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A dynamic model of metabolizable energy utilization in growing and mature cattle. II. Metabolizable energy utilization for gain

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ABSTRACT: Component models were developed to predict the net efficiency of ME utilization for gain in cattle and to predict daily gain using recovered energy as the input. These models were integrated into a single model to predict daily gain from ME available for gain. One component model predicts the net efficiency of ME utilization for gain using constant partial net efficiencies of 0.2 and 0.75 for ME retention as protein and fat, respectively. This model predicts net efficiency of ME utilization for gain as a function of the ratio of the energy recovered in protein to the total energy recovered. The other component model predicts daily gain as a function of recovered energy and is represented by a system of ordinary differential equations that are numerically integrated on a daily basis. This model was developed by reformulating the equations in a published body composition model that uses daily gain to predict composition of gain since recovered energy is a function of gain and composition of gain. The equations in the two component models interact in that net efficiency is used to predict recovered energy from ME for gain, and in turn, recovered energy is used to predict gain in empty BW, which determines net efficiency through composition of gain. The numeric integration procedure provides an iterative solution for net efficiency. Simulated response of net efficiency for Hereford × Angus steers at 400 kg of empty BW decreased from 0.57 to 0.52 on diets with ME densities of 3.1 and 2.6 Mcal/kg of DM, and restricting the lower-quality diet to 75% of ad libitum intake resulted in a simulated net efficiency of 0.47. These responses in net efficiency were shown to be a result of composition of gain, with leaner gains resulting in lower net efficiencies.

Key Words: Beef Cattle, Energy Metabolism, Models, Weight Gain

Introduction

Energy systems have been developed to account for the partitioning of ME intake (MEI) and to predict animal performance and requirements (ARC, 1980; CSIRO, 1990; NRC, 2000). These systems are based on experimental data obtained in feeding trials at specific points in time or over fixed feeding intervals and are therefore static in nature and empirical in their approach. Dynamic simulation models have the advantage of accommodating a wider range of management options and transition states that may be difficult to handle with a static system. These dynamic models are input driven and are ideal for studying animal response to changes in nutritional management. Our overall objective was to develop, test, and evaluate a dynamic simulation model of ME utilization that could accurately predict animal response resulting from either a known MEI or the MEI required to achieve a specified response in growing or mature nonpregnant, nonlactating cattle. In this study, we will assume that feed intake is known and that ME densities of feed ingredients in feed composition tables will be used to calculate MEI. The specific objective of this article is to develop a model to predict changes in empty BW (EBW) using daily MEI that is available for gain (MEg) as the input.

Materials and Methods

Modeling Concepts

Table 1 contains a list of acronyms used in this paper. The EBW of mature cattle that contains 25% ether-extractable lipid is referred to as the standard reference EBW (SREBW). Williams and Jenkins (1997) published estimates of SREBW for several breeds and breed crosses of beef cattle. Major components of EBW are ether-extractable lipid, referred to as empty body fat weight (FAT), and empty body fat-free weight (FFM). Only the protein fraction in FFM (PRO) contains energy; hence, ME is retained in FAT.
Table 1. Glossary of terms

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>FBW</td>
<td>BW of animal that includes contents of the gastrointestinal tract, kg</td>
</tr>
<tr>
<td>EBW</td>
<td>FBW less weight of contents of gastrointestinal tract, kg</td>
</tr>
<tr>
<td>dEBW</td>
<td>Change in EBW/d</td>
</tr>
<tr>
<td>SREBW</td>
<td>EBW of mature cattle that is 25% ether-extractable lipid</td>
</tr>
<tr>
<td>FAT</td>
<td>Weight of ether-extractable lipid in EBW, kg</td>
</tr>
<tr>
<td>dFAT</td>
<td>Change in FAT/d, kg</td>
</tr>
<tr>
<td>FFM</td>
<td>Weight of ether-extractable lipid free mass in EBW, kg</td>
</tr>
<tr>
<td>dFFM</td>
<td>Change in FFM/d, kg</td>
</tr>
<tr>
<td>FFME</td>
<td>Recovered energy in FFM, Mcal/kg</td>
</tr>
<tr>
<td>PRO</td>
<td>Weight of protein in EBW, kg</td>
</tr>
<tr>
<td>dPRO</td>
<td>Change in PRO/d, kg</td>
</tr>
<tr>
<td>MD</td>
<td>ME density of diet, Mcal/kg DM</td>
</tr>
<tr>
<td>MEI</td>
<td>ME intake, Mcal/d</td>
</tr>
<tr>
<td>ME&lt;sub&gt;m&lt;/sub&gt;</td>
<td>ME used for maintenance, Mcal/d</td>
</tr>
<tr>
<td>H&lt;sub&gt;E&lt;/sub&gt;</td>
<td>ME used for support metabolism, Mcal/d</td>
</tr>
<tr>
<td>ME&lt;sub&gt;g&lt;/sub&gt;</td>
<td>ME used for gain, Mcal/d</td>
</tr>
<tr>
<td>RE</td>
<td>Retained or recovered energy, Mcal/d</td>
</tr>
<tr>
<td>RE&lt;sub&gt;p&lt;/sub&gt;</td>
<td>Recovered energy in protein, Mcal/d</td>
</tr>
<tr>
<td>FP</td>
<td>Fraction of protein in FFM</td>
</tr>
<tr>
<td>k&lt;sub&gt;m&lt;/sub&gt;</td>
<td>Net efficiency of ME utilization for maintenance</td>
</tr>
<tr>
<td>k&lt;sub&gt;g&lt;/sub&gt;</td>
<td>Net efficiency of ME utilization for gain</td>
</tr>
<tr>
<td>k&lt;sub&gt;p&lt;/sub&gt;</td>
<td>Net efficiency of ME utilization for protein gain</td>
</tr>
<tr>
<td>k&lt;sub&gt;f&lt;/sub&gt;</td>
<td>Net efficiency of ME utilization for fat gain</td>
</tr>
</tbody>
</table>

and PRO. Daily rates of change in these five components (FBW, EBW, FAT, FFM, PRO) are prefixed with the letter d (e.g., daily rate of change in EBW is dEBW). These daily rates of change are part of a system of differential equations that define the models in this paper and a solution for this system of equations is obtained using a fourth-order Runge-Kutta procedure (Shampine and Watts, 1970) for numerical integration.

Review of Models to Predict dEBW

Current systems that predict dEBW first predict recovered energy (RE), and then use the predicted values of RE to predict dEBW. The partitioning of MEI in these systems was discussed by Williams and Jenkins (2003) and is summarized with the following equation:

\[ RE = k_g \times (MEI - ME_m) \]  

where ME<sub>m</sub> is the amount of MEI used for maintenance, k<sub>g</sub> is the net efficiency of ME utilization for gain, and the term (MEI – ME<sub>m</sub>) is ME<sub>g</sub>. Two of the most widely used models to predict dEBW are from ARC (1980) and NRC (2000). Starting with a known MEI, these models predict dEBW by first estimating ME<sub>m</sub>, and then predicting k<sub>g</sub> from the dietary ME density. These estimates of ME<sub>m</sub> and k<sub>g</sub> are used as inputs to Eq. [1] to estimate RE, and empirical equations are then used to predict dEBW directly from RE.

In the ARC (1980) system, RE is predicted with the following equation:

\[ RE = k_g \times (Q_\times I - FHP/k_m) \]

where Q is the metabolizability of the diet, I is feed intake, FHP is fasting heat production, and k<sub>m</sub> is the efficiency of ME utilization for maintenance. The term Q × I is MEI, and FHP/k<sub>m</sub> is ME<sub>m</sub>, which makes this equation the same as Eq. [1]. The estimate of RE is used to predict dEBW with the following equation:

\[ dEBW = RE/EVG \]

where EVG is the energy value of dEBW and is predicted in the ARC (1980) system with the following equation:

\[ EVG = 5.0 + 0.0389 \times EBW - 0.0000114 \times EBW^2 + 0.1608 \times RE \]

The NRC (2000) system predicts RE with the following equation:

\[ RE = NE_g \times (DMI - NER_m/NE_m) \]

where NER<sub>m</sub> is the NE requirement for maintenance, which is the same as FHP, and NE<sub>g</sub> and NE<sub>m</sub> are the dietary concentrations of NE for gain and maintenance, respectively. Using relationships (NRC, 2000) based on the concentration of ME in diet (MD), NE<sub>g</sub> and NE<sub>m</sub> are equivalent to k<sub>g</sub> × MD and k<sub>m</sub> × MD, respectively, and we can rewrite the above equation as follows:

\[ RE = k_g \times MD \times [DMI - NER_m/(k_m \times MD)] \]

\[ = k_g \times (DMI \times MD - NER_m/k_m) \]

\[ = k_g \times (MEI - ME_m) \]

This equation for RE is the same as Eq. [1], which makes the formulations in ARC (1980) and NRC (2000) the same. The systems differ in the assumptions used to estimate partial efficiencies of ME utilization for
maintenance and gain and the requirements for maintenance.

To predict dEBW, NRC (2000) proposed the following allometric relationship between RE and dEBW:

$$\frac{RE}{EBW^{0.75}} = a \times dEBW^b$$  [2]

Estimates of $a$ and $b$ were obtained by linear regression using the log transformation of Eq. [2], thus:

$$\ln(\frac{RE}{EBW^{0.75}}) = \ln (a) + b \times \ln(dEBW)$$

Estimates of $\ln(a)$ and $b$ were $-2.7566$ and $1.097$, respectively, for medium-frame steers. The reciprocal relationship in the above equation is used to predict dEBW as follows:

$$dEBW = \frac{1}{a}1/ b \times RE^{1/b} \times EBW^{-0.75} \times 1/b = 12.34 \times RE^{0.9116} \times EBW^{-0.6837}$$

Models developed by Notter (1977) and Oltjen et al. (1986) use a more mechanistic approach to predict dEBW. These models use the same method as in Eq. [1] to obtain an estimate of RE, and the approach to predict dEBW is based on using an underlying protein growth curve to estimate the potential dPRO, and dFAT is calculated as a residual as shown in the following equations:

$$dPRO = \text{minimum (potential dPRO, RE/5.7)}$$

$$dFAT = \frac{(RE - dPRO \times 5.7)}{9.5}$$

$$dFFM = \frac{1}{FP} \times dPRO$$

$$dEBW = dFFM + dFAT$$

where FP is the fraction of dFFM that is protein, and 5.7 and 9.5 represent the amount of energy in Mcal/kg of DM of protein and fat, respectively (Brouwer, 1965).

**Proposed Model to Predict dEBW Using ME\(_g\) as the Input**

Components of a model that uses an input value for ME\(_g\) to predict dEBW are illustrated in Figure 1. The first component is the prediction of RE from ME\(_g\), and this is accomplished through the prediction of $k_g$, which is used to predict RE from ME\(_g\). The second component is the prediction of dEBW using RE as the input. This is accomplished by first partitioning RE into energy retained in protein and fat, and then estimating the weights of protein (dPRO) and fat (dFAT) that are retained. The fraction of protein (FP) in dFFM is then estimated and used to calculate dFFM from dPRO. Finally, dEBW is calculated as the sum of dFFM and dFAT. The approach used to predict dEBW based on these two component models is discussed below.

**Prediction of RE Using ME\(_g\) as the Input.** The model to predict RE from ME\(_g\) is based on Eq. [9] of Williams and Jenkins (2003a), where substituting ME\(_g\) for MEI – ME\(_m\) – $H_1E_v$ results in the following equation for RE:

$$RE = k_g \times ME_g$$  [3]

The term $H_1E_v$ is a component of heat production that is attributable to support metabolism. The system used by NRC (2000) assumes that $k_g$ is constant for a specific diet, and the system used by ARC (1980) assumes that $k_g$ is constant for a specific diet fed at a specific level of intake; hence, the relative contributions of protein and fat to RE have no impact on $k_g$ (i.e., composition of gain has no impact on $k_g$). Conversely, experimental results with sheep and cattle show that $k_g$ varies with composition of gain.

Graham (1980) found that $k_g$ increased from 0.32 in weaned lambs at 2 mo to 0.55 for a similar diet given to the same sheep at age 10 mo, and that subsequently, it did not vary for sheep up to 6 yr old. Blaxter et al. (1966) found no significant difference in $k_g$ in cattle aged 15 to 81 wk. Average daily gain in these cattle contained 30.5 kcal of protein energy/100 kcal of retained energy at 15 wk of age, and 24.8 kcal of protein energy/100 kcal of retained energy at 81 wk of age. These results show that there was very little difference in composition of gain in the data, which may explain why differences in $k_g$ were not significant. Other evidence reviewed by Vermorel and Bickel (1980) and studies with Hereford and Holstein steers (Garrett, 1971) indicate that $k_g$ increased with the proportion of fat in gain. Metabolizable energy is retained in protein and fat, and as an animal grows from birth to maturity without any restriction in feed availability, the proportion of fat in dEBW increases. Hence, the above experimental results were interpreted to suggest that ME is
retained in fat with a higher efficiency than in protein. This suggests that \( k_p \) should be weighted by the relative contributions of protein and fat to RE, using separate partial net efficiencies for ME retention in protein (\( k_p \)) and fat (\( k_f \)).

Pullar and Webster (1977) measured energy balance during growth in lean and fatty Zucker rats because the phenotypes differ markedly in the way they partition ME to energy retained in protein and fat. These authors obtained values of 0.45 and 0.75 for \( k_p \) and \( k_f \), respectively, by multiple regression analysis. Accepting a \( k_p \) value of 0.45 for ruminants limits \( k_g \) to a minimal value of 0.45; however, this minimum value would most likely be greater than 0.45 since in growing ruminants, energy retained in protein is never 100% of RE. This minimal \( k_g \) would be much greater than that in the results of Graham (1980) for 2-mo-old weaned lambs. Also, the equation published by NRC (2000) to calculate \( k_g \) gives a value of 0.296 at a ME concentration of 2.0 Mcal/kg of DM. This suggests that in ruminants, energy is retained in protein much less efficiently than in nonruminants.

Ørskov and McDonald (1970), Bickel and Durrer (1974), and Rattray and Joyce (1976), in experiments with ruminants, obtained estimates for \( k_p \) and \( k_f \) that varied from 0.56 to 1.28 and from 0.18 to 0.36, respectively. Geay (1984) reviewed 52 sets of published data in ruminants on energy retention as protein and found that \( k_g \) decreased curvilinearly as the proportion of protein energy in RE increased. Analysis of these data by Geay (1984) resulted in estimates of 0.2 and 0.75 for \( k_p \) and \( k_f \), respectively. These estimates agree fairly well with the data collected in sheep by Ørskov and McDonald (1970), Rattray and Joyce (1976), and Notter et al. (1984). These results suggest that in ruminants, energy is retained in fat with about the same efficiency as that in nonruminants, but energy retention in protein in ruminants is less than half as efficient as that in nonruminants. Feed to gain ratio of cattle on high-energy diets in feedlots is about 6.5:1, and in chickens, it is less than 2:1. This supports the lower efficiency of energy retention as protein in ruminants. Partial net efficiencies of ME utilization of 0.2 for protein gain and 0.75 for fat gain will be used to derive an overall equation to predict \( k_g \) as a function of the proportion of protein energy that is in RE.

Metabolizable energy that is available for gain is recovered in protein and fat, and using the partial net efficiencies for ME recovery as protein energy (\( RE_p \)) and fat energy (\( RE_f \)), RE can be expressed as follows (Geay, 1984):

\[
RE/k_g = RE_p/0.2 + RE_f/0.75 \tag{4}
\]

Solving for \( k_g \) in terms of \( RE_p \) and \( RE \) (\( RE_f = RE - RE_p \)) we get:

\[
k_g = 0.75/(1 + 2.75 \times RE_p/RE) \tag{5}
\]

This estimate of \( k_g \) is used in Eq. [3] to calculate RE. With this equation, if \( RE_p = 0 \), then \( k_g = 0.75 \), and if \( RE_p = RE \), then \( k_g = 0.2 \). The relationship in Eq. [5] between \( k_g \) and \( RE_p/RE \) is plotted in Figure 2, which shows the curvilinear decrease in \( k_g \) from 0.75 to 0.2, as \( RE_p/RE \) increases from 0 to 1. The unknowns in Eq. [5] are \( RE_p \) and RE, and methods to estimate them are discussed in the next section.

Prediction of dEBW Using RE as the Input. The method we will use to predict dEBW as a function of RE is the same as that used by NRC (2000). First, we will predict RE as a function of dEBW, and then we will reformulate the equations and use the reciprocal relationship to predict dEBW as a function of RE. The sum of the energy recovered in fat and protein is RE; therefore, to predict RE as a function of dEBW, we need a model that can predict the composition of dEBW. Keele et al. (1992) and Williams and Jenkins (1997) developed computer simulation models to predict composition of dEBW in growing and mature cattle, respectively, and Williams and Jenkins (1998) integrated these two models into a single model to predict composition of dEBW in cattle of all ages.

The model of Williams and Jenkins (1998) was used to predict RE as a function of dEBW. This model uses dEBW as its input to predict the amount of dFFM in dEBW, and dFAT is obtained as a residual according to the following two equations:

\[
dFFM = b \times dEBW + c \tag{6}
\]

\[
dFAT = dEBW - b \times dEBW - c \tag{7}
\]

The parameters \( b \) and \( c \) model the impact of breed and previous and present level of nutrition on the composition of dEBW. A complete description of the development and parameterization of the model can be found...
in Keele et al. (1992), Williams et al. (1995), and Williams and Jenkins (1997; 1998).

The components of dEBW in Eq. [6] and [7] can be used to estimate RE if the FP in dFFM can be calculated. Data from Buckley (1985) was used to develop an empirical equation to estimate FP. These data contained observed values on the chemical empty body composition of Hereford, Charolais, and Simmental heifers slaughtered at birth, 3, 7, 8, 10, and 14 mo of age, which showed that FP in FFM varied from 20.5% at birth to 24.5% at 14 mo of age. Values of FP in these data were regressed on linear and quadratic terms for UEBW (EBW/SREBW) to obtain the following equation:

\[ FP = 0.204 + 0.102 \times UEBW - 0.055 \times UEBW^2 \]  \[ (R^2 = 0.88, SE = 0.005) \]  \[ 8 \]

and dPRO was predicted as protein weight on day t minus the protein weight on day t − 1, according to the following equation:

\[ dPRO = FFM_t \times FP_t - FFM_{t-1} \times FP_{t-1} \]  \[ 9 \]

With this estimate of dPRO, RE was estimated as follows:

\[ RE = 5.7 \times dPRO + 9.5 \times dFAT \]  \[ 10 \]

where 5.7 × dPRO is REp, and 9.5 × dFAT is REf.

This above system of equations (Eq. [6], [7], [8], [9], [10]) shows the prediction of REp, REf, and RE using dEBW as the input. The predicted values of REp and REf were multiplied by 9.5 and 5.7, respectively, to obtain estimates for REp and REf, and these are summed to obtain RE as shown in Eq. [10].

Recovered energy in dFFM is in the form of protein; hence, the energy density of dFFM (FFME) can be expressed as follows:

\[ FFME = \frac{5.7 \times dPRO}{dFFM} \]  \[ 11 \]

and

\[ FFME \times dFFM = 5.7 \times dPRO \]

We can now rewrite Eq. [10] as follows:

\[ RE = FFME \times dFFM + 9.5 \times dFAT \]  \[ 12 \]

Next, we substitute Eq. [6] and [7] for dFFM and dFAT in Eq. [12] to derive the following:

\[ RE = FFME \times (b \times dEBW + c) + 9.5 \times (dEBW - b \times dEBW - c) \]

Then, collecting terms for dEBW we obtain:

\[ RE = dEBW \times (FFME \times b + 9.5 - 9.5 \times b) + FFME \times c - 9.5 \times c \]

Solving for dEBW, we arrive at the following:

\[ dEBW = \frac{(RE - FFME \times c + 9.5 \times c)}{(FFME \times b + 9.5 - 9.5 \times b)} \]  \[ 13 \]

This equation expresses dEBW as a function of RE and other variables, and it completes the development of the component model to predict dEBW using RE as the input.

Integrating the Component Models. The primary objective is to predict dEBW using MEg as the input. This is achieved by first predicting RE from MEg, and then predicting dEBW from RE. The processes contained in these two component models were integrated into a single model, which is illustrated in Figure 3. The model requires initial values for EBW, PRO, FAT, and the previous level of gain. These initial values were used to calculate starting values for FFME, c, b, FP, and FFM. At the start of the simulation, an initial value for kg was calculated from the ME density of the diet according to NRC (2000). With a fixed input value for MEg, RE is determined according to Eq. [3]. This predicted RE value, along with initial values for FFME, b, and c are used in Eq. [13] to predict dEBW. The predicted dEBW is partitioned into dFFM and dFAT using Eq. [6] and [7], respectively. Both dEBW and dFFM are used to update the integrals EBW and FFM, respectively. The value for EBW is used in Eq. [8] to calculate a new value for FP, and this is used with the updated value for FFM in Eq. [9] to calculate dPRO. Values for dPRO and dFFM are used in Eq. [11] to calculate a new value for FFME. Values for dFAT and dPRO are multiplied by 9.5 and 5.7, respectively, to obtain estimates for REp and REf and these are summed to obtain RE as shown in Eq. [10].

The processes described above show that for a fixed input value for MEg, kg determines RE, and RE determines dEBW, which indirectly determines kg through composition of gain. The model consists of a system of differential equations that are numerically integrated on a daily basis using a fourth-order Runge-Kutta-England routine (Shampine and Watts, 1970). This numeric procedure provides an iterative solution for the interacting components. A maximum step size of 1 d is used, and this routine performs a minimum of nine function evaluations each day. If on a particular day the solutions are not acceptable, step size is halved and 16 function evaluations are done. During a specific function evaluation, the value of RE calculated with Eq. [10] is the same as the beginning value of RE calculated with Eq. [3]. What the model does that is
important is that it predicts how much of the RE from Eq. [3] is in protein and uses both RE and REp in Eq. [5] to calculate a new $k_g$ value. It is this new value for $k_g$ that sets the stage for the next function evaluation, where the same MEg input value is multiplied by the new $k_g$ value to give an updated value for RE with Eq. [3], and the process is repeated until the value of $k_g$ converges.

The input value of MEg would be negative when MEI is less than MEm. In this case, the model allows for the mobilization of body tissues to satisfy the negative MEg, and RE is predicted with the following equation:

$$RE = (ME_g \times k_m)/0.8$$

We assumed that when body tissues are mobilized, only 80% of the energetic value of the tissues would be available, and $k_m$ is used instead of $k_g$ since the energy is being used to satisfy maintenance requirements. The value for RE in this case is negative, and when used in Eq. [13], the predicted value for dEBW would be negative, resulting in EBW loss.

On the beginning day of the simulation, initial conditions are set and usually step size has to be halved before the value of $k_g$ converges. On the next day, starting conditions are more accurate and the $k_g$ value usually converges without halving the step size. This part of the model is based on a very strong relationship between dEBW and composition of dEBW that responds to both previous and current levels of nutrition and breed composition. In other applications, this model, as illustrated in Figure 3, can also be used in the reverse manner to predict MEg using dEBW as the input, thus providing a means to predict a part of the feed requirements to achieve a certain level of response.

Results and Discussion

Response of $k_g$ to different diets and different levels of the same diet was investigated by simulating the growth and body composition of Hereford × Angus steers in three separate runs. In these runs, steers were put on a stocker program at weaning and were offered finishing diets at an average FBW of 340 kg at an average age of 490 d. In the first and second run, steers were given ad libitum access to diets containing 3.1 (H) and 2.6 (L) Mcal of ME/kg of DM, respectively. In the third run, intake was restricted to 75% of the ad libitum intake of the L diet (L75). Simulated values of $k_g$ and empty body fatness at 400 kg of EBW in the finishing phase were 0.57 and 25.5% for the H diet, 0.52 and 23.9% for the L diet, and 0.47 and 20.6% for the L75 diet.

These results show that $k_g$ decreased as the energy density of the diet decreased using constant values for
$k_p$ and $k_f$. The value of $k_g$ is calculated in the model as a function of composition of gain and not energy density of the diet; hence, the lower $k_g$ value obtained with the L diet compared with the H diet is a result of leaner EBW gains with the L diet. This is further illustrated with the lower $k_g$ value obtained with the L75 diet compared with the L diet. In this case, both diets had the same energy density, but steers on the L75 diet had leaner gains compared with steers on the L diet.

The model illustrated in Figure 3 was tested with experimental data (Smith et al., 1976; Cundiff et al., 1981; 1984) on MEI during the finishing period of Hereford $\times$ Angus steers in the first three cycles of the Germplasm Evaluation Program at the U.S. Meat Animal Research Center. Daily ME intake was partitioned to maintenance, support metabolism, and $ME_g$ according to the model developed by Williams and Jenkins (2003), and $ME_g$ was used to simulate growth and body composition of these steers with the model shown in Figure 3. Energy retained in dFAT and dPRO was predicted on a daily basis and used to calculate $k_g$ according to Eq. [5] and also to calculate dEBW using a predicted value for FP according to Eq. [8]. Results of this test showed a predicted value of 233 kg for gain in EBW over the feeding period compared with an observed gain of 234 kg, and this is evidence that the model, as illustrated in Figure 3, was formulated and programmed correctly.

Predicted values for $k_g$ in Figure 4 increased from 0.39 to 0.56 as UEBW increased from 0.34 to 0.7. The rate of increase in $k_g$ decreased up to a value of about 0.55 for UEBW and was almost constant between UEBW values of 0.5 and 0.7. This initial decrease in the rate of increase in $k_g$ is a result of the impact of previous nutrition on the composition of present gains in EBW. In these experiments, steers were conditioned at a low ADG for an average duration of 35 d before starting the finishing phase, and this resulted in high protein gains at the start of the finishing phase. A distributed lag function is used to model the transition from one nutritional level to another (Keele et al., 1992). At the start of the simulation, this results in a larger than normal decrease in the fraction of protein and a larger than normal increase in the fraction of fat in dEBW, and this causes a large increase in the value of $k_g$. As days in the finishing phase increase, both the rate of decrease in the fraction of protein and rate of increase in the fraction of fat in dEBW decrease and gradually approach the values for the present plane of nutrition, and the impact of previous nutritional level decreases and eventually disappears.

The distributed lag function used to model the impact of previous level of nutrition on composition of gain uses a first-order lag constant of 33 d (Keele et al., 1992). This means that 63% of the full response would be achieved in 33 d. At 86 d on feed, 93% of the full response would be achieved, and at this time UEBW was 0.5. Between UEBW values of 0.5 and 0.7, $RE_p$ decreased from 18 to 12% of total RE, and over this range, the rate of increase in $k_g$ was almost constant.

**Implications**

A complete model to predict empty body gain using metabolizable energy available for gain was developed. One of the key concepts in this model is that of net efficiency of metabolizable energy utilization for gain, which is used to calculate recovered energy from metabolizable energy available for gain. Present energy systems use estimates of net efficiency that are constant within diet and are not influenced by composition of gain. In contrast, this model uses separate partial efficiencies for protein and fat retention and composition of gain to estimate net efficiency. A previously published model that uses daily gain as its input to predict composition of gain was reformulated to predict daily gain and composition of this gain from daily recovered energy. This model responds to both previous and present level of nutrition and is used in a dynamic beef production systems model to predict daily gain.

**Literature Cited**


A model of metabolizable energy utilization


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