JOURNAL OF ANIMAL SCIENCE
The Premier Journal and Leading Source of New Knowledge and Perspective in Animal Science

**Use of residual feed intake in Holsteins during early lactation shows potential to improve feed efficiency through genetic selection**

E. E. Connor, J. L. Hutchison, H. D. Norman, K. M. Olson, C. P. Van Tassell, J. M. Leith and R. L. Baldwin VI

*J ANIM SCI* 2013, 91:3978-3988.
doi: 10.2527/jas.2012-5977 originally published online May 8, 2013

# Use of residual feed intake in Holsteins during early lactation shows potential to improve feed efficiency through genetic selection[1]

E. E. Connor,*[2] J. L. Hutchison,† H. D. Norman,† K. M. Olson,‡[3]
C. P. Van Tassell,* J. M. Leith,§ and R. L. Baldwin VI*

*Bovine Functional Genomics Laboratory, and †Animal Improvement Programs Laboratory, Agricultural Research Service, USDA, Beltsville, MD 20705; ‡National Association of Animal Breeders, Columbia, MO 65205; and §Research Support Services, Agricultural Research Service, USDA, Beltsville, MD 20705.

**ABSTRACT:** Improved feed efficiency is a primary goal in dairy production to reduce feed costs and negative impacts of production on the environment. Estimates for efficiency of feed conversion to milk production based on residual feed intake (RFI) in dairy cattle are limited, primarily due to a lack of individual feed intake measurements for lactating cows. Feed intake was measured in Holstein cows during the first 90 d of lactation to estimate the heritability and repeatability of RFI, minimum test duration for evaluating RFI in early lactation, and its association with other production traits. Data were obtained from 453 lactations (214 heifers and 239 multiparous cows) from 292 individual cows from September 2007 to December 2011. Cows were housed in a free-stall barn and monitored for individual daily feed consumption using the GrowSafe 4000 System (GrowSafe Systems, Ltd., Airdrie, AB, Canada). Animals were fed a total mixed ration 3 times daily, milked twice daily, and weighed every 10 to 14 d. Milk yield was measured at each milking. Feed DM percentage was measured daily, and nutrient composition was analyzed from a weekly composite. Milk composition was analyzed weekly, alternating between morning and evening milking periods. Estimates of RFI were determined as the difference between actual energy intake and predicted intake based on a linear model with fixed effects of parity (1, 2, $\geq$ 3) and regressions on metabolic BW, ADG, and energy-corrected milk yield. Heritability was estimated to be moderate (0.36 ± 0.06), and repeatability was estimated at 0.56 across lactations. A test period through 53 d in milk (DIM) explained 81% of the variation provided by a test through 90 DIM. Multiple regression analysis indicated that high efficiency was associated with less time feeding per day and slower feeding rate, which may contribute to differences in RFI among cows. The heritability and repeatability of RFI suggest an opportunity to improve feed efficiency through genetic selection, which could reduce feed costs, manure output, and greenhouse gas emissions associated with dairy production.

**Key words:** dairy cow, feed efficiency, genetic selection, residual feed intake



J. Anim. Sci. 2013.91:3978–3988
doi:10.2527/jas2012-5977

## INTRODUCTION

Rising feed costs and concerns about greenhouse gas emissions and nutrient losses to the environment associated with animal production necessitate identifying the most efficient dairy cattle for milk production. Models from Koch et al. (1963) have been used to calculate the difference between actual feed intake and predicted feed intake for a given level of milk production, BW gain, and maintenance, known as residual feed intake (**RFI**). The trait is defined such that it is not phenotypically correlated with body size, ADG, or milk yield (Van Arendonk et al., 1991) and should be an indication

[1]The authors acknowledge the excellent technical support of Mary Bowman, Marsha Campbell, Dennis Hucht, Mary Niland, Donald Carbaugh, Mike Kemp, Research Support Services staff at the USDA-ARS (Beltsville, MD), Kevin Garossino, Neil Tarrant, and Camiel Huisma who contributed to this project. Thanks also to Dr. Stanislaw Kahl (USDA-ARS, Beltsville, MD) for assistance with statistical analyses. Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture (USDA). The USDA is an equal opportunity provider and employer.

[2]Corresponding author: erin.connor@ars.usda.gov

[3]Current address: ABS Global, Inc., 1525 River Rd., DeForest, WI 53532

Received October 11, 2012.
Accepted April 12, 2013.

of metabolism-related differences among animals rather than differences in production (Crews, 2005).

Research in beef cattle suggests that selection for reduced RFI should reduce animal feed intake by 10 to 12%, greenhouse gas emissions by 25 to 30%, and nutrient losses in manure by 15 to 17% without significant negative impacts on other production traits (Alberta Agriculture, Food and Rural Development, 2006). Factors contributing to differences in RFI among cattle are not well understood but may include differences in feeding behavior and physical activity (Nkrumah et al., 2007; Golden et al., 2008). Reported heritability estimates for RFI in growing beef cattle range from 0.26 to 0.43 (Crews, 2005), although reported estimates for RFI in lactating dairy cattle range from 0.01 to 0.38 (Korver et al., 1991; Van Arendonk et al., 1991; Ngwerume and Mao, 1992; Veerkamp et al., 1995; Vallimont et al., 2011).

Few studies have estimated RFI in lactating dairy cattle, primarily due to a lack of availability of individual feed intake measurements. Our objective was to use the radio-frequency identification-based GrowSafe 4000 System to measure feed intake in Holstein cows during the first 90 d of lactation (**DIM**) to characterize the RFI trait, including heritability, repeatability, and relationship with production and feeding and physical behavior traits. Minimum test duration for RFI measurement also was investigated.

## MATERIALS AND METHODS

All aspects of the study involving the use of animals were approved by the Beltsville Area Animal Care and Use Committee protocol number 10–013.

### *Animals*

Measures of feed intake, animal activity, feeding behavior, BW, and milk production-related traits [yield, composition, and somatic cell count (**SCC**)] were obtained from 453 lactations (214 first-lactation heifers; 131 second-lactation cows; and 108 cows in their third or greater lactation) from September 2007 to December 2011. The total number of unique animals represented in the complete dataset was 292. Five cows lacked pedigree information; thus, 287 cows were used in analyses requiring pedigree information. In this group of 287 cows, 81 sires were represented (with 1 to 22 daughters per bull, and 35 sires represented by a single offspring). A total of 93 maternal grandsires (**MGS**) were represented with 1 to 19 granddaughters represented. Ten cows had unidentified MGS. The pedigree was traced back in the national dairy cattle genetic evaluation database until it terminated with unknown ancestors (G. R. Wiggans, Animal Improvement Programs Laboratory, Agricultural Research Service, USDA, Beltsville, MD, personal communication). The comprehensive pedigree included 9,304 animals with the oldest born in 1930. A total of 161 cows were evaluated in a single lactation, and 96, 28, and 2 cows were evaluated in 2, 3, and 4 consecutive lactations, respectively. Table 1 summarizes the characteristics of the 453 lactations represented in the study.

**Table 1.** Characteristics of Holstein dairy cattle evaluated for residual feed intake (RFI) in the first 90 d of lactation[1]

| Characteristic | Mean ± SD |
|---|---|
| First-lactation heifers (*n* = 214) | |
| Age at calving, yr | 2.0 ± 0.1 |
| BW,[2] kg | 544 ± 43 |
| ADG, kg/d | 0.35 ± 0.40 |
| DMI, kg/d | 19.6 ± 1.6 |
| ME intake, Mcal/d | 55.4 ± 4.6 |
| Energy-corrected milk yield,[3] kg/d | 37.8 ± 4.8 |
| Second-lactation cows (*n* = 131) | |
| Age at calving, yr | 3.3 ± 0.3 |
| BW, kg | 626 ± 49 |
| ADG, kg/d | 0.21 ± 0.41 |
| DMI, kg/d | 24.0 ± 2.6 |
| ME intake, Mcal/d | 67.5 ± 7.6 |
| Energy-corrected milk yield, kg/d | 47.3 ± 6.1 |
| Cows in third or greater lactation (*n* = 108)[4] | |
| Age at calving, yr | 5.3 ± 1.2 |
| BW, kg | 662 ± 53 |
| ADG, kg/d | 0.07 ± 0.50 |
| DMI, kg/d | 23.7 ± 2.8 |
| ME intake, Mcal/d | 66.9 ± 8.1 |
| Energy-corrected milk yield, kg/d | 49.4 ± 7.9 |

[1]Start of data collection averaged (± SD) 7 ± 3 days in milk (DIM) and number of observations within the first 90 DIM averaged (±SD) 79 ± 6 d.

[2]Predicted BW from regression BW = DIM + DIM$^2$ and Predicted BW = intercept + (est_DIM × DIM) + (est_DIM × DIM$^2$).

[3]Energy-corrected milk yield = (0.327 × kg milk) + (12.95 × kg milk fat) + (7.2 × kg milk protein).

[4]*n* = 64 cows in third lactation; *n* = 25 in fourth lactation; *n* = 10 in fifth lactation; *n* = 6 in sixth lactation; 2 in seventh lactation; and 1 in eighth lactation.

Individual daily feed intake and feeding behavior were measured and recorded using the GrowSafe 4000 System (GrowSafe Systems, Ltd., Airdrie, AB, Canada). A total of 33 feeding nodes were arranged in a single line along the center alley of the free-stall barn such that any animal on trial could access any feed bunk. Individual daily animal activity was captured by electronic pedometers (Westfalia-Surge, Inc., Naperville, IL). For each of the 453 lactations included in the study, the data had to meet these quality criteria to be included: a daily feed intake of at least 9 kg to exclude any partial days of intake measurement (e.g., due to an animal being temporarily moved out of the group for veterinary treatment), and feed intake recorded beginning by at least 22 DIM. If on any day intake was < 9 kg, the data for that day were omitted from the dataset. Feed intake data of the entire group were omitted for any day in which data quality was questionable due to errors in operation of the GrowSafe System (e.g., assigned feed disappearance < 93%), as identified by technicians at GrowSafe Systems, Ltd. Once these data points were omitted, a minimum of 57 d of feed intake records for each animal was available during the first 90 d for assessment of RFI.

For estimation of feeding behavior, a meal event was defined as an animal feeding period detected at a feed bunk (or multiple feed bunks if the animal fed from more than a single bunk during the feeding period) with no interruption lasting more than 300 s. If an animal was detected at a feed bunk but did not consume any feed during that time period, then the data during that time period were not included in the estimation of number of meal events, time spent feeding per day, meal duration, or feeding rate. On any given day, each animal had to consume at least 3 meals to be included for the day in the analysis of feeding behavior, as animals were offered fresh feed 3 times daily.

Animals were housed in a single free-stall barn (14.6 m × 25.6 m) in which the number of animals in the group pen averaged 39 and ranged from 28 to 52. As animals calved, they were moved into the feed intake evaluation group and other measurements were recorded until approximately 100 DIM. After 100 DIM, they were returned to the general lactation group within the production herd. Animals were milked twice daily at approximately 0730 and 1930 h.

Individual BW was determined every 10 to 14 d immediately after the morning milking. Predicted daily BW (**$BW_{pred}$**) was estimated for each lactation record by fitting a linear model of individual periodic BW using the equation:

$$BW_{pred} = b_0 + b_1 \times DIM + b_2 \times (DIM)^2,$$

where $b_0$ = intercept, and $b_1$, $b_2$ = coefficients for linear and quadratic effects of DIM, respectively.

Using the $BW_{pred}$ values, ADG was calculated by subtracting $BW_{pred}$ on the first day of available feed intake data from $BW_{pred}$ on the last day of available feed intake data and dividing by the number of days in the test period.

### *Diet and Feed Analysis*

A single total mixed ration (**TMR**) targeting approximately 50% DM was mixed twice daily and fed to all animals 3 times per day at approximately 0700, 1400, and 1730 h. The second daily mix was divided and fed at the mid-day and evening feedings. The diet consisted of 51.7% corn silage, 26.0% grain mix (primarily ground corn and soybean), 10.9% haylage, 2.2% alfalfa hay, 1.9% wheat straw, 1.6% orchard grass hay, 1.2% whole cottonseed, 3.5% sugar blend, and 1.0% citrus pulp on an as-fed basis. A representative grab sample of each TMR mix was collected daily into a 7.6-L bucket and the samples from each daily mix were combined and mixed thoroughly. Duplicate 250-g samples of the TMR were used for daily DM determination and a second 500-g sample was reserved daily to obtain a weekly composite sample of 500 g for nutrient analysis. Feed analysis of weekly composites ($n$ = 225) was provided by Cumberland Valley Analytical Services, Inc. (Hagerstown, MD). The diet fed during the study consisted of (mean ± SE) 50.0 ± 0.1% DM. The diet contained 16.7 ± 0.1% CP and 73.4 ± 0.1% TDN on a DM-basis. The diet contained 1.69, 1.74, and 1.12 Mcal/kg DM of $NE_L$, $NE_M$, and $NE_G$, respectively. Daily ME intake was calculated from weekly feed composite TDN values using the following equations from NRC (2001):

$$DE(Mcal/kg) = TDN\ (\%DM) \times 0.04409, \quad [1]$$

$$ME\ (Mcal/kg) = (DE \times 1.01) - 0.45, \text{ and} \quad [2]$$

$$\text{Energy intake (Mcal)} = ME \times DMI\ (kg). \quad [3]$$

### *Milk Analyses*

Milk yield was electronically recorded at each milking. Composite milk samplers were used during automated milking to obtain samples for analysis once per week, alternating morning and evening milking periods. Analysis of milk fat percentage, protein percentage, and SCC was performed by Dairy One (Hagerstown, MD). Predicted daily milk protein (**$protein_{pred}$**) and fat yield (**$fat_{pred}$**) were estimated for each animal and milking period (morning and evening) by fitting a linear model of individual periodic milk composition using this equation:

$$fat_{pred} \text{ or } protein_{pred}, kg = b_0 + MP + b_1 \times DIM + b_2 \times (DIM)^2,$$

where $b_0$ = intercept, and $b_1$, $b_2$ = coefficients for linear and quadratic effects of DIM, respectively; and MP = milking period defined as morning (1) or evening (2).

Higher-order terms were tested in the model but were negligible. Using the predicted daily milk component values, energy-corrected milk (**ECM**) yield was calculated from the sum of the morning and evening milking periods using the equation ECM yield = (0.327 × daily milk, kg) + (12.95 × $fat_{pred}$, kg) + (7.2 × $protein_{pred}$, kg) from Orth (1992).

### *Calculation of RFI during Lactation*

The GLM procedure (SAS Inst. Inc., Cary, NC) was used to predict average energy intake for each animal by fitting this regression model (adapted from Van Arendonk et al., 1991):

$$\text{Predicted Energy Intake} = b_0 + \text{Parity (1,2,3+)} + b_1 \times \text{metabolic BW} + b_2 \times \text{ADG} + b_3 \times \text{ECM yield} + \text{RFI},$$

where $b_0$ = intercept; Parity = animal parity (1 = first; 2 = second; 3+ = third or greater); $b_1$ = partial regression coefficient of intake on average metabolic BW [$(\text{BW}_{\text{pred}})^{0.75}$, kg]; $b_2$ = partial regression coefficient of intake on ADG (kg/d); and $b_3$ = partial regression coefficient of intake on ECM yield (kg/d).

The RFI (Mcal ME/d) for each animal was then calculated as the difference between actual and predicted average energy intakes during the trial.

### *Estimating Heritability and Repeatability of RFI*

Heritability of RFI was estimated based on a total of 287 individual animals after removal of unregistered animals or those without a known sire from the dataset. The model included the fixed effects of age of cow at calving fit as a linear and quadratic covariate, parity, calving year, and included random effects of cow genetic effect, environmental effect of cow within lactation, and permanent environment of cow across lactations. Variance components were obtained by MTDFREML (Boldman et al., 1995; http://aipl.arsusda.gov/software/mtdfreml/). Heritability was estimated as cow genetic variance divided by the total variance (sum of genetic variance, permanent environmental variances, and residual variance). Repeatability of RFI across lactations was estimated using variance components from the prediction model and calculated as the sum of the genetic variance and the permanent environmental variance across lactation, divided by the total variance. Repeatability of RFI within lactation was calculated as the sum of the genetic variance and permanent environmental variances within and across lactations, divided by the total variance.

### *Determining Minimum Test Duration for Estimating RFI*

Estimates of RFI were calculated as described above using 7-d increments of data, starting with the 7-d period centered at 18 d and progressing through the interval centered at 95 d, with a total of 12 periods in all. Each period was analyzed as a cumulative average through all 12 periods, and the magnitude of variance for each period was plotted over time [similar to Archer et al. (1997) and Wang et al. (2006)], along with correlation coefficients between RFI for each cumulative shortened test period and total RFI during all 12 periods using the corr function in Matlab R2012a (Statistics Toolbox User's Guide, The MathWorks, Inc., Natick, MA; http://www.mathworks.com/help/pdf_doc/stats/stats.pdf). Because only genetic effect and residual variance were estimated in this particular analysis, only the first available lactation observations were included. In addition, correlation coefficients were calculated using the corr function in Matlab R2012a and plotted for the phenotypic correlation between RFI during each 7-d period and total RFI during all 12 periods for each animal using all available lactations. Determination of minimum test length was based on a combination of the time at which residual variance remained relatively small, and the correlation coefficient between RFI for the cumulative shortened test length and RFI through all 12 periods was large [>0.90; similar to Archer et al. (1997) and Wang et al. (2006)].

### *Statistical Analysis*

Correlation was used to evaluate the relationships between RFI and phenotypic measures {BW, ECM yield, ADG, DMI, and gross milk efficiency [ratio of ECM yield (kg)/DMI (kg)]}. Animals with RFI > 0.5 SD above the mean of 0 were categorized as the "low-efficiency group"; those with RFI > 0.5 SD below the mean were categorized as the "high-efficiency group"; and those within ± 0.5 SD of the mean were categorized as the "mid-efficiency group." Mean comparisons of phenotypic measures among the low-, mid-, and high-efficiency groups were made by ANOVA using the GLM procedure (SAS Inst. Inc.). Group was the CLASS variable and the MODEL statement included each phenotypic measure as a dependent variable and group as the independent effect. Further pairwise comparisons of least squares means across groups within each phenotypic measure were performed with SAS using the PDIFF option in the LSMEANS statement.

Multiple regression also was used to evaluate the relationships between RFI and behavioral traits using GLM of SAS. The regression MODEL statement included the random effects of animal, residual variance, and regression effects of meal size, number of meals, time spent feeding, (time spent feeding)$^2$, feeding rate, and pedometer reading. Parity was included as a CLASS variable.

A *P*-value < 0.05 was considered statistically significant.

## RESULTS

### *Effect of Parity on RFI during Milk Production*

There was an effect of parity (1, 2, and 3 or more; *P* < 0.0001) on predicted average energy intake among the 453 lactations in the model used to calculate RFI during milk production (Table 2). Predicted energy intake differed

**Table 2.** Parameter estimates of variables included in the model for estimating predicted average ME intake of Holstein heifers and cows during the first 90 d of lactation ($n$ = 453 lactations)[1]

| Parameter[2] | Estimate | SE | $P$-value |
|---|---|---|---|
| Intercept | 0.70 | 4.23 | 0.868 |
| Parity 1 | −0.58 | 0.86 | 0.504 |
| Parity 2 | 2.82 | 0.64 | < 0.0001 |
| Parity 3+ | 0.00 | | |
| $BW^{0.75}$ | 0.27 | 0.03 | < 0.0001 |
| ADG | 3.74 | 0.54 | < 0.0001 |
| Energy-corrected milk yield | 0.63 | 0.04 | < 0.0001 |

[1]Predicted energy intake = $b_0$ + Parity (1,2,3+) + $b_1 \times BW^{0.75}$ + $b_2 \times$ ADG + $b_3 \times$ energy-corrected milk yield + residual feed intake.

[2]Parity 1 = first-lactation heifer; Parity 2 = cow in second lactation; Parity 3+ = cow in third or greater lactation; and $BW^{0.75}$ = average metabolic BW.

($P$ < 0.0001) between first-lactation heifers and second-lactation cows, and between cows in their second lactation versus those in their third or greater lactation ($P$ < 0.0001). Therefore, parity (1, 2, 3+) was included in the model for estimating average energy intake to maximize residual degrees of freedom and maintain integrity of the model. Table 2 shows the parameter estimates for the variables included in the model for estimating average energy intake, and their effects on the model. Because this model is overparameterized, constraints must be applied to obtain solutions. The final level of parity was set to 0 in the analysis; thus, the solution for the intercept is an estimate of the overall mean plus the effect for parity 3+ cows, and solutions for parity 1 and 2 estimate the difference between cows in those parities and parity 3+.

### *Variation in RFI and Repeatability of Measures by Lactation*

Considerable differences were observed in actual DMI among first-lactation heifers and multiparous cows within the herd, ranging from a difference of 2.2 kg/d between the least and most efficient heifers (±0.5 SD from mean RFI of 0), 2.8 kg/d in DMI between the least and most efficient second-lactation cows, and 4.6 kg/d between the least and most efficient cows in their third or greater lactation. Among all first-lactation heifers, estimates of RFI ranged from −9.53 to 12.62 Mcal ME/d between the most and least efficient animals, respectively, and the SD for RFI among first-lactation heifers was 3.47 Mcal ME/d. Estimates of RFI for second-lactation cows ranged from a minimum of −11.84 to a maximum of 29.96 Mcal ME/d (SD = 5.90) and ranged from −14.51 to 9.89 (SD = 4.98) among cows in their third or greater lactation. The overall SD for RFI was 4.64 Mcal ME/d and the $R^2$ for the model to predict energy intake was 0.72 ($P$ < 0.0001).

First, weekly observations of RFI were used to calculate estimates of variance components. Based on 6,986 weekly observations that included complete lactation records, estimates of additive genetic variance, across lactation cow permanent environmental variance, within lactation cow permanent environmental variance, residual variance, and phenotypic variance of RFI were 4.26, 3.48, 10.69, 20.62, and 39.05, respectively. Heritability (±SE) was estimated at 0.11 ± 0.05, and repeatability was estimated at 0.20 across lactations and 0.47 within lactation.

Next, averages of weekly observations of RFI in the first ~100 DIM were used to calculate estimates of variance components. Because observations were combined in each lactation, within lactation cow permanent environmental effects and variance could not be estimated. Based on 445 averages of weekly observations, estimates of additive genetic variance, across lactation cow permanent environmental variance, residual variance, and phenotypic variance of average RFI were 7.76, 4.03, 9.94, and 21.73, respectively. Heritability (±SE) was estimated at 0.36 ± 0.06, and repeatability was estimated at 0.56 across lactations.

### *Phenotypic Correlations between RFI and Production and Behavior Traits*

There was no correlation between estimates of RFI during milk production and mean $BW_{pred}$, ADG, or mean ECM yield ($r$ = 0.00; $P$ > 0.99), as expected based on how the trait is defined. Estimates of RFI were positively correlated both with DMI ($r$ = 0.41; $P$ < 0.0001) and meal size ($r$ = 0.20; $P$ < 0.0001) and were negatively correlated with gross milk efficiency ($r$ = −0.44; $P$ < 0.0001). There was a positive correlation between RFI and pedometer readings ($r$ = 0.13; $P$ < 0.007) and feeding rate ($r$ = 0.29; $P$ < 0.0001). There was no correlation detected between RFI and average number of meals consumed per day ($r$ = 0.01; $P$ > 0.78), average total time spent feeding each day ($r$ = −0.04; $P$ > 0.41), or meal duration ($r$ = −0.04; $P$ > 0.34).

### *Production and Behavioral Characteristics of RFI Groups*

Table 3 summarizes the production and behavioral characteristics of the high-, mid-, and low-efficiency groups. There was no difference among the groups in ADG, SCC, pedometer readings, average number of meal events per day, meal duration, or time spent feeding per day ($P$ > 0.13). However, there were differences among efficiency groups in mean gross milk efficiency, DMI, ME intake, meal size, and feeding rate ($P \leq 0.001$), as well as BW and ECM yield ($P$ < 0.02). The mean BW and ECM yield of the mid-efficiency group were less ($P$ < 0.04) than in the high- and low-efficiency groups, but no differences ($P$ > 0.53) in mean BW and ECM yield were observed between the high-

**Table 3.** Production and feeding characteristics of high-, mid-, and low-efficiency groups of Holstein heifers and cows during the first 90 d of lactation

| Trait | Efficiency group[1] High (Mean ± SE) | Mid (Mean ± SE) | Low (Mean ± SE) | P-value |
|---|---|---|---|---|
| n | 136 | 202 | 115 | |
| Production trait | | | | |
| BW, kg | 604 ± 6[a] | 584 ± 5[b] | 607 ± 6[a] | 0.006 |
| ADG, kg/d | 0.14 ± 0.04 | 0.22 ± 0.03 | 0.13 ± 0.04 | 0.137 |
| Energy-corrected milk yield, kg/d | 44.0 ± 0.6[a] | 42.1 ± 0.6[b] | 44.6 ± 0.8[a] | 0.015 |
| Somatic cell count, × $10^3$ | 248 ± 29 | 330 ± 41 | 262 ± 34 | 0.227 |
| Gross milk efficiency[2] | 2.14 ± 0.02[a] | 1.96 ± 0.01[b] | 1.84 ± 0.02[c] | < 0.0001 |
| DMI, kg/d | 20.5 ± 0.2[a] | 21.4 ± 0.2[b] | 24.2 ± 0.3[c] | < 0.0001 |
| ME intake, Mcal/d | 57.6 ± 0.6[a] | 60.5 ± 0.5[b] | 68.5 ± 0.8[c] | < 0.0001 |
| Behavioral trait[3] | | | | |
| Pedometer readings | 5.7 ± 0.4 | 5.9 ± 0.3 | 6.5 ± 0.5 | 0.218 |
| No. of meals/d | 10.7 ± 0.3 | 10.8 ± 0.2 | 10.5 ± 0.3 | 0.890 |
| Meal duration, min | 21.2 ± 0.5 | 20.6 ± 0.3 | 20.7 ± 0.4 | 0.409 |
| Meal size, kg | 4.3 ± 0.1[a] | 4.4 ± 0.1[a] | 5.1 ± 0.1[b] | < 0.001 |
| Time spent feeding, min/d | 214.7 ± 3.6 | 211.2 ± 2.8 | 208.3 ± 3.3 | 0.438 |
| Feeding rate, g/s | 3.4 ± 0.1[a] | 3.6 ± 0.1[b] | 4.1 ± 0.1[c] | < 0.0001 |

[1]High-efficiency group = ≤ 0.5 SD below the mean residual feed intake (RFI) value of 0; mid-efficiency group = ± 0.5 SD of the mean RFI value of 0; and low-efficiency group = ≥ 0.5 SD above the mean RFI value of 0.

[2]Ratio of energy-corrected milk yield (kg)/DMI (kg).

[3]Feed quantities related to feeding behavior are on an as-fed basis.

[a–c]Means within a row without a common superscript differ ($P \leq 0.05$).

and low-efficiency groups. Overall, there was a difference in mean DMI of 3.7 kg/d and ME intake of 10.9 Mcal/d between the high- and low-efficiency groups (Table 3).

Table 4 summarizes the regressions for behavior traits on RFI. Regression estimates indicate that keeping all other variables constant, as time spent feeding or feeding rate increased, there was a corresponding increase ($P < 0.0001$) in RFI. There was no relationship ($P > 0.05$) between meal size, number of meals per day, or pedometer reading and RFI. There also was an effect ($P < 0.05$) of parity on RFI with multiparous cows having lower RFI than heifers in their first lactation.

### *Minimum Testing Period for RFI during Milk Production*

Variance components for RFI associated with different test durations are summarized in Table 5. Residual variance decreased from 20.8 at 18 DIM to 8.7 at 53 DIM, then fluctuated around 8.2 as additional data were added to the lactation average values. Heritability estimates showed a corresponding increase wherein estimates steadily increased from 0.23 to 0.45 when including data through 53 DIM, then values stabilized near 0.43

**Table 4.** Regression coefficients for behavior traits on residual feed intake of Holsteins during the first 90 d of lactation ($n$ = 453 lactations)

| Parameter[1] | Coefficient | SE | P-value |
|---|---|---|---|
| Intercept | −119.77 | 11.52 | < 0.0001 |
| Parity 1 | 4.34 | 1.05 | < 0.0001 |
| Parity 2 | −1.37 | 0.67 | 0.04 |
| Parity 3+ | 0.00 | | |
| Meal size, kg | −0.31 | 0.55 | 0.57 |
| No. of meals/d | −0.07 | 0.17 | 0.68 |
| Time spent feeding, min/d | 0.59 | 0.07 | < 0.0001 |
| (Time spent feeding, min/d)$^2$ | 0.00 | 0.00 | < 0.0001 |
| Feeding rate, g/s | 10.45 | 1.08 | < 0.0001 |
| Pedometer reading | −0.02 | 0.16 | 0.92 |

[1]Parity 1 = first-lactation heifer; Parity 2 = cow in second lactation; Parity 3+ = cow in third or greater lactation.

with inclusion of additional data (Table 5). Phenotypic correlations between cumulative periodic measures and full-test RFI (including 12 periods) are illustrated in Fig. 1 and show steady increases; although, there is a diminishing increase as more data are added. The correlation between cumulative average RFI and the full-test period RFI exceeded 0.90 in test periods that included data through 60 DIM (Fig. 1). Evaluated on a weekly basis, RFI estimates during wk 6 of observation (50 to 56 DIM) were correlated most highly ($r$ = 0.83) with average RFI for the full-test period. The correlations by week were generally quite consistent from wk 4 to 7 (36 to 63 DIM) at approximately 0.82. The first week showed the lowest correlation coefficient ($r$ = 0.63), and declined slightly after wk 7 from 0.82 to 0.69 (Fig. 1).

**Table 5.** Effect of test period on variance and heritability estimates for residual feed intake (Mcal/d)[1]

| DIM[2] | Genetic | Residual | Phenotypic | Heritability[3] |
|---|---|---|---|---|
| 18 | 6.30 | 20.85 | 27.15 | 0.23 |
| 25 | 5.97 | 17.18 | 23.15 | 0.26 |
| 32 | 6.74 | 13.79 | 20.53 | 0.33 |
| 39 | 6.34 | 11.52 | 17.86 | 0.35 |
| 46 | 6.52 | 10.11 | 16.63 | 0.39 |
| 53 | 7.02 | 8.73 | 15.75 | 0.45 |
| 60 | 6.26 | 8.56 | 14.82 | 0.42 |
| 67 | 6.13 | 8.23 | 14.36 | 0.43 |
| 74 | 6.18 | 8.04 | 14.21 | 0.43 |
| 81 | 6.18 | 8.09 | 14.27 | 0.43 |
| 88 | 6.16 | 8.27 | 14.44 | 0.43 |
| 95 | 6.41 | 8.19 | 14.60 | 0.44 |

[1]Only the first recorded lactation for each of 287 cows for which pedigree data were available was used in this analysis.

[2]Days in milk.

[3]Heritability = genetic variance/phenotypic variance.

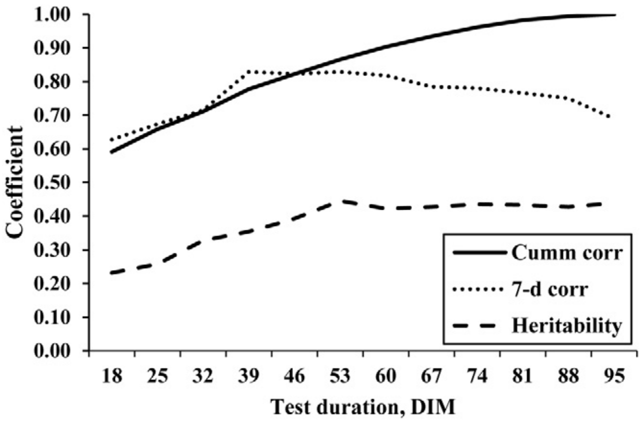


**Figure 1.** Effect of test duration (measured in days in milk; DIM) for estimating residual feed intake (Mcal/d) on estimates of heritability and phenotypic correlations between shorter test lengths and a full-length test through approximately 100 DIM. Estimates of residual feed intake (RFI) were calculated using 7-d increments of data, starting with the 7-d period centered at 18 d and progressing through the interval centered at 95 d. Each period was analyzed as a cumulative average through all 12 periods, and correlation coefficients (Cumm corr) for the relationship between RFI for each cumulative shortened test period and total RFI during all 12 periods was plotted (only the first available lactation observations were included; *n* = 287). Correlation coefficients (7-d corr) were calculated and plotted for the relationship between RFI during each 7-d period and total RFI during all 12 periods for each animal using all available lactations (*n* = 445).

## DISCUSSION

Use of RFI to estimate efficiency of lactating dairy cattle in the conversion of feed to milk production has been described previously using various approaches. However, there is considerable variation across studies in the time over which feed intake was estimated, the methods for measuring feed intake, the diets provided, the stage of lactation evaluated, and the method for estimation of ADG during the test period. For instance, Van Arendonk et al. (1991) estimated RFI during the first 105 d of lactation in first-lactation heifers (mixed breed) using feed intake measures collected on individuals during 2-wk periods at 2, 5, 9, and 13 wk postcalving. Heifers were offered roughage ad libitum and a fixed amount of concentrate daily. Feed intake was measured using an electronically controlled gating system and BW was determined at the start and finish of the feeding trial. In another study, Veerkamp et al. (1995) estimated RFI using 3 different estimation approaches during the first 26 wk of lactation in Holstein-Friesian heifers and multiparous cows of 2 genetic groups selected for milk components yield and fed 1 of 2 TMR formulations ad libitum. In their study, individual feed intake was measured manually for 4 d consecutively each week, and BW was recorded weekly. More recently, Prendiville et al. (2009) estimated RFI in Holstein-Friesian cows on pasture over a full lactation wherein feed intake was calculated using a modified *n*-alkane technique developed by Mayes et al. (1986), but intake was measured only during 5 d corresponding to approximately 51, 108, 149, 198, and 233 DIM. In that study, BW was recorded twice weekly, and BCS also was included in the model for estimating RFI. Therefore, although there are studies examining RFI in lactating dairy cattle, none have evaluated feed intake for consecutive days over several weeks or under conditions highly representative of current management practices on United States dairy farms.

In the present study, RFI was estimated in a high-producing Holstein herd (rolling herd average of 12,050 kg/yr) provided ad libitum access to a TMR and managed under conditions typical of a United States dairy herd. Estimates were obtained for both heifers and multiparous cows during the first 90 DIM using continuous daily measures (approximately every 6 s) of feed intake using a radio-frequency identification-based system (GrowSafe 4000 System; GrowSafe Systems, Ltd.). This computerized feeding system identifies the individual animal when it places its head in the feed bunk by way of an ear tag containing a transponder, then records animal feed intake and behavior using bunk weights continuously monitored via load cells located beneath each bunk. This approach allows any cow to directly feed from any available bunk and, therefore, should reduce impacts of feed intake monitoring on feeding behavior and provide a more accurate and less biased estimate of feed intake compared with electronic gated systems that require animals to "learn" to gain access to feed. Assessment of ADG for the model to predict energy intake also was based on determinations of BW every 10 to 14 d, which were converted to daily estimates by fitting periodic measures to a linear model based on DIM and DIM$^2$.

Using our approach for calculating RFI based on the difference between predicted energy intake and actual energy intake, it was determined that parity had a significant effect on energy intake. Predicted intake was greater in second-lactation cows than first-lactation heifers and cows in their third or greater lactation. Thus, factors other than differences in BW, ECM yield, and ADG contributed to differences in predicted energy intake among the 3 groups. Causative factors responsible for differences in intake are unknown but may include differences in gut capacity (Oldenbroek, 1989; Azizi et al., 2009), or interactions of body composition, body condition (Gallo et al., 1996), or type of growth (e.g., skeletal versus adipose or muscle). Thus, as has been done in other studies estimating RFI within dairy cattle herds (Ngwerume and Mao, 1992; Prendiville et al., 2011), parity should be included in the model for predicting energy intake to account for variation among different parity groups.

In this study, considerable differences were observed in DMI, and thus energy intake, among both first-lactation heifers and multiparous cows within the herd. Coefficients of variation (% CV) associated with DMI were 8.4 and 11.3 for first-lactation and multiparous cows, respectively. This variation in DMI appears to be slightly less than that reported among growing beef cattle evaluated for RFI, which generally ranged from 10.1 to 13.8% (Archer and Bergh, 2000; Arthur et al., 2001b; Basarab et al., 2003; Wang et al., 2006). Standard deviations for RFI in growing beef cattle of various breeds in 1 study also ranged from 0.66 to 0.86 kg/d (Wang et al., 2006) and were slightly less in finishing Limousin × Friesian heifers at 0.59 kg/d (Kelly et al., 2010). Likewise, SD for RFI ranged from 0.50 to 0.74 kg/d across a variety of beef breeds from other studies wherein models varied slightly for estimating predicted feed intake (Archer and Bergh, 2000; Arthur et al., 2001b; Basarab et al., 2003). These values are less than our observed variation in RFI in lactating cows across all parity groups of 1.63 kg/d (based on DMI rather than energy intake; data not shown). Of interest, Carnie et al. (2010) reported a SD for RFI during growth of 0.54 kg/d (range of −2.25 to 1.50 kg/d) in 26-wk-old Holsetin-Friesian heifers based on a 42-d feeding trial. Indeed, the strength of the relationship between RFI in growing dairy heifers and subsequent RFI during milk production is currently unknown and of great interest. This topic is currently under investigation in New Zealand (Waghorn et al., 2012) and our laboratory.

Despite differences in observed variation in RFI in growing beef cattle versus RFI in lactating dairy cattle, heritability estimates for RFI during each condition suggest that there is similar opportunity for genetic selection for RFI. Reported heritability estimates for RFI during milk production vary over a broad range from 0.01 to 0.38, based on very few studies (Korver et al., 1991; Van Arendonk et al., 1991; Ngwerume and Mao, 1992; Veerkamp et al., 1995; Lopez-Villalobos et al., 2008; Vallimont et al., 2011). Our estimate for RFI among Holsteins during early lactation was 0.36, based on a fairly limited number ($n$ = 445) of lactations. This estimate is greater than that of 0.19 for RFI previously reported by Van Arendonk et al. (1991) in 306 lactating dairy heifers during the first 105 d of lactation using similar equations for determining RFI. More similar to our estimate, however, Veerkamp et al. (1995) estimated heritability between 0.30 and 0.38 using 3 different approaches for calculating RFI in 377 lactations of heifers and cows during the first 182 d of lactation but suggested that the estimates are likely inflated due to "large genetic covariances" among traits used to calculate RFI. Among studies of RFI in growing beef cattle, recent heritability estimates (from 2000) based on a fairly large number of studies ranged from 0.16 to 0.39 (Arthur and Macarthur, 2009). Thus, the estimated heritability for RFI during lactation in the present study is within the range reported in other studies in both growing beef cattle and lactating dairy cows and should provide a similar opportunity for genetic improvement as traits such as mature equivalent milk yield, protein yield, and fat yield (Cassell, 2009).

In addition to heritability, repeatability of RFI during lactation was evaluated in the present study to determine the correlation of estimates within individual cows over multiple lactations. Herd et al. (2006) reported positive correlations ($r$ = 0.39) between RFI estimates for growing Angus heifers postweaning and subsequently as mature cows, and a recent study in beef heifers suggested that measures of RFI during growth within individuals from 8 to 11 mo of age are similar to their RFI measures during the finishing phase (Kelly et al., 2010). The authors reported a highly significant correlation of 0.62 between consecutive measures within individuals. On the contrary, a study in growing ewe lambs indicated no relationship between RFI during growth and RFI during maintenance as mature ewes (Redden et al., 2011), although diets differed substantially from a pelleted feed during the growth phase to a hay-based diet during the maintenance phase, which could have impacted results. We found that weekly RFI records during the first 90 DIM had a repeatability of 0.47 within lactation and 0.20 across lactations, suggesting that the trait is only moderately consistent within individual cows over time. However, when these weekly observations were aggregated into a 90-d average RFI, the repeatability across lactations was estimated at 0.56, which is similar to repeatability values reported for traits such as milk yield, milk fat yield, and milk protein percentage in dairy cattle (Roman et al., 2000).

Although RFI during lactation is repeatable within animal over time and moderately heritable, it is important to consider phenotypic correlations with other production traits. We found that measures of RFI during lactation were not phenotypically correlated to traits such as BW, ADG during lactation, or ECM yield, as one would expect based on how the estimate is derived. A positive correlation was observed between RFI during lactation and DMI, and a negative correlation was found between RFI and gross milk efficiency. These results indicate that lower RFI (increased efficiency) is associated with decreased feed intakes and improved gross efficiency. Our findings are consistent with those by Van Arendonk et al. (1991) in lactating heifers evaluated for RFI using a similar methodology. Likewise, our results are in agreement with studies evaluating RFI in growing beef cattle wherein RFI was not phenotypically correlated with traits such as BW or ADG but was positively correlated with DMI and G:F (Arthur et al., 2001b; Nkrumah et al., 2004; Basarab et al., 2007).

To further describe the relationships between RFI and production traits, we compared mean production measures between the most and least efficient animals in our herd (defined as those more than 0.5 SD above or below the herd mean RFI of 0). The traits included ADG, BW, ECM yield, SCC, gross milk efficiency, and feed intake on a DM and ME basis. It was determined that the high- and low-RFI groups did not differ in BW, ADG, or ECM yield, as expected, but low-RFI animals (high efficiency) had significantly greater gross milk efficiency and consumed an average of 15% less feed per day than high-RFI animals (low efficiency). This result is similar to reductions of approximately 11% in feed intake reported in growing beef cattle selected for low RFI relative to those selected for high RFI (Arthur et al., 2001a). Combined, these results support the concept that selection for low RFI among dairy cattle may reduce feed intake of dairy cows with no associated negative impacts on milk yield. Reductions in intake should translate into reduced feed costs, as well as reductions in total manure output and associated greenhouse gas production (Arthur and Macarthur, 2009). In beef cattle, it was determined that actual methane emission is 25 to 28% lower in low RFI steers relative to high RFI steers (Nkrumah et al., 2006; Hegarty et al., 2007). It would be reasonable to expect equivalent reductions in dairy cattle methane production through selection for lower RFI simply due to the decreased DMI.

For other production-related measures, we found no detectable relationship between RFI and SCC, indicating that differences in SCC likely do not contribute to or explain variation observed in the efficiency of feed conversion to milk production among cows. Alternatively, assuming that SCC is an indicator of mastitis susceptibility, this finding supports the hypothesis that differences in susceptibility to mastitis do not exist between low- versus high-RFI heifers and cows. Of interest, however, a recent study in our laboratory examining genetic differences between cows with high and low estimated breeding values for RFI showed that more efficient cows exhibit copy number variations in genes associated with immunity and the inflammatory response (Hou et al., 2012), which could impact their ability to elicit a response to an immune challenge. Therefore, the relationship between immune function and RFI of dairy cattle is a current area of investigation within our laboratory.

In addition to production measures, we sought to determine whether high- and low-RFI animals differed in physical activity as determined by pedometer readings, or feeding behavior as recorded by the GrowSafe System. In a review by Herd and Arthur (2009), positive relationships were reported between RFI and feeding activity of swine and chickens, as well as differences in physical activity between efficient and inefficient mice, as determined by heat loss. In cattle, the authors reported a positive phenotypic correlation between pedometer readings and RFI, which suggested that physical activity may contribute to 10% of the variation in RFI among cattle. In the present study, pedometer readings of lactating dairy heifers and cows had a similar positive phenotypic correlation with RFI; however, no differences were observed among mean pedometer readings of high-, mid-, and low-RFI groups, and multiple regression analysis indicated that, all other variables in the model being equal, pedometer readings were not associated with RFI. A previous report using the GrowSafe System to evaluate feeding behavior in growing beef steers indicated positive phenotypic and genetic correlations between daily feeding duration and RFI, and significant differences among high-, mid-, and low-RFI groups of steers in frequency of feeding events per day and daily feeding duration (Nkrumah et al., 2007). That is, the most efficient steers spent less time daily at the feedbunk and had fewer feeding events per day than the most inefficient steers. In the study by Nkrumah et al. (2007), a feeding event was defined as detection of a steer at a single feedbunk without interruption lasting more than 300 s or interruption by feeding of another animal at the same feedbunk. If the steer moved to another feedbunk, it was considered a separate feeding event. During a feeding event, the animal was present at the feedbunk but may not have been consuming feed (e.g., the steer may have been standing, licking, or chewing). Therefore, this is a slightly different measurement from meal events recorded in the present work. However, the authors suggested that differences in feeding behavior may impact animal metabolism and contribute to differences in growth efficiency of beef cattle.

In the present study of lactating dairy cattle, average number of meals consumed per day did not differ among RFI groups, and there was no relationship detected between number of meals per day or average meal size and RFI, as determined by multiple regression. However, mean DMI, ME intake, and meal size were significantly less in low-RFI (more efficient) versus high-RFI (less inefficient) animals. Furthermore, metabolic inefficiency (high RFI value) was associated with more total time spent feeding each day. This finding is consistent with reported positive phenotypic or genetic correlations between RFI and time spent feeding in finishing beef cattle (Robinson and Oddy, 2004), growing beef cattle (Basarab et al., 2007; Nkrumah et al., 2007; Lancaster et al., 2009), and pregnant beef cows (Basarab et al., 2007). On the contrary, Bingham et al. (2009) found that daily feeding duration was greater in low-RFI growing beef heifers compared with high-RFI heifers. In their study, feeding behavior was assessed by human observers using video recordings, and heifers were fed using Calan gate feeders (American Calan, Inc., Northwood, NH) where there was 1 feedbunk per animal. Hence, their experimental design may have affected outcomes relative to studies using the GrowSafe System or similar systems where there is more than 1 animal per feedbunk (i.e., there is competition for access to feed) and occupancy at the bunks is automatically detected by a transponder. Thus, our results and those reported among beef cattle suggest that additional energy expenditure associated with increased feeding activity may contribute to decreased metabolic efficiency of cattle.

When feeding rate (grams consumed on an as-fed basis per second) was calculated from meal duration (minutes per meal) and meal size (kilograms consumed on an as-fed basis per meal), the rate of feed consumption had a strong relationship to efficiency, wherein more efficient (low RFI) heifers and cows consumed feed at a slower rate than less efficient (high RFI) animals. Similarly, a positive phenotypic correlation between feeding rate during the finishing period and RFI in beef heifers divergently selected for RFI was recently reported by Kelly et al. (2010). Likewise, Robinson and Oddy (2004) reported a positive phenotypic correlation between RFI and feeding rate in finishing beef cattle and Bingham et al. (2009) reported a faster feeding rate in high-RFI versus low-RFI heifers during growth. On the contrary, Lancaster et al. (2009) found no difference in feeding rate between high- versus low-RFI bulls during growth and no phenotypic correlation between RFI and feeding rate. Likewise, Golden et al. (2008) found no difference in feeding rate of growing steers with high- versus low-RFI. Due to the relationship between passage rate of feed and its digestibility, slower feeding rates may contribute to increased DM digestibility in efficient animals. Indeed, because this is the first study examining detailed feeding behavior of a relatively small number of lactating dairy cattle and its relationship to feed efficiency, and there are conflicting reports among beef cattle on the relationship between feeding rate and RFI; additional study is warranted in this area of research.

Lastly, a question of importance regarding estimation of RFI in lactating dairy cattle is the minimum duration of the testing period. Despite the major improvements in assessing individual feed intake using automated radio-frequency-based systems, a shorter time period should permit more animals to be evaluated within a given time frame and reduce labor associated with assessing feed intake. Based on measures using the GrowSafe System to assess RFI in hybrid beef steers, Wang et al. (2006) deduced that a 63-d test period would provide estimates of RFI that are as reliable as a 91-d test period. Similarly, prior research in beef cattle by Archer et al. (1997) indicated a 70-d test is as informative as a 119-d test period. Much the same, we found that a test period through 53 DIM provided 81% of the information provided by a test through 90 DIM, and residual variance also remained fairly stable for this test length. Furthermore, we found that by the sixth week of lactation, weekly RFI estimates were well correlated with RFI estimates based on cumulative data through 90 DIM. Based on weekly measures of RFI, wk 6 of lactation was most highly correlated with RFI by 90 DIM. However, because the shape of the lactation yield curve and extent of mobilization of body fat do change during the typical 305-d lactation, it is not known what specific time frame during the lactation cycle is most representative of efficiency during the full 305-d lactation. We chose to evaluate the first 90 DIM because this period contains the peak in milk yield, and, generally, lactating dairy cows have overcome negative energy balance and returned to a neutral energy balance by about 16 wk postpartum (Bauman and Currie, 1980). Further evaluation of the correlations between RFI estimates during different periods of the lactation cycle versus a complete 305-d lactation is needed.

In conclusion, given the moderate heritability of RFI, its association with reduced feed intake without associated impacts on milk yield, and its potential to reduce associated greenhouse gas emissions and manure production, our findings suggest that RFI during lactation could be a valuable target for genetic selection. Mechanisms contributing to differences in RFI among dairy cattle should be investigated further and may include differences in feeding behavior between efficient and inefficient animals. Impacts of selection for low RFI in dairy cattle on body condition and other health traits, such as metabolic disease and fertility should also be considered in future investigations. Based on the identified benefits of selection for improved feed efficiency based on RFI in beef cattle production, it appears that selection for improved RFI in dairy cattle could have similar benefits without negative correlated responses in animal size or milk production. Genetic markers associated with RFI are currently being investigated and could improve the accuracy of selection and rate of improvement for the trait due to relative increases in predictive data density in younger animals.

## LITERATURE CITED

Alberta Agriculture, Food and Rural Development. 2006. Residual feed intake (net feed efficiency) in beef cattle. AGRI-FACTS, July 2006, Agdex 420/11–1.

Archer, J. A., P. F. Arthur, R. M. Herd, P. F. Parnell, and W. S. Pitchford. 1997. Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in British breed cattle. J. Anim. Sci. 75:2024–2032.

Archer, J. A., and L. Bergh. 2000. Duration of performance tests for growth rate, feed intake and feed efficiency in four biological types of beef cattle. Livest. Prod. Sci. 65:47–55.

Arthur, P. F., J. A. Archer, R. M. Herd, and G. J. Melville. 2001a. Response to selection for net feed intake in beef cattle. Proc. Assoc. Adv. Anim. Breed. Gen. 14:135–138.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001b. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805–2811.

Arthur, P. F., and E. Macarthur. 2009. Reduction in greenhouse gas emissions associated with selection for residual feed intake in beef cattle in Alberta. Science Coordination Workshop, March 16, 2009, Leduc, AB, Canada.

Azizi, O., O. Kaufmann, and L. Hasselmann. 2009. Relationship between feeding behaviour and feed intake of dairy cows depending on their parity and milk yield. Livest. Sci. 122:156–161.

Basarab, J. A., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87:489–502.

Basarab, J. A., M. A. Price, J. A. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189–204.

Bauman, D. E., and W. B. Currie. 1980. Partitioning of nutrients during pregnancy and lactation: A review of mechanisms involving homeostasis and homeorhesis. J. Dairy Sci. 63:1514–1529.

Bingham, G. M., T. H. Friend, P. A. Lancaster, and G. E. Carstens. 2009. Relationship between feeding behavior and residual feed intake in growing Brangus heifers. J. Anim. Sci. 87:2685–2689.

Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassell, and S. D. Kachman. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances [DRAFT]. Agric. Res. Serv., U.S. Dep. of Agric., Washington, DC.

Carnie, K. R., S. R. Davis, K. A. Macdonald, G. C. Waghorn, V. V. Obolonkin, and R. J. Spelman. 2010. Brief Communication: Variation in feed conversion efficiency in Holstein-Friesian heifer calves. Proc. N. Z. Soc. Anim. Prod. 70:250–252.

Cassell, B. 2009. Using heritability for genetic improvement. Va. Coop. Ext. Publ. 404-084.

Crews, D. H., Jr. 2005. Genetics of efficient feed utilization and national cattle evaluation: A review. Genet. Mol. Res. 4:152–165.

Gallo, L., P. Carnier, M. Cassandro, R. Mantovani, L. Bailoni, B. Contiero, and G. Bittante. 1996. Change in body condition score of Holstein cows as affected by parity and mature equivalent milk yield. J. Dairy Sci. 79:1004–1015.

Golden, J. W., M. S. Kerley, and W. H. Kolath. 2008. The relationship of feeding behavior to residual feed intake in crossbred Angus steers fed traditional and no-roughage diets. J. Anim. Sci. 86:180–186.

Hegarty, R. S., J. P. Goopy, R. M. Herd, and B. McCorkell. 2007. Cattle selected for lower residual feed intake have reduced daily methane production. J. Anim. Sci. 85:1479–1486.

Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. J. Anim. Sci. 87:E64–E71.

Herd, R., P. F. Arthur, and J. A. Archer. 2006. Repeatability of residual feed intake and interaction with level of nutrition in Angus cows. Aust. Soc. Anim. Prod. Short Comm. 80.

Hou, Y., D. M. Bickhart, H. Chung, J. L. Hutchison, H. D. Norman, E. E. Connor, and G. E. Liu. 2012. Analysis of copy number variations in Holstein cows identify potential mechanisms contributing to differences in residual feed intake. Funct. Integr. Genomics. 12:717–723.

Kelly, A. K., M. McGee, D. H. Crews, Jr., T. Sweeney, T. M. Boland, and D. A. Kenny. 2010. Repeatability of feed efficiency, carcass ultrasound, feeding behavior, and blood metabolic variables in finishing heifers divergently selected for residual feed intake. J. Anim. Sci. 88:3214–3225.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of food use in beef cattle. J. Anim. Sci. 22:486–494.

Korver, S., E. A. M. Van Eekelen, H. Vos, G. J. Nieuwhof, and J. A. M. Van Arendonk. 1991. Genetic parameters for feed intake and feed efficiency in growing heifers. Livest. Prod. Sci. 29:49–59.

Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, L. O. Tedeschi, and D. H. Crews Jr. 2009. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass traits in growing bulls. J. Anim. Sci. 87:1528–1539.

Lopez-Villalobos, N., D. P. Berry, B. Horan, F. Buckley, J. Kennedy, M. O'Donovan, L. Shalloo, and P. Dillon. 2008. Genetics of residual energy intake in Irish grazing dairy cows. Proc. N. Z. Soc. Anim. Prod. 68:97–100.

Mayes, R. W., C. S. Lamb, and P. M. Colgrove. 1986. The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. J. Agric. Sci. 107:161–170.

Ngwerume, F., and I. L. Mao. 1992. Estimation of residual energy intake for lactating cows using an animal model. J. Dairy Sci. 75:2283–2287.

Nkrumah, J. D., J. A. Basarab, M. A. Price, E. K. Okine, A. Ammoura, S. Guercio, C. Hansen, C. Li, B. Benkel, B. Murdoch, and S. S. Moore. 2004. Different measures of energetic efficiency and their phenotypic relationships with growth, feed intake, and ultrasound and carcass merit in hybrid cattle. J. Anim. Sci. 82:2451–2459.

Nkrumah, J. D., D. H. Crews, Jr., J. A. Basarab, M. A. Price, E. K. Okine, Z. Wang, C. Li, and S. S. Moore. 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J. Anim. Sci. 85:2382–2390.

Nkrumah, J. D., E. K. Okine, G. W. Mathison, K. Schmid, C. Li, J. A. Basarb, M. A. Price, Z. Wang, and S. S. Moore. 2006. Relationships of feedlot feed efficiency, performance, and feeding behavior with metabolic rate, methane production, and energy partitioning in beef cattle. J. Anim. Sci. 85:145–153.

NRC 2001. Nutrient Requirements of Dairy Cattle. 7th rev. ed. Natl. Acad. Sci., Washington, DC.

Oldenbroek, J. K. 1989. Parity effects on feed intake and feed efficiency in four dairy breeds fed ad libitum two different diets. Livest. Prod. Sci. 21:115–129.

Orth, R. 1992. Sample day and lactation report. DHIA 200 Fact Sheet A-2. Mid-states DRPC, Ames, IA.

Prendiville, R., K. M. Pierce, and F. Buckley. 2009. An evaluation of production efficiencies among lactating Holstein-Friesian, Jersey, and Jersey × Holstein-Friesian cows at pasture. J. Dairy Sci. 92:6176–6185.

Prendiville, R., K. M. Pierce, L. Delaby, and F. Buckley. 2011. Animal performance and production efficiencies of Holstein-Friesian, Jersey and Jersey × Holstein-Friesian cows throughout lactation. Livest. Sci. 138:25–33.

Redden, R. R., L. M. M. Surber, B. L. Roeder, B. M. Nichols, J. A. Paterson, and R. W. Kott. 2011. Residual feed efficiency established in a post-weaning growth test may not result in more efficient ewes on the range. Small Ruminant Res. 96:155–159.

Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livest. Prod. Sci. 90:255–270.

Roman, R. M., C. J. Wilcox, and F. G. Martin. 2000. Estimates of repeatability and heritability of productive and reproductive traits in a herd of Jersey cattle. Genet. Mol. Biol. 23:113–119.

Vallimont, J. E., C. D. Dechow, J. M. Daubert, M. W. Dekleva, J. W. Blum, C. M. Barlieb, W. Liu, G. A. Varga, A. J. Heinrichs, and C. R. Baumrucker. 2011. Short communication: Heritability of gross feed efficiency and associations with yield, intake, residual intake, body weight, and body condition score in 11 commercial Pennsylvania tie stalls. J. Dairy Sci. 94:2108–2113.

Van Arendonk, J. A. M., G. J. Nieuwhof, H. Vos, and S. Korver. 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. Livest. Prod. Sci. 29:263–275.

Veerkamp, R. F., G. C. Emmans, A. R. Cromie, and G. Simm. 1995. Variance components for residual feed intake in dairy cows. Livest. Prod. Sci. 41:111–120.

Waghorn, G. C., K. A. Macdonald, Y. Williams, S. R. Davis, and R. J. Spelman. 2012. Measuring residual feed intake in dairy heifers fed an alfalfa (*Medicago sativa*) cube diet. J. Dairy Sci. 95:1462–1471.

Wang, Z., J. D. Nkrumah, C. Li, J. A. Basarab, L. A. Goonewardene, E. K. Okine, D. H. Crews, and S. S. Moore. 2006. Test duration for growth, feed intake, and feed efficiency in beef cattle using the GrowSafe System. J. Anim. Sci. 84:2289–2298.