Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers

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ABSTRACT: This study examined the relationship of feed efficiency and performance with feeding behavior, blood metabolic variables, and various body composition measurements in growing beef heifers. Individual DMI and growth were measured in yearling Limousin × Holstein-Friesian heifers [n = 86; initial BW = 191.8 (SD = 37) kg] fed a TMR diet comprising 70:30 concentrate:corn silage on a DM basis (ME of 2.65 Mcal/kg of DM; DM of 580 g/kg) for 82 d. Meal duration (min/d) and meal frequency (events/d) were calculated for each animal on a daily basis using an Insentec computerized feeding system. Physical measurements as well as ultrasonic fat and muscle depths were recorded on 3 equally spaced occasions during the experimental period. Blood samples were collected by jugular venipuncture on 4 equally spaced occasions and analyzed for plasma concentrations of IGF-I, insulin, leptin, and various metabolites. Phenotypic residual feed intake (RFI) was calculated for all animals as the residuals from a multiple regression model regressing DMI on ADG and midtest BW0.75. Overall, ADG, DMI, feed conversion ratio (FCR), and RFI were 1.51 (SD = 0.13), 6.74 (SD = 0.99), 4.48 (SD = 0.65), and 0.00 (SD = 0.48) kg/d, respectively. Residual feed intake was positively correlated with DMI (r = 0.47) and FCR (r = 0.46), but not with ADG or midtest BW. Positive correlations (ranging from r = 0.27 to r = 0.63) were estimated between ultrasonic measures of final lumbar fat and lumbar fat accretion over the test period and DMI, FCR, and RFI. The inclusion of gain in lumbar fat to the base RFI model increased R² (0.77 vs. 0.80) value for the degree of variation in DMI not explained by midtest BW and ADG alone. The Pearson rank correlation between RFI and carcass-adjusted RFI (RFIc) was high (r = 0.93). From the plasma analytes measured, NEFA (r = −0.21; P < 0.05) and β-hydroxybutyrate (r = 0.37; P < 0.05) concentrations were correlated with RFI. Plasma leptin (r = 0.48), glucose:insulin (r = −0.23), NEFA (r = −0.32), and β-hydroxybutyrate (r = 0.25) were associated with FCR. However, systemic IGF-I and insulin were unrelated (P > 0.05) to any measure of feed efficiency. The feeding behavior traits of eating rate, daily feeding events, and nonfeeding events were positively correlated (P < 0.05) with RFI and RFIc. This multifactorial study provides new information on some of the biological processes responsible for variation in feed efficiency in beef cattle.

Key words: beef cattle, body composition, feed efficiency, feeding behavior, plasma analyte

INTRODUCTION

Feed is the major cost in beef production and is thus a significant determinant of profitability. To improve the economic and environmental sustainability of the enterprise, cattle that are more efficient at utilizing feed resources must be identified. Traditionally, feed conversion efficiency was expressed as the ratio of feed intake to BW gain (FCR), but it has been suggested that selection for this trait may be confounded with maturity patterns and body size (Arthur et al., 2001a),

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thus contributing to greater maintenance energy requirements and a greater environmental impact of the breeding herd (Herd and Arthur, 2009). An alternative measure of feed efficiency proposed is residual feed intake (RFI), defined as the difference between actual feed intake of an animal and its predicted intake based on body size and level of performance. This trait is moderately heritable and genetically independent of growth and body size (Crews, 2005). However, knowledge of the underlying biological mechanisms controlling RFI are yet to be fully understood (Herd and Arthur, 2009; Moore et al., 2009).

Animal behavioral responses can alter physical activity and thus influence total energy expenditure and feed efficiency (Susenbeth et al., 1998). For example, studies show that feed-efficient animals typically engage in less daily feeding activity (Golden et al., 2008), which may have evolved as an energy-sparing mechanism. Additionally, body composition plays a key role in defining energetic efficiency and is in turn influenced by diet, physiological state, and genotype (Basarab et al., 2003). Furthermore, systemic concentrations of key metabolic hormones associated with feed intake, growth, fat accumulation, nutrient repartitioning, and nutrient utilization have been examined with a view to identifying potential physiological markers of feed efficiency along with improving our understanding of the metabolic basis of the trait in cattle (Wood et al., 2003). However, results to date are contradictory. The objective of this study was to examine the relationship between RFI, feeding behavior, blood metabolic variables, and various ultrasonic and body measurements in growing beef heifers.

**MATERIALS AND METHODS**

All procedures involving animals were approved for the use of live animals in experiments by the Animal Research Ethics Committee, University College Dublin, Belfield, Dublin, Ireland, and were licensed by the Irish government’s Department of Health and Children, in accordance with the Cruelty to Animals Act (Ireland 1897) and European Community Directive 86/609/EC.

**Animals and Management**

Female progeny born to Holstein-Friesian dams and sired by Limousin bulls were identified and sourced from Irish commercial dairy herds in spring 2006. Sire selection was based on the estimated breeding value for RFI, calculated using a data set from the Irish National Beef Bull Performance Test Station, Tully, Co. Kildare. In total, 90 calves were purchased from 18 dairy herds and transferred to University College Dublin, Research Centre, Lyons Estate, at 3 to 5 wk of age. Calves were reared indoors on a standardized feeding protocol (Fallon and Harte, 1987) using a computerized calf rearing system (Foerster Technik, Engen, Germany), before being turned out to pasture at a mean age of 17 wk. At pasture, animals were offered ad libitum pasture and supplemented with 2 kg of concentrate daily. Calves were treated with ivermectin (Qualimec, Janssen Animal Health, Janssen-Cilag Ltd., High Wycombe, Bucks, UK) at 3, 8, and 13 wk after turnout for the control of external and gastrointestinal parasites. All calves grazed together at pasture until housed at 7 mo of age.

On arrival at the feed intake research facility, each animal was fitted with a passive radio frequency transponder button ear tag. Animals were penned (21 × 17 m) as 1 group bedded on peat mulch and had ad libitum access to 15 electronic feeding stations (Insentec, Marknesse, the Netherlands). Animals were managed and tested for growth and feed intake under a standardized feeding, housing, and management environment.

Briefly, animals were given an adaptation period of 30 d, during which the concentrate proportion in the diet was gradually increased while the forage proportion was concurrently reduced. This pretest adjustment period allowed them to become acclimatized to the ad libitum feeding regimen and adapt to the test facility. Ad libitum feed intake was reached at 20 d after the beginning of the acclimatization period; thus, animals were on ad libitum intake for approximately 10 d before the experimental recording period, which lasted for 82 d (i.e., 112-d period in total). The mean age at the beginning of the performance test was 247 d (SD = 15) and the mean BW was 192 kg (SD = 36.9). During the test period, animals had ad libitum access to a TMR composed of concentrate pellet and corn silage on a 70:30 concentrate:forage ratio (DM basis). The diet had a DM of 580 g/kg, 182 g/kg of CP, and an estimated ME concentration of 2.65 Mcal/kg of DM (NRC, 2000; Table 1). The dietary ingredients were mixed and dispensed using a feeding wagon and were offered in 1 feeding daily at 0900 h. Each feed station was filled to 110% of the weight of material removed on the previous day to ensure that all animals had constant and unrestricted access to feed. All feed stations were calibrated twice weekly using known weight. Animals also had ad libitum access to fresh drinking water.

Samples of the TMR diet were taken twice weekly from 3 locations within each of the 15 feed stations. Samples were composited on a weekly basis and stored at −20°C pending analysis for DM, CP, ADF, NDF, water-soluble carbohydrate, ether extract, ash, and GE. Samples were milled through a 1-mm screen using a Christy and Norris hammer mill (Christy and Norris Process Engineers Ltd., Chelmsford, UK); DM was determined by oven drying at 104°C for a minimum of 16 h. Ash was determined on all materials after ignition of a known weight of ground material in a muffle furnace (Nabertherm, Bremen, Germany) at 550°C for 4 h. The NDF and ADF concentrations of feed were obtained using an Ankom-200 fiber analyzer (Ankom Technology, Fairport, NY) according to the method of Van Soest et al. (1991). The CP (total N × 6.25)
was determined using the method of Sweeney (1989) with a Leco FP 528 nitrogen analyzer (Leco Instruments UK Ltd., Newby Road, Hazel Grove, Stockport, Cheshire, UK). Water-soluble carbohydrate content of all feedstuffs was also established in duplicate using a modification of the method of Birch and Mwangelwa (1974). Ether extract was determined with a Sortex instrument (Tecator, Höganäs, Sweden), whereas GE was determined with a Parr 1201 oxygen bomb calorimeter (Parr, Moline IL).

Feed Intake and Growth Data

Feed intake was measured for each animal with an Insentec monitoring system, validated previously by Chapinal et al. (2007). Briefly, the system consisted of 15 feed bins (1.00 m wide, 0.75 m high, and 0.84 m deep), a data-logging reader panel connected to each feed node, and a personal computer and Insentec Data Acquisition and Analysis Software. When an animal approached the feed bin, an antenna detected the unique passive transponder of the animal and lowered the barrier, allowing the animal access to the feed. For each visit to the bin, the system recorded the animal number, bin number, initial and final times, and weight of contents, and calculated the visit duration and quantity of material removed during a visit.

Animals were weighed in the morning, at 14-d intervals using calibrated electronic scales, resulting in 7 records per animal during the test period. Animals were weighed on 2 consecutive days at the beginning and again at the end of test.

Feeding Behavior

Feeding behavior traits were evaluated in this study using feed bin attendance data. The number of daily feeding events was calculated as the number of times an animal entered the feed bin and consumed a minimum of 100 g of feed. Nonfeeding events were calculated as the number of times an animal entered the feed bin without feed consumption occurring or when less than 100 g of feed was consumed. Daily feeding duration was computed as the total daily time taken to consume the recorded intake (min/d). Eating rate was calculated as total DMI per day divided by total daily duration of eating (meal) activity (kg/min).

Skeletal and Muscular Scores and Ultrasound Measurements

To provide a more objective description of animal morphology, linear body measurements (Campion et al., 2009) were recorded on all animals on 3 separate occasions throughout the experimental period. The measurements taken were height at the withers, chest girth, length of the back, chest depth, and pelvic width. A digital calipers was used to record height at the with-
ers, chest depth, and width of the pelvis, and a metal tape was used to measure chest girth and length of the back.

Animals were scored linearly at 11 mo of age by a trained Irish Cattle Breeding Federation assessor as described by Drennan et al. (2008). Skeletal scores on a scale of 1 (short/narrow) to 10 (long/wide) were taken at 3 locations (height at the withers, length of the back, and width at the hips). Muscular scores were assigned on a scale of 1 (hollow, poorly muscled) to 15 (wide, heavily muscled) at 4 locations on the body (width behind the withers, loin development, development of the hindquarter, and hindquarter width). Subjective scores on a scale of 1 to 10 for docility (1 to 2 = aggressive; 3 to 4 = flighty/wild; 5 to 6 = nervous; 7 to 8 = restless; 9 to 10 = docile) were also assigned to each animal.

At the time of linear body measurement (i.e., 3 occasions), each animal was ultrasonically scanned (Aquila Vet real-time ultrasound scanner, with a 3.5-MHz transducer, Esaote Pie Medical, Pie Medical Equipment B.V., Maastricht, the Netherlands) to obtain LM depth and fat depth. Scanning was carried out on the right side of each animal. The LM depth was measured at the third lumbar vertebra, where depth of this muscle is greatest. Measurement was from the bottom of the third lumbar vertebra, where depth of this muscle is greatest. Measurement was from the bottom of the backfat layer to the top of the bone. Three fat depth measurements were taken at the third lumbar vertebra and a further 4 were taken at the Ausmeat P8 site (rump) as described by Robinson et al. (1992). Lumbar and rump fat depths were calculated as the means of the values recorded.

**Blood Collection and Analysis**

Blood was sampled by jugular venipuncture in the morning on 4 equally spaced occasions (d 1, 30, 60, and 82) during the experimental period. Samples (10 mL) were collected into heparinized evacuated tubes (170-IU lithium heparin Vacutainers, Becton Dickinson Vacutainer Systems, Plymouth, UK) for plasma concentrations of IGF-I, insulin, leptin, glucose, NEFA, and β-hydroxybutyrate (BHB). On collection, samples were immediately stored in ice water and centrifuged at 1,500 × g at 4°C for 15 min. The plasma was then split into borosilicate glass scintillation vials and stored at −20°C until analysis.

Plasma IGF-I concentrations were determined by RIA after an acid-ethanol extraction procedure, as described previously by Spicer et al. (1988). Intraassay CV for IGF-I were 12.4, 11.5, and 7.1% for low, medium, and high standards, respectively. Interassay CV were 12.3, 11.9, and 7.1% for low, medium, and high standards, respectively. Glucose and urea were analyzed using reagents supplied by Olympus Diagnostics (Tokyo, Japan; catalog numbers OSR6121 and OSR6134). Concentrations of BHB and NEFA were analyzed using reagents supplied by Randox Laboratories (Crumlin, Co. Antrim, Northern Ireland, UK; catalog numbers RD1007 and FA115). All plasma metabolite concentrations were quantified by enzymatic colorimetry using an AV400 clinical analyzer (Olympus Diagnostics). Plasma insulin was quantified by fluoroimmunoassay (AutoDELFIA, PerkinElmer Life and Analytical Sciences, Turku, Finland; catalog number B080-101) and validated for bovine plasma (Ting et al., 2004). Intraassay CV for insulin were 6.4, 3.6, and 2.5% for the low, medium, and high standards, respectively. Corresponding interassay CV were 6.3, 3.5, and 2.5%. Leptin was assayed in a double-antibody RIA as described by Wylie et al. (2008). The primary antibody (GP-OL3) was raised in guinea pigs against recombinant ovine leptin. The second antibody was donkey anti-guinea pig IgG. Intraassay CV for leptin ranged from 4.88 to 8.58% (mean, 6.58%); the interassay CV was 8.75%. Assay sensitivity (defined as zero-binding counts less than 2 SD) was between 0.5 and 0.6 ng/mL.

**Traits and Their Derivations**

Average daily gain during the test period for each animal was computed as the coefficient of the linear regression of BW (kg) on time by using the REG procedure (SAS Inst. Inc., Cary, NC). Midtest metabolic BW (MBW) was represented as BW0.75 t 41 d before the end of the test, which was estimated from the intercept and slope of the regression line after fitting a linear regression through all BW0.75 observations. Total daily DMI was calculated as the sum of all the meals consumed within the day corrected for DM content. Average daily ME intake (Mcal/kg of DM) per unit of MBW (MEI) was estimated using the following equation: MEI = {GE × DE (NRC, 2000)} × 0.82)/MBW, as described by El-Meccawi et al. (2009). Feed conversion ratio of each animal was computed as the ratio of daily DMI to ADG. The additional growth traits of Kleiber ratio (KR) and relative growth rate (RGR) were examined because they are considered to be indirect measures of feed efficiency, without the requirement of feed intake measurement (Fitzhugh and St. Taylor, 1971; Bergh et al., 1992); RGR, growth relative to instantaneous body size, and KR were computed as follows: RGR = 100 × [log(end BW) − log(beginning BW)]/days on test, and KR = ADG/MBW.

Residual feed intake was computed for each animal and was assumed to represent the residuals from a multiple regression model regressing DMI on ADG and MBW. The base model used was

\[ Y_j = \beta_0 + \beta_1 MBW_j + \beta_2 ADG_j + e_j \]

where \( Y_j \) is the standardized DMI of the jth animal, \( \beta_0 \) is the regression intercept, \( \beta_1 \) is the regression coefficient on MBW, \( \beta_2 \) is the regression coefficient on ADG, and \( e_j \) is the uncontrolled error of the jth animal.

Standard deviations above and below the mean were used to group animals into high RFI (RFI > 0.5 SD above the mean), medium RFI (RFI ± 0.5 SD above and below the mean), and low RFI (RFI < −0.5 SD below the mean).
below the mean). An alternative RFI estimate ($RFI_c$) was computed from expected DMI adjusted for ultrasound estimated carcass composition. Initially, stepwise regression analysis was performed (REG procedure of SAS) to determine the order of inclusion of ultrasound carcass composition traits into the base model. With this order, ultrasound composition traits were sequentially added and the resulting change in coefficient of determination was used to determine their relative importance, to account for additional variation in DMI. Similarly, feeding behavior traits were added to the carcass-adjusted regression (i.e., $RFI_c$) to evaluate the relevance of feeding behavior traits to explain additional variation in RFI. Gain in backfat, muscle thickness, and linear measurement for each individual animal was predicted from regression equations of measurements on time (days).

**Statistical Analysis**

Data were checked for normality and homogeneity of variance by histograms, qqplots, and formal statistical tests as part of the UNIVARIATE procedure of SAS. Data that were not normally distributed were transformed by raising the variable to the power of lambda. The appropriate lambda value was obtained by conducting a Box-Cox transformation analysis using the TRANSREG procedure of SAS. The natural logarithmic transformations of insulin and NEFA were used to normalize data distributions for these 2 variables because preliminary analyses revealed that the distribution of values for both analytes was positively skewed. All feeding behavior-related traits required a transformation and were raised to the power of 0.25, with the exception of daily feed consumption, which required a logarithmic transformation. The transformed data were used to calculate $P$-values. However, the corresponding least squares means and SE of the nontransformed data are presented in the results for clarity. Least squares procedures using the MIXED procedure of SAS were used to examine the effect of RFI group on performance, intake, feed efficiency, and body composition measures. The statistical model used included the fixed effect of RFI group (high, medium, and low). A random sire effect was included in the final model for all traits except relative growth rate or KR. Animal age at the beginning of test was included in the model as a linear covariate. Variables having more than 1 observation per subject, such as feeding behavior and plasma analytes, were analyzed using repeated measures ANOVA (MIXED procedure), with terms for RFI group, day of test, and their interaction included in the model and animal within RFI group set as the error term. The interaction term if not statistically significant ($P > 0.05$) was subsequently excluded from the final model. The type of variance-covariance structure used was chosen depending on the magnitude of the Akaike information criterion (AIC) for models run under compound symmetry, unstructured, autoregressive, or Toeplitz variance-covariance structures. The model with the least AIC value was selected. Differences in RFI group were determined by $F$-tests using Type III sums of squares. The PDIF option and the Tukey test were applied as appropriate to evaluate pairwise comparisons between RFI group means. Pearson correlation coefficients among traits were determined using the CORR procedure of SAS. Repeated measures of the blood analytes and feeding behavior traits for the entire experimental period were used in the correlation analyses.

**RESULTS**

**Performance and Feed Efficiency**

Animals in this study had an overall mean DMI of 6.74 kg/d (SD = 0.99), an ADG of 1.51 kg/d (SD = 0.13), and an FCR of 4.48 kg of DMI/kg of BW gain (SD = 0.65). Residual feed intake averaged 0.00 kg/d (SD = 0.48) and ranged from −1.25 to 1.87 kg/d, representing a difference of 3.12 kg of feed per day between the greatest and least ranked animals. Differences in intake, performance, and feed efficiency traits are presented in Table 2.

Low-RFI heifers consumed 8.5 and 15.9% less feed than their counterparts ranked as either medium or high RFI, respectively ($P < 0.001$). Least squares means for MEI, RFI, and FCR were greater ($P < 0.001$) for high-RFI heifers than for medium-RFI heifers, which in turn were greater ($P < 0.001$) than for low-RFI heifers. Average daily gain, initial BW, MBW, and final BW did not differ ($P > 0.10$) between the high-, medium-, and low-RFI groups. Relative growth rate or KR did not differ between the RFI groups.

Residual feed intake was not correlated with MBW or ADG, but was correlated ($P < 0.001$) with DMI ($r = 0.47$) and FCR ($r = 0.46$). Dry matter intake was strongly correlated ($P < 0.001$) with FCR ($r = 0.79$), initial BW ($r = 0.65$), final BW ($r = 0.86$), and MBW ($r = 0.83$), and was moderately correlated ($P < 0.001$) with ADG ($r = 0.37$). Feed conversion ratio was negatively associated ($P < 0.05$) with ADG ($r = −0.28$).

**Body Composition Traits**

Of the body composition variables measured, the inclusion of gain in lumbar fat into the base model accounted for the largest increment in explained variation (3 percentage units; $P < 0.05$) in DMI beyond ADG and MBW. In the current study, differences between RFI groupings were not detected ($P > 0.10$) for either muscle depth or deposition over the trial period (Table 3). Correlation analysis indicated positive associations ($P < 0.01$) between final muscle depth with DMI ($r = 0.60$), ADG ($r = 0.29$), and FCR ($r = 0.43$); an association with RFI or $RFI_c$ was not observed (Table 4).

Change in muscle deposition was positively associated ($P < 0.05$) with ADG ($r = 0.33$), negatively associated with FCR ($r = −0.23$), and tended to be associated
with RFI (r = 0.20; P = 0.06). However, there was no association between RFI, and muscle deposition (r = 0.15; P = 0.52). High-RFI heifers had a 38% greater (P < 0.05) lumbar fat thickness and 59% greater lumbar fat gain (P < 0.05) compared with low-RFI heifers (Table 3). Furthermore, rump fat accretion tended (P = 0.09) to be greater in high-RFI heifers compared with values for the low and medium groupings. Generally, positive (P < 0.05) correlations (ranging from r = 0.27 to r = 0.63) between absolute fat depths and estimated fat gains with DMI, RFI, and FCR were observed, but an association with ADG and RFIc was not detected (Table 5).

There was no difference (P > 0.10) between RFI groupings in body measurements (Table 3), although moderate/strong positive associations (P < 0.01) existed between the end-of-test body measurements and DMI and FCR (Table 4). Positive correlations were also observed between ADG and estimated gain in both chest depth (r = 0.22) and girth (r = 0.36). From the linear scores assessed, loin development was greater (P < 0.05) in high-RFI than low-RFI heifers. There was a positive association (P < 0.05) between RFI (r = 0.24) and RFIc (r = 0.22) with the muscular score for loin development. The remaining muscular traits scored were uncorrelated (P > 0.10) to RFI. Relationships between DMI, ADG, and FCR with the various skeletal traits scored were generally positive (P < 0.05), but no such relationships with RFI existed. Moderate positive correlation coefficients (P < 0.05) were generally observed between the muscular trait scores and DMI and FCR, but not ADG (Table 4).

**Blood Hormones and Metabolites**

Metabolic hormone and metabolite data for animals with low, medium, or high RFI are presented in Table 5. Correlation coefficients between performance, feed efficiency traits, and metabolic hormones over the test period are presented in Table 6. Concentrations of all analytes increased (P < 0.001) with time over the experimental period. There was an RFI phenotype × day of test interaction (P < 0.001) for IGF-I (Figure 1), whereby concentrations were greater for the high- than the low-RFI group on the final sampling day but did not differ between groups before this time. A positive but weak association was observed between IGF-I and ADG (r = 0.26; P < 0.05), but associations with DMI, FCR, RFI, and RFIc were not detected (P > 0.10). Grouping by RFI did not affect (P > 0.40) the plasma concentrations of leptin, insulin, glucose, or urea, nor did it affect the ratio between plasma glucose and insulin (glucose:insulin). Correlation analysis indicated moderate positive associations (P < 0.001) between leptin concentrations and DMI (r = 0.43) and FCR (r = 0.48), but not (P > 0.10) ADG, RFI, or RFIc. Correlations between insulin and intake, performance, and the feed efficiency traits measured were not different from zero (P > 0.10). Circulating glucose was not associated (P > 0.10) with DMI, ADG, FCR, RFI, or RFIc. Weak positive correlations (P < 0.001) existed between glucose:insulin and FCR (r = −0.23; P < 0.05) and DMI (r = −0.21; P = 0.08), but not (P > 0.10) ADG, FCR, RFI, or RFIc. Over the test period, urea was positively correlated (P < 0.01) with DMI (r = 0.46) and FCR (r = 0.42), but not with ADG, RFI, or RFIc. An effect (P < 0.05) of RFI phenotype was detected for circulating NEFA concentrations, with increased concentrations observed in the low-RFI grouping compared with their high counterparts. Accordingly, NEFA demonstrated negative phenotypic associations with DMI (r = −0.31; P < 0.01), FCR (r = −0.32; P < 0.01), and RFI (r = −0.21; P = 0.07), but not with ADG or RFIc. The plasma concentrations of BHB were greater (P < 0.001) in high-RFI than low-RFI heifers. Positive correlations were detected between BHB with DMI (r = 0.34; P < 0.01), FCR (r = 0.25; P < 0.05), RFI (r = 0.37; P < 0.001), and RFIc (r = 0.31; P < 0.01).

**Table 2. Characterization of intake, performance, and energetic efficiency traits in growing beef heifers with high, medium, and low residual feed intake (RFI)**

<table>
<thead>
<tr>
<th>Trait</th>
<th>RFI group†</th>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of animals</td>
<td>High</td>
<td>Medium</td>
<td>Low</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual feed intake, kg/d</td>
<td>23</td>
<td>42</td>
<td>21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed conversion ratio, kg of DM/kg of BW gain</td>
<td>0.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.00&lt;sup&gt;b&lt;/sup&gt;</td>
<td>−0.63&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.05&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>DMI, kg/d</td>
<td>4.86&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.61&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.04&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.10&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>ME intake, kcal/(kg&lt;sup&gt;0.75&lt;/sup&gt;·d)</td>
<td>7.34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.75&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.17&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.17&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>0.26</td>
<td>0.25</td>
<td>0.26</td>
<td>0.04&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>0.36</td>
</tr>
<tr>
<td>Kleiber ratio</td>
<td>0.02</td>
<td>0.02</td>
<td>0.02</td>
<td>0.00&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>0.15</td>
</tr>
<tr>
<td>Metabolic BW, kg&lt;sup&gt;0.75&lt;/sup&gt;</td>
<td>63.47</td>
<td>63.53</td>
<td>62.84</td>
<td>1.24&lt;sup&gt;SE&lt;/sup&gt;</td>
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<td>ADG, kg/d</td>
<td>1.52</td>
<td>1.49</td>
<td>1.54</td>
<td>0.03&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>0.41</td>
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<tr>
<td>Initial BW, kg</td>
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<td>197</td>
<td>192</td>
<td>6.44&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>0.81</td>
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<tr>
<td>Final BW, kg</td>
<td>314</td>
<td>313</td>
<td>312</td>
<td>7.01&lt;sup&gt;SE&lt;/sup&gt;</td>
<td>0.97</td>
</tr>
</tbody>
</table>

*†Least squares means within a row with different superscripts differ (P < 0.05).*  
†High = RFI was >0.5 SD above the mean; medium = RFI was ±0.5 SD above and below the mean; low = RFI was <−0.5 SD below the mean.  
<sup>SE</sup> = pooled SE.
Feeding Behavior

There was an RFI phenotype × day of test interaction \((P < 0.01)\) for the average quantity of food consumed per minute on a daily basis (eating rate; Figure 2); eating rate was generally greatest for high-RFI, intermediate for medium-RFI, and least for low-RFI animals, with the exception of the last 20 d of the experimental period, during which eating rate was not different between RFI phenotypes. There was an effect of time on trial on eating rate, with the rate increasing as time on trial progressed. Eating rate was positively associated with DMI \((r = 0.56; \ P < 0.001)\), FCR \((r = 0.54; \ P < 0.001)\), RFI \((r = 0.26; \ P < 0.05)\), and RFI \((r = 0.22; \ P < 0.05)\), but not with ADG \((P > 0.10; \ Table \ 7)\). Significant effects were observed for RFI, day of test, and RFI phenotype × day of test \((P < 0.01)\) for the number of feed events per day. High-RFI animals \([68.1 \text{ events/d (SE = 3.01)}\] consistently had more feeding events per day during the experimental period compared with medium-ranked \([55.6 \text{ events/d (SE = 3.06)}\] and low-ranked \([53.4 \text{ events/d (SE = 2.90)}\] animals (Figure 2). Correlation analysis indicated weak to moderate positive relationships between daily feed events and DMI \((r = 0.24; \ P < 0.05)\), RFI \((r = 0.45; \ P < 0.001)\), and RFI \((r = 0.39; \ P < 0.01)\), although relationships with ADG and FCR were not detected \((P > 0.10)\). There was an effect of day of test \((P < 0.01)\) on the number of daily nonfeeding events, with overall frequency of nonfeeding events decreasing with time on trial. There was no effect of RFI phenotype or RFI phenotype × day of test (Figure 2) on the occurrence of nonfeeding events. Nonfeeding events (Table 7) were positively correlated with both RFI \((r = 0.23; \ P < 0.05)\) and RFI \((r = 0.18; \ P < 0.05)\), but were negatively correlated with DMI \((r = -0.30; \ P < 0.001)\). Daily feeding duration did not differ \((P = 0.84)\) between animals ranked as high \([116.9 \text{ min/d (SE = 4.52)}\], medium \([114.2 \text{ min/d (SE = 4.74)}\], or low \([116.2 \text{ min/d (SE = 4.94)}\] RFI. Correspondingly, correlations coefficients between feeding duration and intake or the feed efficiency traits measured were not different from zero \((P > 0.10; \ Table \ 7)\).
Inclusion of daily feeding events in the carcass-adjusted regression model used to compute RFI accounted for the largest additional variation (0.80 vs. 0.84; \( P < 0.05 \)) in DMI beyond ADG, MBW, and gain in lumbar fat. Docility score was unaffected (\( P = 0.47 \)) by phenotypic ranking on RFI, and correlations between docility score

Table 4. Correlations of intake, performance, and feed efficiency traits with ultrasound, linear measurement, and body composition scores across all animals

<table>
<thead>
<tr>
<th>Trait</th>
<th>DMI</th>
<th>ADG</th>
<th>FCR¹</th>
<th>RFI²</th>
<th>RFIc³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ultrasound measurement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Final lumbar fat thickness, mm</td>
<td>0.57***</td>
<td>−0.07</td>
<td>0.63***</td>
<td>0.27*</td>
<td>0.00</td>
</tr>
<tr>
<td>Lumbar fat thickness, mm/d</td>
<td>0.48***</td>
<td>−0.06</td>
<td>0.53***</td>
<td>0.33**</td>
<td>0.00</td>
</tr>
<tr>
<td>Final rump fat thickness, mm</td>
<td>0.54**</td>
<td>0.02</td>
<td>0.54**</td>
<td>0.20*</td>
<td>0.10</td>
</tr>
<tr>
<td>Rump fat thickness, mm/d</td>
<td>0.40***</td>
<td>0.03</td>
<td>0.39***</td>
<td>0.27*</td>
<td>0.10</td>
</tr>
<tr>
<td>Final muscle depth thickness, mm</td>
<td>0.60**</td>
<td>0.29**</td>
<td>0.43***</td>
<td>0.11</td>
<td>0.08</td>
</tr>
<tr>
<td>Muscle depth thickness, mm/d</td>
<td>0.00</td>
<td>0.33***</td>
<td>−0.24*</td>
<td>0.20*</td>
<td>0.15</td>
</tr>
<tr>
<td>Linear measurement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Final height at withers, mm</td>
<td>0.57***</td>
<td>0.05</td>
<td>0.55***</td>
<td>−0.08</td>
<td>−0.08</td>
</tr>
<tr>
<td>Height at withers, mm/d</td>
<td>−0.01</td>
<td>−0.04</td>
<td>0.00</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>Final depth of chest, mm</td>
<td>0.68***</td>
<td>0.11</td>
<td>0.65***</td>
<td>−0.02</td>
<td>−0.02</td>
</tr>
<tr>
<td>Depth of chest, mm/d</td>
<td>−0.10</td>
<td>0.22*</td>
<td>−0.27*</td>
<td>0.14</td>
<td>0.11</td>
</tr>
<tr>
<td>Final pelvic width, mm</td>
<td>0.55***</td>
<td>0.07</td>
<td>0.54***</td>
<td>0.04</td>
<td>0.05</td>
</tr>
<tr>
<td>Pelvic width, mm/d</td>
<td>−0.05</td>
<td>0.09</td>
<td>−0.13</td>
<td>0.14</td>
<td>0.10</td>
</tr>
<tr>
<td>Final length of back, mm</td>
<td>0.62***</td>
<td>0.11</td>
<td>0.58***</td>
<td>−0.02</td>
<td>−0.01</td>
</tr>
<tr>
<td>Length of back, mm/d</td>
<td>−0.06</td>
<td>0.10</td>
<td>−0.14</td>
<td>0.07</td>
<td>0.11</td>
</tr>
<tr>
<td>Final chest girth, mm</td>
<td>0.79***</td>
<td>0.13</td>
<td>0.75***</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>Chest girth, mm/d</td>
<td>0.08</td>
<td>0.36***</td>
<td>−0.15</td>
<td>0.10</td>
<td>0.14</td>
</tr>
<tr>
<td>Skeletal score</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height of withers</td>
<td>0.68***</td>
<td>0.34**</td>
<td>0.51***</td>
<td>−0.05</td>
<td>−0.08</td>
</tr>
<tr>
<td>Length of back</td>
<td>0.61***</td>
<td>0.23*</td>
<td>0.52***</td>
<td>−0.09</td>
<td>−0.07</td>
</tr>
<tr>
<td>Width at hips</td>
<td>0.53***</td>
<td>0.17</td>
<td>0.49***</td>
<td>−0.14</td>
<td>−0.13</td>
</tr>
<tr>
<td>Muscular score</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width behind withers</td>
<td>0.55***</td>
<td>−0.12</td>
<td>0.65***</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>Loin development</td>
<td>0.53***</td>
<td>−0.05</td>
<td>0.58***</td>
<td>0.24*</td>
<td>0.22*</td>
</tr>
<tr>
<td>Development of hindquarter</td>
<td>0.18†</td>
<td>−0.09</td>
<td>0.24*</td>
<td>0.12</td>
<td>0.07</td>
</tr>
<tr>
<td>Thigh and hindquarter width</td>
<td>0.72***</td>
<td>0.21I</td>
<td>0.62***</td>
<td>0.15</td>
<td>0.08</td>
</tr>
</tbody>
</table>

1FCR = feed conversion ratio.
2RFI = base model residual feed intake.
3RFIc = RFI trait adjusted for carcass composition.

† \( P < 0.10 \); * \( P < 0.05 \); ** \( P < 0.01 \); *** \( P < 0.001 \).

Table 5. Characterization of metabolic hormones and metabolites in animals with high, medium, and low residual feed intake (RFI)¹

<table>
<thead>
<tr>
<th>Trait</th>
<th>RFI group²</th>
<th>Day</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High</td>
<td>Medium</td>
<td>Low</td>
</tr>
<tr>
<td>No. of animals</td>
<td>23</td>
<td>42</td>
<td>21</td>
</tr>
<tr>
<td>BHB,³ mmol/L</td>
<td>0.49a</td>
<td>0.46c</td>
<td>0.41b</td>
</tr>
<tr>
<td>Glucose, mmol/L</td>
<td>5.10</td>
<td>5.05</td>
<td>5.13</td>
</tr>
<tr>
<td>Urea, mmol/L</td>
<td>5.12</td>
<td>5.24</td>
<td>5.04</td>
</tr>
<tr>
<td>Leptin, ng/mL</td>
<td>2.66</td>
<td>2.43</td>
<td>2.39</td>
</tr>
<tr>
<td>IGF-I, ng/mL</td>
<td>288.7</td>
<td>283.3</td>
<td>277.8</td>
</tr>
<tr>
<td>Log, insulin</td>
<td>2.60</td>
<td>2.73</td>
<td>2.65</td>
</tr>
<tr>
<td>Insulin, µIU/mL</td>
<td>14.67</td>
<td>15.28</td>
<td>14.16</td>
</tr>
<tr>
<td>Log, glucose:insulin</td>
<td>−1.08</td>
<td>−1.11</td>
<td>−1.02</td>
</tr>
<tr>
<td>Glucose:insulin</td>
<td>0.34</td>
<td>0.33</td>
<td>0.36</td>
</tr>
<tr>
<td>Log, NEFA</td>
<td>−2.63a</td>
<td>−2.67a</td>
<td>−2.51b</td>
</tr>
<tr>
<td>NEFA, mmol/L</td>
<td>0.07</td>
<td>0.07</td>
<td>0.08</td>
</tr>
</tbody>
</table>

²Least squares means within a row with different superscripts differ (\( P < 0.05 \)).
³Back-transformed least squares means are presented where appropriate.
⁴High = RFI was >0.5 SD above the mean; medium = RFI was ±0.5 SD above and below the mean; low = RFI was −0.5 SD below the mean.
⁵SE = pooled SE.
⁶P × D = phenotype (high RFI; medium RFI; low RFI) × day (1 d; 30 d; 60 d; 82 d) interaction.
⁷BHB = β-hydroxybutyrate.
⁸NS = \( P > 0.05 \).
and DMI, ADG, FCR, RFI, and RFI_c were not different from zero.

**Multitrait Equation**

After stepwise multiple regression analysis, it was estimated that daily feeding events, overall trial period mean plasma BHB concentrations, and lumbar fat accretion explained 35% of the observed variation in RFI and that there was no advantage in including further variables in the regression model. Therefore, the best multitrait equation (with R^2 = 0.35), taking colinearity among variables into account, was found to be: RFI = −1.63 + (1.66 × BHB) + (0.01 × daily feeding events) + (6.32 × lumbar fat accretion).

**DISCUSSION**

Animals with poor feed efficiency have a greater environmental impact (Nkrumah et al., 2006) and a greater cost of production (Crews, 2005). In beef cattle production, feed accounts for up to 80% of the variable costs (Arthur et al., 2004) and of this up to 75% of total dietary energy consumed is used for maintenance energy requirements (nonproductive purposes). By definition, therefore, increased feed efficiency, without increased maintenance energy costs, reduces the excretion of nutrients to the environment; thus, it is an economically relevant trait to consider when developing genetic selection programs.

In the current study, the base RFI regression model (DMI explained by MBW and ADG) accounted for 77% of the variation in DMI, similar to other published reports (Arthur et al., 2001a,b; Basarab et al., 2003; Nkrumah et al., 2007a). By design, phenotypic correlations between RFI and ADG and body size were unsurprisingly near to zero. Residual feed intake has been found to be genetically independent of growth and body size in growing bulls (Arthur et al., 2001a,b) and steers (Nkrumah et al., 2004), although some studies have re-

**Table 6.** Correlations of intake, performance, and feed efficiency traits with metabolic hormones and metabolites across all animals

<table>
<thead>
<tr>
<th>Trait</th>
<th>DMI</th>
<th>ADG</th>
<th>FCR^1</th>
<th>RFI^2</th>
<th>RFI^3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insulin</td>
<td>0.13</td>
<td>−0.01</td>
<td>0.12</td>
<td>0.07</td>
<td>0.06</td>
</tr>
<tr>
<td>IGF-I</td>
<td>0.14</td>
<td>0.26*</td>
<td>−0.03</td>
<td>0.06</td>
<td>0.05</td>
</tr>
<tr>
<td>Leptin</td>
<td>0.43***</td>
<td>−0.02</td>
<td>0.48***</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>Glucose</td>
<td>−0.07</td>
<td>0.17</td>
<td>−0.19</td>
<td>−0.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Glucose:insulin</td>
<td>−0.21</td>
<td>0.03</td>
<td>−0.23*</td>
<td>−0.10</td>
<td>−0.09</td>
</tr>
<tr>
<td>Urea</td>
<td>0.46***</td>
<td>0.13</td>
<td>0.42***</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>NEFA</td>
<td>−0.31**</td>
<td>0.00</td>
<td>−0.32**</td>
<td>−0.21*</td>
<td>−0.18</td>
</tr>
<tr>
<td>BHB</td>
<td>0.34**</td>
<td>0.14</td>
<td>0.25*</td>
<td>0.37***</td>
<td>0.31**</td>
</tr>
</tbody>
</table>

^1FCR = feed conversion ratio.
^2RFI = base model residual feed intake.
^3RFI = RFI trait adjusted for carcass composition.
^4BHB = β-hydroxybutyrate.

†P < 0.10; *P < 0.05; **P < 0.01; ***P < 0.001.

**Figure 1.** Plasma concentrations of IGF-I (ng/mL) of heifers with high, medium, and low residual feed intake (RFI) measured on d 1, 30, 60, and 82 of the experimental period (*P < 0.01). High RFI = RFI was >0.5 SD above the mean; medium RFI = RFI was ±0.5 SD above and below the mean; low RFI = RFI was <−0.5 SD below the mean.
ported weak genetic correlations between RFI and BW (Herd and Bishop, 2000; Schenkel et al., 2004). The range in performance and feed efficiency data recorded in the present experiment is similar to those of previous international studies (Arthur et al., 1999; Archer and Bergh, 2000; Liu et al., 2000). In agreement with our findings, Arthur et al. (2001a,b), Hoque et al. (2005), and Nkrumah et al. (2007a), using diverse breeds of cattle, reported positive phenotypic correlations ranging from 0.60 to 0.72 between RFI and DMI, indicating that selection for more favorable RFI phenotypes should result in significant reductions in feed intake. Residual feed intake was moderately correlated (r = 0.46) with FCR, concurring with the data of Lancaster et al. (2009). However, stronger associations have been reported in growing bulls (r = 0.53) and steers (r = 0.62; Arthur et al., 2001b; Nkrumah et al., 2004). Our DMI and FCR data for heifers are consistent with the

Table 7. Correlations of intake, performance, and feed efficiency traits with feeding behavior or activities across all animals

<table>
<thead>
<tr>
<th>Trait</th>
<th>DMI</th>
<th>ADG</th>
<th>FCR</th>
<th>RFI</th>
<th>RFIc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding duration</td>
<td>0.08</td>
<td>0.19</td>
<td>0.03</td>
<td>0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>Eating rate</td>
<td>0.56</td>
<td>0.09</td>
<td>0.54</td>
<td>0.26</td>
<td>0.22</td>
</tr>
<tr>
<td>Feeding events</td>
<td>0.24</td>
<td>0.16</td>
<td>0.14</td>
<td>0.45</td>
<td>0.39</td>
</tr>
<tr>
<td>Nonfeeding events</td>
<td>-0.30</td>
<td>-0.03</td>
<td>-0.15</td>
<td>0.23</td>
<td>0.18</td>
</tr>
<tr>
<td>Docility</td>
<td>0.07</td>
<td>0.17</td>
<td>0.01</td>
<td>0.00</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

1FCR = feed conversion ratio.
2RFI = Base model residual feed intake.
3RFIc = RFI trait adjusted for carcass composition.
†P < 0.10; *P < 0.05; ***P < 0.001.

Figure 2. Least squares means of daily DMI (pooled SE = 0.17), eating rate (pooled SE = 0.003), nonfeeding events per day (pooled SE = 1.22), and feed events per day (pooled SE = 2.83) for high, medium, and low residual feed intake (RFI) heifers (**P < 0.01). High RFI = RFI was >0.5 SD above the mean; medium RFI = RFI was ±0.5 SD above and below the mean; low RFI = RFI was <−0.5 SD below the mean.
findings of Nkrumah et al. (2004), who indicated that steers of high RFI fed a concentrate-based diet consumed 15% more feed and had a 17% greater FCR compared with low-RFI steers despite the lack of difference in BW and growth. Recent studies have reported negative phenotypic and genetic correlations for FCR and ADG (Arthur et al., 2001a,b; Schenkel et al., 2004). Those findings are consistent with the results of the present study and indicate that applying selection pressure for FCR would likely result in increased growth rates and mature size, leading to greater maintenance energy costs and thus an increased feed requirement, particularly in the breeding herd (Arthur et al., 2004). Interestingly, the lack of a relationship between RFI and initial age and BW herein indicates that RFI may be unaffected by variation in the pretest environment and is a much more robust index compared with other measures of efficiency, concuring with the results of Nkrumah et al. (2004) and Lancaster et al. (2009).

Reports on the relationship between RFI and carcass characteristics have been contentious. Numerous studies have observed weak positive phenotypic and genetic correlations between RFI and measures of body fat content (Richardson et al., 2001; Basarab et al., 2003; Schenkel et al., 2004). In agreement, Herd and Bishop (2000) reported negative phenotypic (r = −0.22) and genetic (r = −0.43) associations between RFI and carcass lean content. In the current study, the provision of a high-energy diet should have allowed any genetic differences, for age, in fat accretion potential to be expressed. The correlation coefficients between feed efficiency traits and ultrasonically measured fatness generally agree with published estimates, with low-RFI animals having less backfat compared with their greater ranking counterparts. Although potentially beneficial from a feed energy utilization viewpoint, appreciable reductions in body fat depot could be a counterproductive approach for both carcass quality in terminal animals (Nkrumah et al., 2004) and fertility of the breeding herd (Dakin and Morris, 2008). Encouragingly, however, results from divergent selection studies for postweaning RFI to date have shown no compromise in meeting market specifications for feedlot steers (Richardson et al., 1998) and no reduction in subcutaneous fat depths in beef cows (Arthur et al., 1999). Refining RFI by adjusting for carcass traits should be considered (Basarab et al., 2003). Results from stepwise regression analysis in our study indicate that of the body composition variables assessed, gain in lumbar backfat accounted for the largest additional variation (3 percentage units in the coefficient of determination) in predicted DMI beyond ADG and MBW. The Pearson phenotypic correlation between the base model (RFI) and RFI adjusted for lumbar backfat gain (RFL) was strong (r = 0.93), implying that they are more or less the same trait. Similar rank correlation coefficients (r = 0.87 to 0.92) have been reported in growing bulls (Lancaster et al., 2009) and growing steers (Basarab et al., 2003).

Differences between RFI groupings were not observed in either LM depth or growth in steers, bulls, or heifers (Arthur et al., 2001a; Basarab et al., 2003; Nkrumah et al., 2004), as in the present study. We did, however, observe a trend toward a positive association between RFI and muscle deposition in the uncorrected base RFI model, but not the body composition-corrected model. Weak positive phenotypic and genetic correlations between RFI and change in ribeye area have also been detected previously (Crews et al., 2003; Lancaster et al., 2009). Relationships detected here between ADG and DMI with ultrasound muscle depth and fat thickness are similar to those in other studies with steers (Nkrumah et al., 2004) and bulls (Schenkel et al., 2004), indicating that faster growing cattle would consume more feed and have greater muscle development and greater fat accretion at the end of the performance test period.

Body dimensions or linear measurements are used to supplement BW as a measure of productivity (Gilbert et al., 1993) or as easily measured indicators of growth rate and BW (Drennan et al., 2008). Generally, the phenotypic correlations in the present study showed that ranking on the basis of RFI had little or no bearing on either the linear measurements or the descriptive physical scores examined. Only the loin development scores were slightly less for the low- compared with high-RFI phenotypes, quite possibly because of the moderate significant association (r = 0.52) of this trait with final ultrasonic lumbar fat.

Systemic concentrations of metabolic hormones and metabolites, mediators of nutrient uptake as well as inhibitors of tissue catabolism, have been examined with a view to identifying potential physiological biomarkers for feed efficiency in cattle (Richardson et al., 2004; Wood et al., 2004; Nkrumah et al., 2007b). Insulin-like growth factor-I, a known mitogen for cell proliferation, was determined to be genetically (Moore et al., 2005) and phenotypically (Brown et al., 2004) correlated in a positive manner with RFI in growing bulls and heifers. However, a relationship between overall plasma IGF-I concentration with FCR and RFI was not evident in the present study. The likely explanation for this inconsistency is that, in most studies to date in which IGF-I was correlated with RFI, the animals were measured at a young age shortly after weaning (Moore et al., 2005), animals were consuming a roughage-based diet (Brown, 2005), and consequently, animals might be expected to have a greater rate of lean tissue gain and reduced carcass fatness. Despite this, we did detect a phenotype × day of test interaction on the final sampling day, with greater IGF-I concentrations detected in the high-RFI grouping. Furthermore, the end-of-test IGF-I concentrations were positively correlated with RFI (r = 0.27) and RFI, (r = 0.24), indicating that more efficient cattle would have less plasma IGF-I. However, it could be argued that interpretation of endocrine variables based on a single within-day (blood) sample might be...
misleading (Richardson et al., 2002) because systemic concentrations of these metabolite variables are more under environmental (i.e., diet, energy status, stressful sampling procedure) than under genetic control. Recently, Johnston et al. (2007) reported that as cattle became more physiologically mature, the genetic relationship between plasma IGF-I concentration and RFI became less positive, indicating that the many genes responsible for systemic IGF-I concentration differed between the postweaning and finishing stages of development. Therefore, IGF-I may not be as informative as a predictor of RFI as originally thought.

Leptin functions as a regulator of BW, feed intake, energy expenditure (Houseknecht et al., 1998), reproduction (Garcia et al., 2002), and immunocompetence (Lord et al., 1998). Its concentration in plasma is related to the extent of body lipid depots (Ji et al., 1997; Chillard et al., 1998; Minton et al., 1998), which is consistent with our findings (data not presented). The magnitude of the relationships between circulating leptin and DMI, ADG, and FCR in the current study is similar to the findings of Richardson et al. (2004). However, in contrast, these authors also observed a significant phenotypic correlation ($r = 0.31$) between serum leptin and RFI. Alternatively, Brown et al. (2004) reported that systemic leptin concentrations were unrelated to intake, performance, and feed efficiency traits. Furthermore, SNP in the promoter region of the bovine leptin gene have been shown to be associated with body fatness, growth rate, and feed intake, but not with measures of feed efficiency (Nkrumah et al., 2005).

Previous studies (Richardson et al., 2004; Brown, 2005) have reported greater systemic insulin concentrations in high-RFI steers at the end of a feedlot test, which have been attributed to a decrease in leanness resulting from increased fat deposition because insulin can reduce lipolysis and stimulate lipogenesis in adipose tissue. However, in contrast, the present results indicate that plasma insulin concentrations were unrelated to intake, performance, or feed efficiency traits.

Blood metabolites could be useful to the overall metabolic characterization of animals divergent in feed efficiency. In agreement with the findings of the present study, Richardson et al. (2004) reported that glucose concentrations measured at weaning were not correlated with performance or feed efficiency traits. The glucose:insulin, an indicator of glucose metabolism, was unaffected by RFI ranking, consistent with the report of Kolath et al. (2006). However, glucose:insulin was negatively correlated with FCR and tended to be correlated with DMI. Based on these results, more efficient cattle, as measured by FCR, may have an altered glucose metabolism, providing further evidence that FCR and RFI are different traits.

We did not observe any effect of RFI phenotype on systemic urea concentration. Despite this, previous reports in cattle (Richardson et al., 1996, 2004) have found greater blood concentrations of urea in less efficient genotypes. This may be credited to a greater protein intake in high-RFI animals, a greater rate of body protein degradation, or deviation in the supply of AA due in part to variation in the efficiency of microbial protein production in the rumen (Lush et al., 1991; Kahn, 2000). Additionally, the moderate positive correlation between blood urea, FCR, and DMI is probably consistent with the positive association between urea and dietary nitrogen intake (Walsh et al., 2008; Clarke et al., 2009).

Nonesterified fatty acid concentration, a product of body fat mobilization, was greater in the low-RFI group, and negative correlations were detected with DMI, FCR, and RFI. This supports the conclusion of Richardson et al. (2004) that high-RFI steers had 27% less plasma triglyceride concentrations than low-RFI steers. These authors attributed this finding to a greater fat content in high-RFI animals together with a greater energy requirement by muscle due to greater protein turnover rate.

There are few reports in the literature on the relationship between RFI phenotype and systemic concentrations of BHB. Richardson et al. (2004) reported a positive phenotypic ($r = 0.55$) correlation at weaning between RFI and BHB. Consistent with these findings, the present study reported positive relationships for BHB with DMI ($r = 0.34$), FCR ($r = 0.25$), RFI ($r = 0.37$), and RFIc ($r = 0.31$). A likely explanation for these relationships is the difference between RFI groupings with respect to DMI. Overall, the presence of significant effects on blood metabolite concentrations was not unanticipated because feed intake, diet composition, and physical activity, rather than genotype of the animal, are the main determinants of blood metabolite concentration (Beeby et al., 1988; Spicer et al., 1990). Moreover, the interactions between homeostatic control mechanisms within the animal and factors governing rumen function contribute to the complexity of interpreting metabolic profiles, leaving cause-and-effect relationships difficult to elucidate (Kelly, 1997).

Differences in feeding behavior and activity (eating time, eating rate, eating frequency) may also contribute to variation in energetic efficiency between animals. Reports on nonruminant species such as pigs (de Haer et al., 1993) and poultry (Luiting et al., 1991) reveal that physical activity contributes to a substantial proportion of the variation in RFI. Indeed, recent work in cattle from the United States (Lancaster et al., 2005; Golden et al., 2008) and Canada (Nkrumah et al., 2006, 2007a), as well as the present study, show a distinct difference in diurnal feeding behavior, with energetically efficient animals typically engaging in 22% fewer daily feeding events compared with their inefficient counterparts. Furthermore, positive relationships were observed between RFI and daily feeding events ($r = 0.45$), nonfeeding events ($r = 0.23$), and daily eating rate ($r = 0.26$). Concurring, Robinson and Oddy (2004) reported positive genetic and phenotypic correlations between RFI and daily feeding duration, eating sessions per day, and rate of eating (g/min). Collectively, these results
indicate an increase in feeding-associated activities for the inefficient phenotype; thus, low-RFI animals may spend more time being sedentary, thereby utilizing less energy for activity. The inclusion of daily feeding events into the RFI model accounted for the explanation of an additional 20% of the variation in DMI. Correspondingly, in pigs (de Haer et al., 1993) and cattle (Lancaster et al., 2009), it has been documented that feed-related activities accounted for 44 and 35%, respectively, of the variation in daily feed intake not explained by MBW, ADG, and ultrasound traits. In a recent review, Herd and Arthur (2009) documented that differences in energy expenditure associated with physical activity and feeding pattern accounted for 10 and 2%, respectively, of the variation in energetic efficiency. Residual feed intake appears to be a trait that reflects inherent interanimal variation in biologically relevant processes related to feed efficiency. Further research is required to enhance our understanding of the underlying genetic and physiological mechanisms affecting feed intake and related traits.

The multitrait RFI regression analysis identified the relative importance of factors related to feeding activity (daily feeding events), body composition (lumbar fat accretion, BHB), and tissue anabolism (lumbar fat accretion, BHB) in the explanation of interanimal variation in RFI. The best multivariate model explained 0.35 of the observed variation in RFI, of which 0.22 was attributed to daily feeding events, 0.07 to circulating BHB concentration, and 0.05 to lumbar fat accretion. The remaining two-thirds of the variation is likely to be associated with other physiological processes such as protein turnover, ion pumping, proton leakage, thermoregulation, and stress responses (Richardson and Herd, 2004). In fact, it has been proposed that protein turnover, ion pumping, and proton leakage can account for approximately 60 to 70% of the total energy requirements for maintenance, which, in essence, symbolizes the energetic inefficiency of an animal (Bottje and Carstens, 2009).

The results from this study confirmed that significant differences in performance and feed efficiency measures exist in growing beef heifers. The data also indicated that RFI has the potential to allow producers to select for more efficient cattle that eat less than expected for their given level of production. Overall, the multifactorial approach taken enhanced our understanding and tested the potential for some more easily measured predictors of RFI to be used in future work. For example, feeding behavior traits symptomatic of activity level and appetite, carcass composition measures, and systemic concentrations of blood metabolites, mediators of nutrient uptake as well as inhibitors of tissue catabolism, have been shown to contribute to variation in RFI and merit additional study. However, future research is warranted to unravel the remaining unexplained variation in energetic efficiency to provide more cost-effective methodologies for wide-scale identification of animals with superior genetic merit for RFI earlier in life.

LITERATURE CITED


Richardson, E. C., R. M. Herd, P. F. Arthur, J. Wright, G. Xu, K. Dibley, and V. H. Oddly. 1996. Possible physiological indicators...


