A meta-analysis of energy and protein requirements for maintenance and growth of Nellore cattle

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ABSTRACT: A meta-analysis was conducted to determine NE and net protein requirements of growing bulls, steers, and heifers of Nellore purebred and Nellore × Bos taurus crossbreds. A database of 16 comparative slaughter studies (n = 389 animals) was gathered to provide enough information to develop equations to predict the requirements of NEm, NEg, and net protein for maintenance (NPm) and growth (NPg). The data were analyzed using a random coefficients model, considering studies as random effects, and sex and castrate status (bulls, steers, and heifers; n = 262, 103, and 24, respectively) and breeds as fixed effects. There were no differences in NEm requirements among sex and castrate status (P = 0.73) and breeds (P = 0.82). The combined data indicated a NEm requirement of 75 kcal/kg0.75 of empty BW (EBW) with a partial efficiency of use of ME for NEm of 0.67. The NEg requirement was different (P = 0.009) among sex and castrate status and tended (P = 0.06) to be different among breeds. The equation for NEg requirement for bulls was 0.0514 × EBW0.75 × EWG1.070; for steers, it was 0.0700 × EBW0.75 × EWG1.070; and for heifers, it was 0.0771 × EBW0.75 × EWG1.070, where EWG = EBW gain (kg/d). The partial efficiency of use of ME for NEg was not different among sex and castrate status (P = 0.20) and averaged 0.44. There were no differences in NPm requirement among sex and castrate status (P = 0.59) and breeds (P = 0.92); the overall NPm requirement was 1.74 g of NP/kg0.75 of EBW·d−1. The overall MP requirement for maintenance was 2.59 g of MP/kg0.75 EBW·d−1. The NPg requirement (g/d) was not different among sex and castrate status (P = 0.59) and breeds (P = 0.14); the overall equation was EWG × [217 – (12.8 × RE/EWG)], where RE = retained energy (Mcal/d). The percentage of RE deposited as protein (%REp) decreased exponentially as the content of RE in the gain (REc, Mcal/kg of EWG) increased. Because no study effect was observed, we pooled the data across studies and the overall equation to predict %REp was 10.1 + 167e(−0.66 × REc). Our results do not support the hypothesis that bulls have greater NEm requirements than steers and heifers. Likewise, no significant differences in the NPm requirements among bulls, steers, and heifers were detected. Nonetheless, the NEg requirement of steers was greater than bulls and less than heifers. Even though the %REp was negatively correlated with the concentration of energy in the EWG, our findings indicated no differences in NPg requirement among bulls, steers, and heifers.

Key words: Bos indicus, comparative slaughter, growth, Nellore, net energy, net protein

INTRODUCTION

The Bos indicus cattle and their crossbreds are commonly used in beef production systems in tropical regions. They possess abilities to withstand hot and humid weather, to tolerate intense sunshine, to resist parasites, and to utilize poor quality forages (Turner, 1980).

The National Research Council guidelines for beef cattle production (NRC, 2000) are widely adopted to formulate diets around the world; however, energy and nutrient requirements are based on Bos taurus data. The NRC (2000) indicates that B. indicus breeds require about 10% less NEm than beef breeds of B. taurus. Tedeschi et al. (2002) indicated that steers and bulls of Nellore, a B. indicus breed, had NEm requirements similar to that adopted by the NRC (2000). Additionally, it has been recognized that sex and castrate status (castrate or intact male or female) influences growth
of body tissues, affecting carcass composition and feed efficiency (Berg and Butterfield, 1976) and the NE\textsubscript{m} requirement (ARC, 1980; NRC, 2000). Therefore, improvements in the beef cattle production in tropical and subtropical regions require an accurate assessment of energy and protein requirements of cattle.

The metabolism of fat and protein involves contributions of various organs that are highly dynamic in terms of energy expenditure; consequently, they should be evaluated together. Several studies have been independently conducted to determine energy and protein requirements of \textit{B. indicus} purebreds and their crosses with \textit{B. taurus}. A meta-analysis of this data is necessary to provide an overall summary, and its interpretation can provide directions for future experiments. Therefore, the objective of this study was to perform a meta-analysis to determine energy and protein requirements for maintenance and growth of bulls, steers, and heifers of Nellore and Nellore × \textit{B. taurus} crossbreds from independent studies that used the comparative slaughter technique to measure energy and protein balances.

**MATERIALS AND METHODS**

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from previously published sources, as described below.

**Data Collection**

A database that included general information (e.g., title, author name, date of publication), qualifying (e.g., breed, sex and castrate status, treatment), and necessary quantitative data were gathered for this study. Quantitative information included days on feed, mean intake of ME and N, initial and final shrunk BW (SBW), empty BW (EBW), and content of ether extract and CP of the EBW for each animal. Studies that provided enough information to compute these variables were included. Data from individual animals were obtained from 16 studies (Ferreira et al., 1999; Paulino et al., 1999, 2004; Martins, 2001; Véras et al., 2001; Putrino et al., 2006; Silva et al., 2002; Tedeschi et al., 2002 (3 studies); Veloso et al., 2002; Freitas, 2004; Backes et al., 2005; Paulino, 2006; Chizzotti et al., 2007; Marcondes, 2007), resulting in 389 animal records. Animals from all studies were individually fed, and no implants were used. Breeds were coded as Nellore purebred and Nellore crossbred with Angus, Red Angus, Simmental, Limousin, or Brangus. Table 1 contains the descriptive statistics of the database classified by breed and sex and castrate status.

**Data Calculation and Analyses**

The procedures used to compute energy requirements for maintenance and growth were similar to those described by Lofgreen and Garrett (1968), except we used data from the baseline animals (within each study) to develop linear regression equations, by study, to determine the initial EBW and initial composition of the EBW of growing animals rather than using the mean SBW and body composition, as described by Tedeschi et al. (2002). The initial EBW was computed from SBW using the appropriate equation for each trial, and then initial empty body fat and protein were estimated for each animal from their predicted initial EBW using the regression equations of the empty body fat or empty body protein on the EBW of the baseline animals. Empty BW gain (EWG) and empty gains of body fat and protein were calculated as the difference between final and initial BW of the respective body components. The caloric values of retained fat and protein were assumed to be 9.367 (Blaxter and Rook, 1953) and 5.686 (Garrett, 1958) Mcal/kg, respectively.

Linear and nonlinear regressions were used to estimate energy and protein utilization. The models that best described the data with a minimal possible number of parameter estimates were determined based on Akaike’s information criteria (AIC) and Schwartz’s Bayesian information criteria (BIC; Mills and Prasad, 1992).

Heat production (HP, kcal/kg\textsuperscript{0.75} of EBW) was calculated as the difference between ME intake (ME\textsubscript{I}, kcal/kg\textsuperscript{0.75} of EBW) and retained energy (RE, kcal/kg\textsuperscript{0.75} of EBW). The average of the antilog of the intercept confidence interval (95\%) of the linear regression between the log of HP and ME\textsubscript{I} was used to estimate the requirement for NE\textsubscript{m} (kcal/kg\textsuperscript{0.75} of EBW; Lofgreen and Garrett, 1968). The ME required for maintenance (ME\textsubscript{m}) was calculated by iteration, assuming that the maintenance requirement is the value at which HP is equal to ME\textsubscript{I} (kcal/kg\textsuperscript{0.75} of EBW-d\textsuperscript{−1}), as shown in the Eq. [1]:

\[ HP = \beta_0e^{(\beta_1 \times MEI)}, \]

where HP = heat production (Mcal/d); \( \beta_0 \) and \( \beta_1 \) = coefficients; \( e \) = the natural log; and ME\textsubscript{I} is ME intake (Mcal/d).

The efficiency of ME utilization for maintenance (k\textsubscript{m}) was calculated as the NE\textsubscript{m} requirement divided by the ME\textsubscript{m} requirement. The slope of the regression of RE on ME\textsubscript{I} was assumed to be the efficiency of energy utilization for growth (k\textsubscript{g}). An alternative method, the intercept divided by the slope (k\textsubscript{g}), was used to compute the ME\textsubscript{m} requirement, which was then multiplied by the k\textsubscript{m} to estimate the NE\textsubscript{m} requirement. This second approach of calculating the NE\textsubscript{m} requirement was compared with the NE\textsubscript{g} requirement estimated using the regression of the log of HP on ME\textsubscript{I}.

The net requirement of protein for maintenance (NP\textsubscript{m}, g·kg\textsuperscript{−0.75}·(EBW·d\textsuperscript{−1})) was assumed to be the intercept of the linear regression of the retained N (g·kg\textsuperscript{−0.75}·(EBW·d\textsuperscript{−1}) on N intake (g·kg\textsuperscript{−0.75}·(EBW·d\textsuperscript{−1}), multiplied by 6.25 to convert to protein.

Animals fed at the maintenance level were not utilized in the calculations of the growth requirement. The NE\textsubscript{g} requirement (Mcal/d) was calculated as shown in
Table 1. Description of the database by breed and sex or castrate status

<table>
<thead>
<tr>
<th>Item</th>
<th>iSBW</th>
<th>fSBW</th>
<th>iEBW</th>
<th>fEBW</th>
<th>ADG</th>
<th>EWG</th>
<th>RE</th>
<th>MEI</th>
<th>NI</th>
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</thead>
<tbody>
<tr>
<td>Nellore (n = 271)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Mean</td>
<td>296</td>
<td>392</td>
<td>255</td>
<td>351</td>
<td>0.82</td>
<td>0.84</td>
<td>3.72</td>
<td>16.5</td>
<td>163</td>
</tr>
<tr>
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<td>210</td>
<td>135</td>
<td>178</td>
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<td>−0.06</td>
<td>−1.30</td>
<td>6.93</td>
<td>111</td>
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<tr>
<td>Maximum</td>
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<td>533</td>
<td>366</td>
<td>469</td>
<td>2.25</td>
<td>2.25</td>
<td>9.79</td>
<td>36.6</td>
<td>278</td>
</tr>
<tr>
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<td>63.4</td>
<td>44.4</td>
<td>57.5</td>
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<td>0.43</td>
<td>2.19</td>
<td>4.88</td>
<td>37.5</td>
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<tr>
<td>Nellore × B. taurus (n = 118)</td>
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<td></td>
<td></td>
<td></td>
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<tr>
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<td>439</td>
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<td>389</td>
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<td>1.01</td>
<td>3.81</td>
<td>17.3</td>
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<tr>
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<td>129</td>
<td>175</td>
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<td>−0.05</td>
<td>−0.41</td>
<td>5.96</td>
<td>115</td>
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<tr>
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<td>337</td>
<td>466</td>
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<td>2.05</td>
<td>8.76</td>
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<td>80.4</td>
<td>42.2</td>
<td>74.9</td>
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<td>0.45</td>
<td>1.96</td>
<td>5.27</td>
<td>34.2</td>
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<td>0.97</td>
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<tr>
<td>Minimum</td>
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<td>178</td>
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<tr>
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<td>2.25</td>
<td>9.79</td>
<td>36.6</td>
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<td>67.0</td>
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<td>0.43</td>
<td>2.14</td>
<td>5.27</td>
<td>34.2</td>
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</tr>
<tr>
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<td>347</td>
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<td>0.73</td>
<td>3.95</td>
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<td>158</td>
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<tr>
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<td>155</td>
<td>201</td>
<td>−0.36</td>
<td>−0.04</td>
<td>−0.33</td>
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<td>111</td>
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<tr>
<td>Maximum</td>
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<td>520</td>
<td>352</td>
<td>469</td>
<td>1.72</td>
<td>1.62</td>
<td>7.47</td>
<td>23.2</td>
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<tr>
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<td>40.5</td>
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<td>37.8</td>
<td>54.4</td>
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<td>0.39</td>
<td>2.01</td>
<td>4.07</td>
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<td>Heifers (n = 24)</td>
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<tr>
<td>Mean</td>
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<td>3.56</td>
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</tr>
<tr>
<td>Minimum</td>
<td>194</td>
<td>187</td>
<td>129</td>
<td>175</td>
<td>−0.31</td>
<td>−0.06</td>
<td>−0.02</td>
<td>5.96</td>
<td>112</td>
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<tr>
<td>Maximum</td>
<td>342</td>
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<td>296</td>
<td>397</td>
<td>1.75</td>
<td>1.68</td>
<td>7.43</td>
<td>20.6</td>
<td>159</td>
</tr>
<tr>
<td>SD</td>
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<td>63.1</td>
<td>40.8</td>
<td>56.6</td>
<td>0.52</td>
<td>0.48</td>
<td>2.32</td>
<td>4.54</td>
<td>14.7</td>
</tr>
</tbody>
</table>

1iSBW and fSBW = initial and final shrunk BW (kg); iEBW and fEBW = initial and final empty BW (kg); EWG = empty BW gain (kg/d); MEI = ME intake (Mcal/d); NI = N intake (g/d), total n = 142 (Nellore n = 85, Nellore × Bos taurus n = 57; Bulls n = 91, steers n = 32, heifers n = 19).

Eq. [2], and the net protein requirement for gain (NPg, g of NPg/d) was calculated as shown in Eq. [3]:

\[ \text{NE}_{g} = a \times \text{EBW}^{0.75} \times \text{EWG}^{b}, \]  \[ \text{NP}_{g} = c + d \times \text{RE} + e \times \text{EWG}, \]  

where \( a \) and \( b \) = the antilog of the intercept and the slope of the linear regression of the logarithm of the RE (Mcal·kg\(^{-0.75}\) of EBW·d\(^{-1}\)) on the logarithm of the EWG, respectively; and \( c, d, \) and \( e \) = the intercept and slopes of the multiple regression of the retained protein (g/d) on EWG, kilograms per day, and RE (Mcal/d), respectively.

The partitioning of MEI to RE as fat and protein was computed using a multiple regression, as shown in Eq. [4]:

\[ \text{MEI} = \beta_0 + \beta_1 \times \text{RE}_f + \beta_2 \times \text{RE}_p, \]  

where \( \text{MEI} = \text{ME intake (Mcal·kg}^{-0.75}\text{ of EBW}^{-1}\text{)}; \) \( \text{RE}_f \) and \( \text{RE}_p = \text{the RE (Mcal·kg}^{-0.75}\text{ of EBW}^{-1}\) as fat and protein, respectively.

The intercept (\( \beta_0 \)) of Eq. [4] was assumed to be the estimate of the \( \text{ME}_{}\), and the coefficients \( \beta_1 \) and \( \beta_2 \) represented the amounts of ME required to deposit 1 Mcal of ME as fat or protein, respectively. The efficiencies of RE as fat and protein (\( K_f \) and \( K_p \), respectively) were calculated as the inverse of the coefficients \( \beta_1 \) and \( \beta_2 \), respectively.

Statistical Analysis

A random coefficients model was used assuming a random variation for the effect of study (Littell et al., 2006). The general statistical model used is shown in Eq. [5]:

\[ Y_{ij} = \beta_0 + \beta_1 X_{ij} + \beta_2 S_i + \beta_3 S_i X_{ij} + \varepsilon_{ij}, \]  

where \( Y_{ij} = \) the dependent variable \( Y \) at level \( j \) of the independent variable \( X \) in the study \( I; \) \( \beta_0 = \) the overall intercept with fixed effect; \( \beta_1 = \) the overall slope that results from regressing \( Y \) on \( X \) across all studies with fixed effect; \( X_{ij} = \) the observed value \( j \) of the independent variable \( X \) in the study \( I; \) \( \beta_2 = \) the effect of study \( i (S_i) \) on the intercept; \( \beta_3 = \) the effect of study \( i \) on the slope of the regression of \( Y \) on \( X \) in study \( I; \) and \( \varepsilon_{ij} = \) the random, unexplained error.

An initial analysis was conducted assuming random slope and intercept effects, including a possible covariance between the slope and intercept using an unstructured variance-covariance matrix. The MIXED procedure (SAS Inst. Inc., Cary, NC) was used in the random coefficients model analysis. The covariance parameter was considered different from zero if the \( P \)-value was less than 0.10. A greater \( P \)-value than the traditional \( P = 0.05 \) was used, because accurate estimations of variances and covariances require a considerable number of observations. In instances in which the covariance parameters were not different from zero, a vari-
ance components structure of the variance-covariance matrix was used. The NL MIXED procedure of SAS was used to fit nonlinear models, and the Gauss method was selected for convergence. Outliers were identified and removed if the studentized residue was greater than 2.5 or less than –2.5 (Neter et al., 1996).

RESULTS AND DISCUSSION

BW Measurements

Regression equations have been developed to estimate EBW from BW (NRC, 1984, 2000). According to Owens et al. (1995), EBW is the most precise index of energy and nutrient content of the body, because the digesta are totally washed out from the gastrointestinal tract after animals are slaughtered, and only tissues are weighed and chemically analyzed. Neither effects of breeds \((P = 0.30)\) nor sex and castrate status \((P = 0.22)\) in the prediction of EBW from SBW values were found. The overall equation is shown in Eq. [6] \((n = 385)\). This equation resulted in predictions of EBW within the range reported by Owens et al. (1995) and NRC (2000), in which the EBW was about 85 to 95% of the SBW:

\[
\text{EBW} = -15.6 \pm 3.71 + 0.928 \pm 0.009 \times \text{SBW}, \quad [6]
\]

where EBW = empty BW (kg) and SBW = shrunk BW (kg).

Similarly, the intercept was not different from zero \((P = 0.23)\), and there were no effects of sex and castrate status \((P = 0.24)\) or breed \((P = 0.24)\) on the estimates of the EWG from the ADG. The overall equation is shown in Eq. [7] \((n = 385)\). The NRC (2000) assumes that EWG is \(0.951 \times \text{ADG}\), which is very close to our findings:

\[
\text{EWG} = 0.961 \pm 0.027 \times \text{ADG}, \quad [7]
\]

where EWG = empty BW gain (kg/d).

Energy Requirement for Maintenance

The nonlinear regression indicated that HP increased exponentially as MEI increased. Ferrell (1988) reported that energy intake affects HP due to an increase on mass and metabolic activity of visceral organs. The intercept and the slope of the regression of the log of HP on MEI and NE\(_{\text{m}}\) requirements are shown in Table 2. There were no differences in NE\(_{\text{m}}\) requirements between breeds \((P = 0.82)\). The combined data indicated a NE\(_{\text{m}}\) requirement of 75 kcal-kg\(^{-0.75}\) of EBW-d\(^{-1}\), which is slightly lower than the NE\(_{\text{m}}\) of 77 kcal-kg\(^{-0.75}\) of EBW-d\(^{-1}\) reported by Lofgreen and Garrett (1968) using data from 5 studies involving 208 \(B. \text{taurus}\) heifers and steers. Freitas et al. (2006) found no differences in NE\(_{\text{m}}\) requirement among Nellore purebred and Nellore \(\times B. \text{taurus}\) bulls. Ferrell and Jenkins (1998) reported an average value of NE\(_{\text{m}}\) requirement of 74.5 kcal-kg\(^{-0.75}\) of EBW-d\(^{-1}\) for \(B. \text{indicus}\) crossbred steers. There were no differences in NE\(_{\text{m}}\) requirements among sex and castrate status \((P = 0.73)\). The NRC (2000) assumed that steers have NE\(_{\text{m}}\) requirements 15% less than bulls. Because animals from our database were individually fed in stalls, the absence of difference among sex and castrate status may be attributed to physical activity and other interactions among bulls when fed in groups.

Similarly, the estimate of ME\(_{\text{m}}\) requirement based on the linear relationship between RE and MEI indicated no differences in the ME\(_{\text{m}}\) requirement among breeds and sex and castrate status (Table 3). The overall estimate of ME\(_{\text{m}}\) requirement was smaller than the exponential relationship between HP and MEI \((107 \pm 112 \text{ kcal-kg}^{-0.75} \text{ of EBW-d}^{-1}\), respectively). Similarly, Ferrell and Jenkins (1998) reported that the estimates of NE\(_{\text{m}}\) requirement, calculated as the MEI at which energy gain equals to zero, resulted in the same ranking among sire breeds but lower values than those estimated from the regression of the log of HP on MEI.

Using the linear regression of RE on MEI, the NE\(_{\text{m}}\) was 71.7 kcal-kg\(^{-0.75}\) of EBW-d\(^{-1}\), which is close to the proposed value for \(B. \text{indicus}\) breeds \((70 \text{ kcal-kg}^{-0.75} \text{ of EBW-d}^{-1}\) by the NRC (2000). This method tends to yield lower values for NE\(_{\text{m}}\) because of the positive linear relationship between RE and MEI, whereas the log of HP on MEI has a nonlinear, ever-decreasing HP value as MEI diminishes. Sainz et al. (2005) also reported a lesser NE\(_{\text{m}}\) requirement of Nellore bulls than that of \(B. \text{taurus}\) breeds and suggested that the lower maintenance expenditure might partially be explained by the lower protein turnover (one of the major contributors to endogenous energy expenditures) reported in Nellore cattle. Ferrell and Jenkins (1998) found that NE\(_{\text{m}}\) requirement differed \((P < 0.05)\) among \(B. \text{taurus}\) and \(B. \text{indicus}\) sire breeds. The authors also found an effect of breed sire on weight of the liver and visceral organs in which the liver and the gastrointestinal compartments of Tuli-sired steers fed for ad libitum intake represented 1.16 and 5.64% of the EBW vs. 1.27 and 6.1% of the EBW of Angus-sired steers, respectively. Although visceral tissues represent approximately 6% of EBW, their energy expenditure can account for more than 40% of total energy utilized for maintenance (Ferrell, 1988).

The partial efficiency of conversion of ME to NE\(_{\text{m}}\) was similar among sex and castrate status and breeds with an average value of 67% (Table 2). Similar to these results, Freitas et al. (2006) reported a k\(_{\text{m}}\) of 67% and found no differences between Nellore purebred and Nellore \(\times B. \text{taurus}\) bulls. Ferrell and Jenkins (1998) reported similar values of k\(_{\text{m}}\) (ranging from 65 to 69%) in crossbreds of \(B. \text{indicus} \times B. \text{taurus}\) and \(B. \text{taurus} \times B. \text{taurus}\) steers.

We concluded the use of log of HP on MEI to determine NE\(_{\text{m}}\) is likely to be more adequate than using a relationship between RE and MEI because of the nonlinear relationship between these variables. Furthermore, the regression of the logarithm of HP on MEI

\[\text{HP} = 1.16 - 0.75 \times \text{EBW}, \quad [5]\n
where HP = HP (mg/L), and EBW = EBW (kg).
resulted in an intercept of \(1.87 \pm 0.01\) (0.5% of the intercept estimate; Table 2), whereas the prediction of \(\text{ME}_m\) based on the regression of \(\text{RE}\) on MEI was calculated using an intercept of \(-4.75 \pm 0.89\) (18.7% of the intercept estimate) and a slope of \(0.44 \pm 0.03\) (6.8% of the slope estimate; Table 3). Therefore, the prediction of \(\text{NE}_m\) using the nonlinear regression of HP on MEI might be less variable and more precise. In addition, our results indicated no differences among sex and castrate status and between Nellore purebred and Nellore \(\times \) B. taurus on \(\text{NE}_m\) and energy efficiency for maintenance.

**Protein Requirement for Maintenance**

The \(\text{NP}_m\) requirement is usually assumed to be the sum of endogenous urinary N, metabolic fecal N, and dermal (scurf and hair) N losses, multiplied by the factor 6.25 (NRC, 1985). Alternatively, the \(\text{NP}_m\) requirement might be estimated as the intercept of the regression of retained N on N intake, which should be similar to the N losses at zero N intake. The main difference is that retained N is the amount of N retained by the animal and does not account for losses such as hair and scurf.

Our results indicated an overall \(\text{NP}_m\) requirement of \(1.74 \pm 0.41\) g of \(\text{NPkg}^{-0.75}\) of \(\text{SBWd}^{-1}\) with no differences in \(\text{NP}_m\) requirement among sex and castrate status (\(P = 0.59\)) and breeds (\(P = 0.92\)). Assuming an efficiency of use of M to \(\text{NP}_m\) of 0.67 (NRC, 2000) and converting the EBW to SBW according to Eq. [6], the overall MP requirement for maintenance was \(2.30\) g of \(\text{MPkg}^{-0.75}\) of \(\text{SBWd}^{-1}\). This value is lower than the recommendation of NRC (2000) of \(3.8\) g of \(\text{MPkg}^{-0.75}\) of \(\text{SBWd}^{-1}\). The Institute National de la Recherche Agronomique (INRA, 1988) used N balance studies to determine the maintenance requirement of \(3.25\) g of \(\text{MPkg}^{-0.75}\) of \(\text{SBWd}^{-1}\). Similarly, Smuts (1935) determined a value of \(3.52\) g of \(\text{MPkg}^{-0.75}\) of \(\text{SBWd}^{-1}\).

**Energy Requirement for Growth**

The coefficients to predict the \(\text{NE}_g\) requirement from the \(\text{RE}\) are listed in Table 4. Rates of protein deposition increase at decreasing rates, whereas rates of fat deposition increase at increasing rates with the rate of gain (Byers, 1982). Consequently, the \(\text{NE}_g\) requirement was exponentially related to the EWG. The regression of the logarithm of \(\text{RE}\) on the logarithm of EWG indicated

Table 2. Regression of logarithm of heat production on ME intake to estimate the NE requirements for maintenance by breed and sex or castrate status

<table>
<thead>
<tr>
<th>Item</th>
<th>Intercept</th>
<th>Slope × 1,000</th>
<th>(\text{NE}_m)</th>
<th>(\text{ME}_m)</th>
<th>(\text{k}_m)</th>
<th>(n)</th>
<th>Intercept</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nellore</td>
<td>1.88 ± 0.03</td>
<td>1.56 ± 0.08</td>
<td>75.1 ± 112</td>
<td>0.67</td>
<td>268</td>
<td>0.82</td>
<td>0.80</td>
<td></td>
</tr>
<tr>
<td>Nellore × Bos taurus</td>
<td>1.88 ± 0.02</td>
<td>1.57 ± 0.07</td>
<td>76.3 ± 116</td>
<td>0.67</td>
<td>118</td>
<td>0.59</td>
<td>0.59</td>
<td></td>
</tr>
<tr>
<td>Bulls</td>
<td>1.86 ± 0.03</td>
<td>1.60 ± 0.09</td>
<td>73.0 ± 109</td>
<td>0.67</td>
<td>258</td>
<td>0.73</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>Heifers</td>
<td>1.88 ± 0.04</td>
<td>1.44 ± 0.15</td>
<td>75.4 ± 108</td>
<td>0.70</td>
<td>24</td>
<td>0.73</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>Steers</td>
<td>1.88 ± 0.02</td>
<td>1.43 ± 0.08</td>
<td>76.7 ± 110</td>
<td>0.69</td>
<td>103</td>
<td>0.73</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>Overall</td>
<td>1.87 ± 0.01</td>
<td>1.55 ± 0.04</td>
<td>75.0 ± 112</td>
<td>0.67</td>
<td>386</td>
<td>0.73</td>
<td>0.13</td>
<td></td>
</tr>
</tbody>
</table>

1Using a variance components variance-covariance matrix and random interaction of study and intercept. Intercept and slope values are mean ± SEM. The \(\text{NE}_m\), kcal/kg\(^{-0.75}\) of empty BW (EBW), was calculated as the antilog of the intercept. The \(\text{ME}_m\), kcal/kg\(^{-0.75}\) of EBW, was calculated by iteration assuming heat produced is equal to ME intake at maintenance. The efficiency of use of ME for \(\text{NE}_m\) (\(\text{k}_m\)) was calculated as \(\text{NE}_m/\text{ME}_m\).

2\(P\)-values for fixed effects of intercept and slope by breed or sex and castrate status.

Table 3. Regression of retained energy (RE) on ME intake to describe energy utilization by breed and sex or castrate status

<table>
<thead>
<tr>
<th>Item</th>
<th>Intercept × 100</th>
<th>Slope</th>
<th>(\text{K}_g)</th>
<th>(\text{ME}_m)</th>
<th>(n)</th>
<th>Intercept</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nellore</td>
<td>-4.13 ± 2.07</td>
<td>0.42</td>
<td>± 0.08</td>
<td>0.42</td>
<td>98.8</td>
<td>223</td>
<td>0.24</td>
</tr>
<tr>
<td>Nellore × Bos taurus</td>
<td>-6.70 ± 1.81</td>
<td>0.52</td>
<td>± 0.07</td>
<td>0.52</td>
<td>128.2</td>
<td>95</td>
<td>0.24</td>
</tr>
<tr>
<td>Bulls</td>
<td>-4.07 ± 1.61</td>
<td>0.41</td>
<td>± 0.06</td>
<td>0.41</td>
<td>99.3</td>
<td>201</td>
<td>0.68</td>
</tr>
<tr>
<td>Heifers</td>
<td>-5.31 ± 2.47</td>
<td>0.49</td>
<td>± 0.10</td>
<td>0.49</td>
<td>107.6</td>
<td>20</td>
<td>0.68</td>
</tr>
<tr>
<td>Steers</td>
<td>-5.41 ± 1.29</td>
<td>0.50</td>
<td>± 0.05</td>
<td>0.50</td>
<td>108.9</td>
<td>97</td>
<td>0.68</td>
</tr>
<tr>
<td>Overall</td>
<td>-4.75 ± 0.89</td>
<td>0.44</td>
<td>± 0.03</td>
<td>0.44</td>
<td>106.8</td>
<td>318</td>
<td>0.68</td>
</tr>
</tbody>
</table>

1Using an unstructured variance-covariance matrix and random interactions of study and intercept and study and slope. \(\text{K}_g\) = efficiency of use of ME for \(\text{NE}_g\) requirement and calculated as the slope of the regression of \(\text{RE}\) (kcal/kg\(^{-0.75}\) of empty BW (EBW)) on ME intake (kcal/kg\(^{-0.75}\) of EBW). The \(\text{ME}_m\) was calculated as the ME intake when \(\text{RE}\) is equal to zero.

2\(P\)-values for fixed effects of intercept and slope by breed or sex and castrate status.
might be accounted for by differences in fat distribution
Angus reported a greater fat content in the empty body in
Nellore crossbred data set (Table 1). Solis et al. (1988)
in Nellore crossbreds than in Nellore purebreds. This
was greater than 1 kg/d, the RE in the EWG was greater
than that of Nellore crossbreds (9% greater than that of
Nellore purebreds). The NEg requirement between breeds
was 18% greater and lesser NEg requirements than steers
for heifers and 10% greater than that for steers. These
findings are in agreement with the differences in car-
cass composition and rates of fat accretion among sex
and castrate status reported by Berg and Butterfield
(1976). These authors indicated that fat deposition was
greater (in a decreasing order) for heifers, steers, and
bulls.

There was a tendency (P = 0.06) of difference in the
NEg requirement between breeds. The regression of the
logarithm of RE on the logarithm of EWG using a com-
mon slope and difference intercept among sex and castrate status
was

\[
\text{NE}_g = a \times \text{EBW}^{0.75} \times \text{EWG}^{1.070}, \quad [8]
\]

where \(\text{NE}_g\) = net energy for gain (Mcal/d); \(\text{EBW}\) = empty
BW (kg); \(\text{EWG}\) = empty BW gain (kg/d); and \(a\) = either
0.0514, 0.0700, or 0.0771 for bulls, steers, or heifers, re-
spectively.

According to the NRC (2000), heifers and bulls have
18% greater and lesser NEg requirements than steers
at the same BW, respectively. Our data indicated that
the NEg requirement for bulls was 27% less than that
for heifers and 10% greater than that for steers. These
findings are in agreement with the differences in car-
cass composition and rates of fat accretion among sex
and castrate status reported by Berg and Butterfield
(1976). These authors indicated that fat deposition was
greater (in a decreasing order) for heifers, steers, and
bulls.

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Table 4. Regression of logarithm of the retained energy on logarithm of the empty body
and coefficients to predict retained energy from empty BW gain and empty BW by
breed and sex or castrate status

<table>
<thead>
<tr>
<th>Item</th>
<th>Coefficients</th>
<th>Intercept Slope</th>
<th>P-value²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a  b  n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nellore</td>
<td></td>
<td>-1.19 ± 0.06  1.03 ± 0.08</td>
<td>0.0640 1.031 191</td>
</tr>
<tr>
<td>Nellore × Bos taurus</td>
<td></td>
<td>-1.33 ± 0.05  1.13 ± 0.07</td>
<td>0.0469 1.128 104</td>
</tr>
<tr>
<td>Bulls</td>
<td></td>
<td>-1.29 ± 0.05  1.07 ± 0.08</td>
<td>0.0514 1.071 214</td>
</tr>
<tr>
<td>Heifers</td>
<td></td>
<td>-1.12 ± 0.06  0.99 ± 0.21</td>
<td>0.0766 0.992 16</td>
</tr>
<tr>
<td>Steers</td>
<td></td>
<td>-1.15 ± 0.04  1.08 ± 0.07</td>
<td>0.0701 1.076 65</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>-1.22 ± 0.03  1.06 ± 0.03</td>
<td>0.0609 1.062 295</td>
</tr>
</tbody>
</table>

Using a common slope for sex and castrate status

<table>
<thead>
<tr>
<th>Item</th>
<th>Coefficients</th>
<th>Intercept Slope</th>
<th>P-value²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bulls</td>
<td></td>
<td>-1.29 ± 0.05   1.07 ± 0.03</td>
<td>0.0514 1.070 214</td>
</tr>
<tr>
<td>Heifers</td>
<td></td>
<td>-1.11 ± 0.06  1.07 ± 0.03</td>
<td>0.0771 1.070 16</td>
</tr>
<tr>
<td>Steers</td>
<td></td>
<td>-1.15 ± 0.04  1.07 ± 0.03</td>
<td>0.0700 1.070 65</td>
</tr>
</tbody>
</table>

¹Using a variance components variance-covariance matrix and random interaction of study and intercept.
²P-values for fixed effects of intercept or slope by breed or sex and castrate status.

Protein Requirement for Growth

Protein deposition in the empty body has been esti-
mated using the rate of ADG and the composition of
the gain (NRC, 2000; Table 5). The composition of the
gain depends on physiological maturity of the animal,
which is affected by sex and castrate and breed of
the animal (NRC, 1984). The NPg requirement was
not different among sex and castrate status (P = 0.59)
and breeds (P = 0.14), suggesting that energy retained
and EWG can account for a significant amount of the
variation in the protein retention due to breeds and sex
and castrate status (Eq. [9]):

\[
\text{NP}_g = \text{EWG} \times [217 - (12.8 \times \text{RE/EWG})], \quad [9]
\]

where \(\text{NP}_g\) = net protein requirement for growth (g/d)
and \(\text{EWG}\) = empty BW gain (kg/d).

The percentage of RE deposited as protein (\%REp)
decreased exponentially as the content of RE in the
gain (Mcal/kg of EWG) increased (Figure 1). The \%REp
can be used to compute the partial efficiency of ME to
NE for growth (Williams and Jenkins, 2003; Tedeschi
et al., 2004). Because no study effect was observed, we
pooled the data across studies to develop Eq. [10].

\[
\text{\%RE}_p = 10.1 + 166.7 \times e^{-0.660 \times \text{REc}}, \quad [10]
\]

where \(\text{REc}\) = the concentration of RE in the empty BW
gain (Mcal/kg) and \(e\) = the natural log.

Our findings are not in agreement with those re-
ported by Geay (1984), who reported that \%REp was
Table 5. Regression of retained protein on retained energy (RE) and empty BW gain (EWG) to estimate the net protein requirements for gain by breed and sex or castrate status.

<table>
<thead>
<tr>
<th>Item</th>
<th>Intercept$^2$</th>
<th>Coefficients</th>
<th>$P$-value$^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$d$</td>
<td>$e$</td>
</tr>
<tr>
<td>Nellore</td>
<td>0.20 ± 11.2</td>
<td>-10.9 ± 5.0</td>
<td>214 ± 25</td>
</tr>
<tr>
<td>Nellore × Bos taurus</td>
<td>-17.3 ± 10.0</td>
<td>-18.7 ± 4.6</td>
<td>233 ± 22</td>
</tr>
<tr>
<td>Bulls</td>
<td>-1.74 ± 10.3</td>
<td>-12.1 ± 4.5</td>
<td>218 ± 26</td>
</tr>
<tr>
<td>Heifers</td>
<td>-22.6 ± 26.3</td>
<td>-13.0 ± 8.1</td>
<td>217 ± 53</td>
</tr>
<tr>
<td>Steers</td>
<td>6.45 ± 8.73</td>
<td>-12.0 ± 3.9</td>
<td>191 ± 23</td>
</tr>
<tr>
<td>Overall</td>
<td>-1.40 ± 4.48</td>
<td>-12.8 ± 2.0</td>
<td>217 ± 10</td>
</tr>
</tbody>
</table>

1Using a variance components variance-covariance matrix and random interaction of study and slopes $d$ and $e$. Intercepts and coefficients $d$ and $e$ are from the multiple regression of the retained protein ($NP_{p, g/d}$) on the RE (Mcal/d) and EWG (kg/d), respectively: $NP_p = \text{intercept} + (d \times \text{RE}) + (e \times \text{EWG})$.

2Intercepts were not different from zero ($P = 0.75$).

3$P$-values for fixed effects of slopes $d$ and $e$ by breed or sex and castrate status.

Greater for bulls than for heifers likely because of greater protein content of protein in the gain. This is possible when animals have similar maturity degree, in which the composition of gain is identical and the RE concentration is comparable.

Efficiencies of Fat and Protein Accretion

The analysis of the partition of MEI above maintenance to protein and fat deposition based on Eq. [4] is shown in Table 6. Based on this multilinear approach, the energetic efficiencies of protein and fat deposition were not different among breeds and sex and castrate status and were on average 0.34 and 0.79, respectively. Owens et al. (1995) reported that protein accretion had an average efficiency of 0.47 and the efficiency of fat accretion was 0.79, which is identical to our finding. Geay (1984) reported efficiencies of protein and fat accretion of 0.20 and 0.75, respectively, using data from 52 experiments. The efficiency of protein accretion is highly variable and depends on physiological stage, nutritional status, and protein turnover. Unlike protein, fat accretion efficiency is thought to be less variable (CSIRO, 1990). According to Tedeschi et al. (2004), the

Figure 1. Relationship between the percentage of retained energy (RE) as protein and the RE concentration (REc) in the empty BW gain (EWG). Symbols are data from bulls (□ and ■), steers (○ and ●), and heifers (◇ and ◆). Opens symbols are data from Nellore purebreds, and solid symbols are data from Nellore × Bos taurus crossbreds. The solid line is the predicted values using the following equation: \(%RE_p = 10.1 (±0.1) + \{166.7 [±15.8] \times e^{[±0.660 (±0.045) \times \text{REc}]})\).
ME for fat deposition has a greater efficiency than for protein likely due to the cost of protein turnover. The variation in efficiency of protein accretion is related to the variations in turnover rate, because faster protein turnover at greater accretion rates will increase HP and decrease GE efficiency (Owens et al., 1995). Our efficiency of protein accretion was greater than that observed by Geay (1984) (0.34 vs. 0.20, respectively); this was likely because of lower rates of protein turnover of Nellore cattle in comparison with B. taurus breeds (Sainz et al., 2005).

**Efficiencies of Retained Energy**

The partial efficiency of use of ME to NE\( _g \) estimated as the slope of the linear regression of RE on MEI was not different among sex and castrate status (\( P = 0.33 \)) and breeds (\( P = 0.20 \)) and averaged 0.44 (Table 3). Ferrell and Jenkins (1998) reported a nonlinear regression in which energy gain increased asymptotically as MEI increased. However, the linear regression of the RE on MEI fit better in our data set than the exponential regression, because it had smaller values of AIC and Schwartz’s BIC (Mills and Prasad, 1992).

Even though Ferrell (2003) reported that variations in body composition and composition of the gain can affect the partial efficiency of energy utilization, the ARC (1980), CSIRO (1990), AFRC (1993), and NRC (2000) compute \( K_p \) based on biological values of the diet. Because the energy content of the fat and lean tissue differs, Tedeschi et al. (2004) suggested that \( K_p \) depends on the composition of EWG. Assuming the equation proposed by Tedeschi et al. (2004, 2005) to compute partial efficiency of NE for growth \( \left[ K_p = (K_f \times K_p) / (K_p + (%RE_p/100) \times (K_f - K_p)) \right] \) and the \( K_f \) and \( K_p \) values found in this study, the \( K_p \) can be estimated from Eq. [11].

\[
K_p = 0.2686/[0.34 + 0.45 \times (%RE_p/100)], \quad [11]
\]

where \( %RE_p \) = the percentage of protein energy in the retained energy (Mcal/Mcal). The use of \( K_p \) based on the EWG composition might be preferable to a single efficiency to compute ME to NE\( _g \) based on diet ME content. As expected, Eq. [11] will yield greater \( K_p \) than the equation proposed by Tedeschi et al. (2004) at the same \( RE_p \). In addition, as \( RE_p \) increases, the difference between \( K_p \) predicted by Eq. [11] and the equation of Tedeschi et al. (2004) increases.

**Energy Partition of the MEI**

The most efficient animal is the one that converts ME to RE more efficiently by expending less energy for maintenance (Herd et al., 2004). The percentage of the MEI utilized for HP and RE was plotted against MEI to evaluate differences in efficiency among breeds and sex and castrate status (Figure 2).

There were no effects of sex and castrate status (\( P = 0.36 \)) and breeds (\( P = 0.91 \)) on the energy partitioning. Nonlinear equations that were fitted to HP \( [0.729 + 0.70 \times e^{-11.8 \times MEI}] \), AIC = −830.7 and BIC = −815.6 and \( RE [0.271 \times (1 - 2.57 \times e^{-11.8 \times MEI}] \), AIC = −830.7 and BIC = −815.6 data (Figure 2) indicated the maximum RE was 27.1% and the minimum HP was 72.9% of the MEI (Mcal-kg\(^{-0.75} \) of EBW\(^{-1} \)). However, the quadratic model fit slightly better than the nonlinear model to describe the relationships between the percentage of MEI used as HP or RE and MEI. The quadratic equations were 1.15 (±0.06) – 2.67 (±0.52) × MEI + 4.48 (±1.16) × MEI\(^2 \) for HP (AIC = −831.7 and BIC = −816.6) and −0.15 (±0.06) + 2.67 (±0.52) × MEI − 4.48 (±1.16) × MEI\(^2 \) for RE (AIC = −831.7 and BIC = −816.6).

Our data suggested that HP increases exponentially with MEI (Table 2), and, although RE increases with increased MEI (Table 3), it happens at a lesser incremental rate than that with HP. This occurs because as MEI increases, the energy utilized for feed intake, digestion, absorption, and metabolism of nutrients also increases. In addition, the metabolic activity of the visceral organs increases with MEI, resulting in a greater HP. Ferrell and Jenkins (1998) reported that HP increased exponentially and energy gain increased asymptotically as DMI increased above maintenance.
Figure 2. Relationship between ME intake (MEI, Mcal·kg\(^{-0.75}\) of empty BW·d\(^{-1}\)) and the percentages of MEI retained in the body (RE, bottom data points) and lost as heat (HP, top data points). Symbols are data from bulls (○ and □), steers (○ and ◆), and heifers (○ and ◆). Open symbols are data from Nellore purebreds, and solid symbols are data from Nellore × Bos taurus crossbreds. Quadratic equations (dotted lines) are HP = 1.15 (±0.06) − [2.67 (±0.52) × MEI] + [4.48 (±1.16) × MEI\(^2\)] (top data points) and RE = −0.15 (±0.06) + [2.67 (±0.52) × MEI] − [4.48 (±1.16) × MEI\(^2\)] (bottom data points). Nonlinear equations (solid lines) are HP = 0.729 (±0.02) + {0.70 [±0.24] × e\(^{-11.8 (±3.35) × MEI}\)} (top data points) and RE = 0.271 (±0.02) × (1 − [2.57 [±1.07] × e\(^{-11.8 (±3.35) × MEI}\}]) (bottom data points).

supporting the quadratic behavior when HP and RE are expressed as percentage of MEI. Assuming the quadratic model, the maximum proportion of the MEI deposited in the body (maximum growth efficiency) does not occur at the maximum energy intake level; the quadratic equation suggested that at the MEI of 0.298 Mcal·kg\(^{-0.75}\) of EBW·d\(^{-1}\), animals retained the greatest portion of the ME consumed (or lost the least portion of MEI as heat).

In conclusion, our results do not support the hypothesis that bulls have greater NE\(_m\) requirements than steers and heifers. Similarly, no differences in the NP\(_m\) among bulls, steers, and heifers were detected. Nonetheless, the NE\(_g\) requirement of steers was greater than bulls and lower than heifers. The %RE\(_g\) was negatively, nonlinearly correlated with the concentration of energy in the EWG, but our findings indicated no differences in NP\(_g\) among bulls, steers, and heifers. The greatest energy efficiency did not occur at the maximum MEI.

LITERATURE CITED


Marondes, M. I. 2007. Desempenho de bovinos Nellore alimentados individualmente ou em grupo, exigências nutricionais e avaliação de alimentos para ruminantes. MS Diss. Universidade Federal de Viçosa, Brazil.


