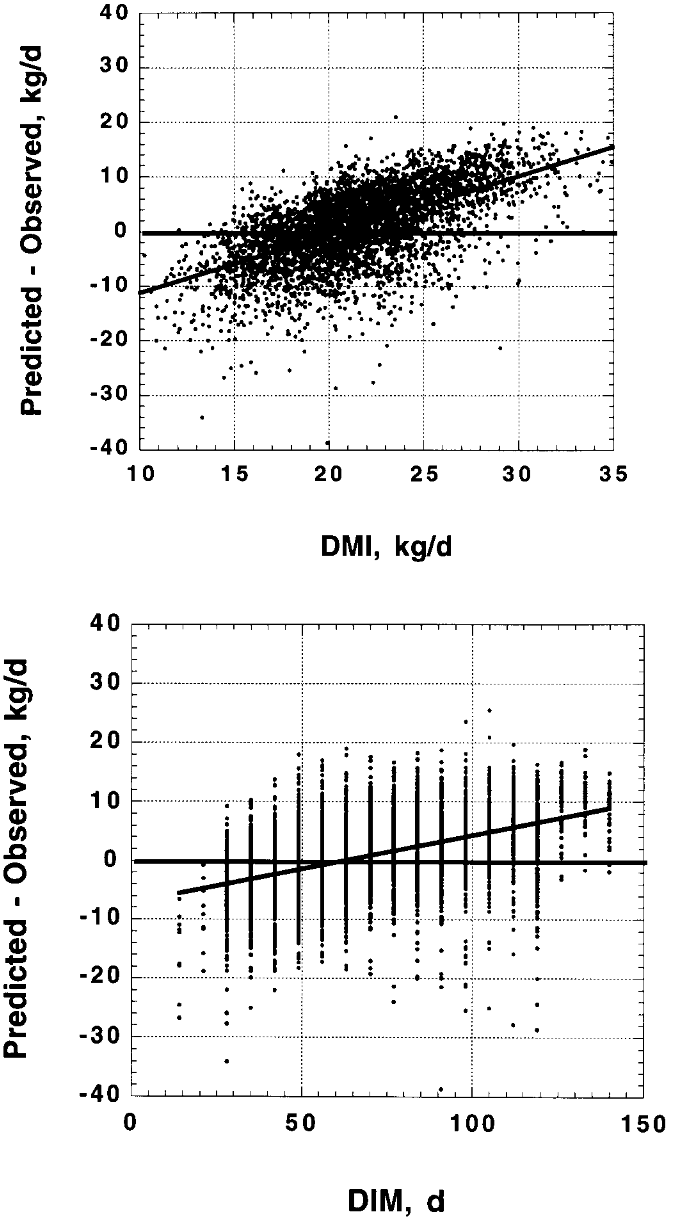

Figure 3. The allowable minus observed milk production (limited by energy or absorbed protein) predicted by the NRC model (16) versus DMI (top; $r^2 = 0.38$) or DIM (bottom; $r^2 = 0.22$). Data shown are for individual weeks of observations on individual cows (Purina Mills, Inc., St. Louis, MO).

Comparison with Other Studies

In contrast to the results reported in this paper, the CNCPS frequently recommends feeding less protein than the NRC model does because the CNCPS predicts higher microbial growth (12). The aforementioned comparison of the models with respect to duodenal flows demonstrates an overprediction of microbial CP (Table 1). Results reported previously (14) showed little relationship between observed and CNCPS predicted values for microbial CP flows for lactating dairy cows, although the model was robust in that it predicted differences in CP flows associated with different DMI among animals ranging from young beef calves to lactating Holsteins (17). Their study used estimates for feed composition when data were not available in the CNCPS feed dictionary.

Wu et al. (23) reported that the CNCPS model and feed dictionary predicted greater protein-allowable milk production than was observed. However, these observed results could have been caused by feeding more than enough protein. Kalscheur et al. (12) showed that the CNCPS predicted lower protein requirements than the NRC model because of higher prediction of microbial CP. These observations contradict the production results elaborated upon previously in this paper. For the previous production results, the CNCPS appeared to underpredict microbial CP especially on diets with high fat content fed to cows with high levels of milk production and BW gain. Each of these variables affects the prediction of microbial CP and was described as causing an underprediction of allowable milk (Table 8) for the CNCPS.

It is difficult to evaluate whether production responses are due to the protein component of a diet or to some other management factor. Observations of cows that are not fed protein-limiting diets are of limited value for use to compare models to balance protein requirements. In such cases, the model used to formulate the diets will appear to be the most accurate because the diets are designed to make the lead model match the observed milk production. To some extent, this effect was observed when several empirical models were compared (22). A model that suggests that less protein would have been sufficient is not tested when feeding the greater amount of protein required of a different model. However, in the present case, the CNCPS predicted that the observed milk production was impossible unless more protein was fed, and, in this sense, the CNCPS model can be invalidated for these diets.

A production trial was conducted using low protein diets based on corn, which resulted in milk production losses compared with results using a control group of cows fed high protein diets (12). The diets were isocaloric so that energy-allowable milk production did not need to be considered, and metabolizable protein or Lys was usually the first-limiting nutrient. There were no significant changes in BW. Allowable milk production was overestimated by 9 or 35%, and model prediction error excluding mean bias was 2.84 and 4.35 kg/d for the NRC model and CNCPS, respectively. In the study of Kalscheur et al. (12), a different set of circumstances resulted in a completely different bias for the CNCPS, and the residual errors for both models were lower than the results reported in this paper. The experimental design that they used explains much of the difference between that study and the present one. The diets were predicted to be Lys limiting instead of Met limiting, and the accuracy of the predicted requirements for Lys may differ from the predictions for Met. Their study ensured that milk production was limited by protein availability so that differences between allowable and observed milk production were entirely due to the model performance and not to overfeeding protein. In addition, many of the other contributors to model error (ADG estimation, energy effects) were controlled so that only the protein aspects of the model were evaluated.

The comparisons reported here were focused on typical diets, animals, and environments. Many of the innovations of the CNCPS relate to improving predictions in atypical conditions (i.e., large or small breeds, hot or cold environmental temperature, small particle size of forage, and unusual feeds). Therefore, the CNCPS might have performed better than the NRC under these conditions, but this topic was not investigated here and has not been reported elsewhere. The NRC model does not address many of the potential limitations of some diets or management conditions, and so more complex models are needed to identify why some herds appear to underperform. For example, the CNCPS and Molly might be able to identify that diets are grossly imbalanced in amino acid availability or ruminally available energy, and they might identify when environmental temperature limits intake. Unless these situations arise, the NRC model appears to be adequate.

There are numerous occasions when milk production responses are observed or not observed because of different dietary treatments. Mechanistic models are routinely used in research and extension to explore and explain these responses. If the models initially fail to explain observations, the models can be adjusted until they do, and this practice further helps the user explain the cause of observed effects. When models fail to reinforce observed or expected results

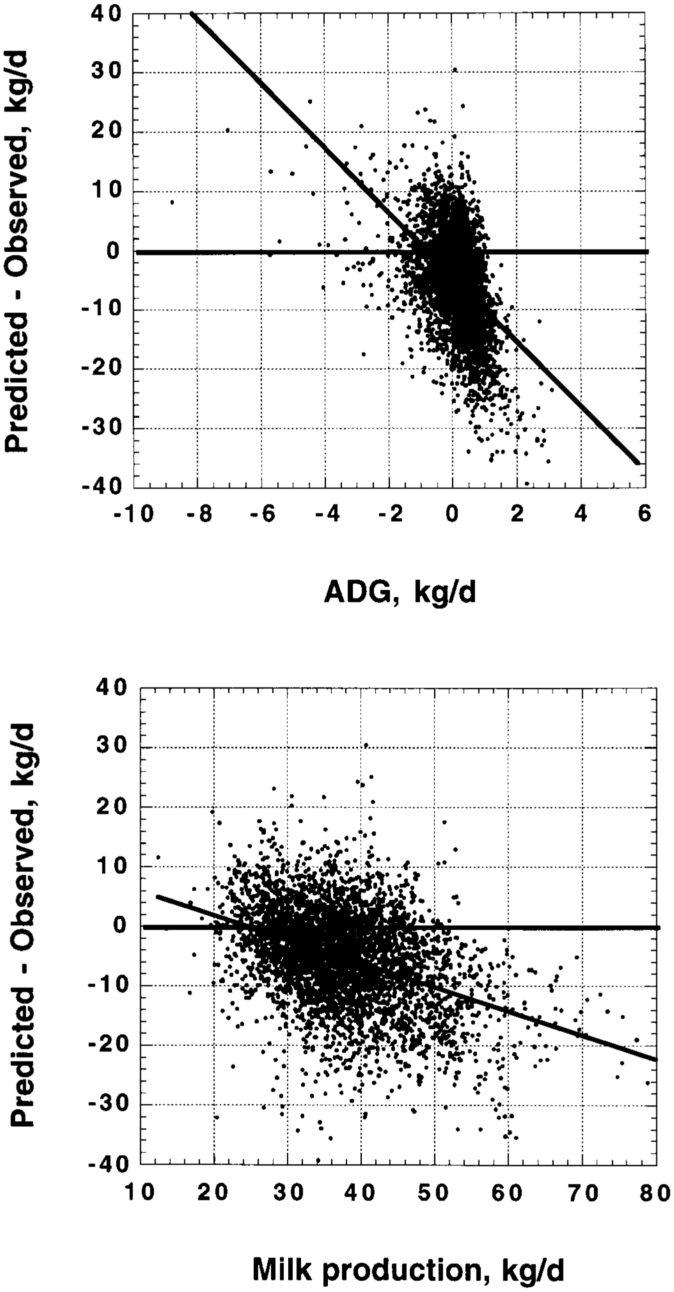

Figure 4. The allowable minus observed milk production (limited by energy, metabolizable protein, Met, or Lys) predicted by the Cornell Net Carbohydrate and Protein System (11, 17, 19, 21) versus average daily gain (top; $r^2 = 0.24$) or milk production (bottom; $r^2 = 0.15$). Data shown are for individual weeks of observations on individual cows (Purina Mills, Inc., St. Louis, MO).

even after the adjustment process, the model predictions would not be considered relevant to the interpretation of results and would not be considered further. Although this practice prevents reference to models that may not appropriately explain a given experiment, it might also enhance confidence in theories and models that are only sometimes accurate. The use of a model to explore biological concepts should not be confused with model evaluation.

CONCLUSIONS

The NRC model was the most accurate for diet formulation for standard conditions but lacked a means to evaluate mechanisms in nutrition. The CNCPS was less accurate for routine diet formulation, stemming largely from the inaccuracy of the microbial protein prediction, but is invaluable for exploring mechanisms of digestion and passage. Molly is the most mechanistic model and incorporates a great deal of fundamental research, but, currently because of a lack of a feed dictionary and the requirement of special software, Molly is not used routinely in the field as of the writing of this article. Although there are a number of advantages to using the mechanistic models for research and teaching purposes, the empirical approach is more accurate for routine diet formulation at the present time.

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