Residual feed intake is repeatable for lactating Holstein dairy cows fed high and low starch diets

S. B. Potts, J. P. Boerman, A. L. Lock, M. S. Allen, and M. J. VandeHaar¹

Department of Animal Science, Michigan State University, East Lansing 48824

ABSTRACT

Residual feed intake (RFI) is a tool to quantify feed efficiency in livestock and is commonly used to assess feed efficiency independent of production level, body weight (BW), or BW change. Lactating Holstein cows ($n = 109$; 44 primiparous and 65 multiparous), averaging (mean $\pm$ standard deviation, SD) 665 ± 77 kg of BW, 42 ± 9 kg of milk/d, and 120 ± 30 d postpartum, were fed diets of high (HI) or low (LO) starch content in 4 crossover experiments with two 28-d treatment periods. The LO diets were $\sim 40\%$ neutral detergent fiber (NDF) and $\sim 14\%$ starch and the HI diets were $\sim 26\%$ NDF and $\sim 30\%$ starch. Individual dry matter intake (DMI) of a cow was modeled as a function of milk energy output, metabolic BW, body energy change, and fixed effects of parity, experiment, cohort nested within experiment, and diet nested within cohort and experiment; RFI for each cow was the residual error term. Cows were classified as high (>0.5 SD of the mean), medium (± 0.5 SD of the mean), or low (<-0.5 SD of the mean) RFI. On average, for the linear model used to determine RFI for individual cows, each unit increase in milk energy output, metabolic BW, or body energy gain was associated with 0.35, 0.09, or 0.05 kg increase in DMI, respectively. When compared with LO diets, HI diets increased energy partitioning to body energy gain and tended to increase DMI. The correlation between RFI when cows were fed HI diets and RFI when cows were fed LO diets was 0.73 and was similar across each parity and experiment. Fifty-six percent of cows maintained the same RFI classification (high, medium, or low RFI) and only 4 of 109 cows changed from high RFI to low RFI or vice versa when diets were changed. Milk:feed, income over feed cost, and DMI were also highly repeatable ($r = 0.72, 0.84$, and 0.92 , respectively). We achieved significant changes in milk yield and component concentration as well as energy partitioning between HI and LO diets and still determined RFI to be repeatable across diets. We conclude

that RFI is reasonably repeatable for a wide range of dietary starch levels fed to mid-lactation cows, so that cows that have low RFI when fed high corn diets will likely also have low RFI when fed diets high in nonforage fiber sources.

Key words: dairy cow, residual feed intake, feed efficiency, repeatability, dietary starch

INTRODUCTION

Residual feed intake (RFI) is calculated as the residual in the linear model to predict feed intake of individual animals, and thus is essentially the difference between an individual's observed feed consumption and its predicted feed consumption. An animal with a negative RFI consumes less than expected for its level of production and thus is more efficient when RFI is used to define feed efficiency. Because RFI is independent of production level, recent attention has been given to using RFI as a tool to assess feed efficiency in dairy cattle for purposes of genetic selection (Connor et al., 2013; Green et al., 2013; Macdonald et al., 2014). The heritability of RFI is 0.15 to 0.19 in lactating dairy cattle (van Arendonk et al., 1991; Tempelman et al., 2015) and 0.22 to 0.38 in growing dairy heifers (Williams et al., 2011; Pryce et al., 2012). If RFI is to be used in selection strategies, it is important to know if it is repeatable across the range of diets commonly used on commercial dairy farms.

Residual feed intake was moderately repeatable across 2 consecutive feeding periods for replacement beef heifers classified as high (>0.5 SD), medium (± 0.5 SD), and low (<-0.5 SD) RFI (Durunna et al., 2012). However, in that study, only 49% of all heifers maintained their feed efficiency classification from one period to the next; 28% of all heifers changed their RFI ranking by more than ± 1 SD, but only 6% of heifers changed from the high RFI group to the low RFI group or vice versa. Connor et al. (2013) determined that RFI was repeatable across weeks (0.47) for Holstein dairy cows in early lactation. Kelly et al. (2010a,b) investigated repeatability of RFI in beef heifers across growing and finishing stages when fed grower and finisher diets and determined that RFI measured during the growing pe-

Received October 26, 2014.

Accepted February 18, 2015.

¹Corresponding author: mikevh@msu.edu

riod and RFI measured during the finishing period were moderately correlated ($r = 0.62$). However, Durunna et al. (2011) examined the repeatability of RFI between 2 consecutive periods for beef steers fed a grower diet, and subsequently a finisher diet, and observed that RFI was less repeatable ($r = 0.33$).

Many of the dairy cows used in current estimates of RFI were fed diets that were high in concentrate. In the future, competition for feed grains might limit their availability for use in dairy cattle diets. The goal in selecting for feed efficiency in dairy cows is to find cows that are efficient across many types of diets, so that those efficient when fed the high starch diets typical of the Midwestern United States at present will also be efficient when consuming lower starch diets that might be fed currently in other areas of the world or in the future when high starch concentrates could be less available. The objective of this experiment was to determine if RFI is repeatable when lactating dairy cows are fed diets that differ markedly in starch content. We hypothesized that RFI and other measures of feed efficiency would be repeatable across high and low starch diets fed to lactating dairy cows.

MATERIALS AND METHODS

Cows, Experimental Design, and Diets

Experimental procedures were approved by the Institutional Animal Care and Use Committee of Michigan State University. Data from 4 separate crossover experiments were used to determine the repeatability of RFI across high and low starch diets. Lactating Holstein cows were fed diets that differed in starch content in experiments 1 ($n = 32$; 22% primiparous), 2 ($n = 25$; 40% primiparous), 3 ($n = 32$; 50% primiparous), and 4 ($n = 20$; 55% primiparous). Treatment effects for experiments 1 and 3 have been reported as separate publications (Boerman et al., 2015a,b). Mean DIM, BW, and milk yield for cows across all 4 experiments (mean $\pm$ SD) were 120 ± 30 d, 665 ± 77 kg, and 42 ± 9 kg/d, respectively, at the beginning of the first experimental period. Each experiment consisted of two 28-d treatment periods during which experimental diets were fed. During each experiment, cows were fed a common diet for 3 to 14 d before the first treatment period (14, 5, 7, or 3 d for experiments 1, 2, 3, and 4, respectively). Because individual RFI is relative to cohorts, which were defined as cows that consumed the same diet at the same time (i.e., same diet sequence within an experiment), it was not necessary to include a wash-out period between the 2 treatment periods. Because all cows within a cohort underwent diet changes at the

same time, this probably had a minimal effect on RFI ranking within cohort.

Within each experiment, cows were blocked based on parity as well as BW and milk yield data from the common-diet-period and randomly assigned to treatment sequence. Throughout each experiment, cows were housed in individual tie stalls in the same barn and milked twice daily (0300 and 1430 h). Water was available ad libitum and feed was offered once daily at 1000 h (experiments 2 and 4) or 1200 h (experiments 1 and 3) at $>110\%$ of expected intake based on intake of the previous day. Tie stalls were equipped with a double-cupped watering system to prevent contamination of feed with water and with side panels and a front gate to prevent other cows from stealing feed during cow movements.

During the 28-d treatment periods for each experiment, cows were fed high (**HI**) or low (**LO**) starch diets, which were formulated to be markedly different in starch content. Ingredient and nutrient composition of HI and LO diets fed throughout each of the 4 experiments are shown in Table 1. On average, all HI diets contained about 30 to 35% corn grain and were measured to be about 26% NDF and 30% starch. The LO diet in experiment 1 was formulated to be 12% starch by replacing ground corn with soybean hulls. The LO diet in experiment 2 was formulated to be 16% starch by replacing ground corn and wheat straw with soybean hulls. The LO diet in experiment 3 was 16% starch and was formulated by replacing ground corn and portions of high moisture corn and wheat straw with legume silage, soybean hulls, whole cottonseed, and a palmitic acid enriched FA supplement (98% total FA). In experiment 4, the LO diet was 12% starch, being derived by replacing ground corn, wheat straw, and portions of both corn and legume silages with soybean hulls and whole cottonseed. Although diets across experiments were formulated with different concentrations of ingredients, distinct differences in starch content between HI and LO were achieved within the experiment, and in all cases milk production or nutrient partitioning was altered by diet. Diets were adjusted for changes in forage DM concentration twice weekly to maintain the desired composition.

Sample Collection and Analysis

Cows were fed once per day and orts were removed and weighed daily before feeding. Milk yield was recorded electronically at each milking, and milk samples were obtained from 4 consecutive milkings per week (d 6, 7, 13, 14, 20, 21, 27, and 28 of each period in experiments 1, 2, and 4; d 4, 5, 11, 12, 18, 19, 25, and 26 of each period in experiment 3). Milk samples were

Table 1. Composition of high and low starch diets fed during each experiment^{1,2}

Item	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	HI	LO	HI	LO	HI	LO	HI	LO
Ingredient, % of DM								
Corn silage	23.9	24.3	23.6	23.8	23.7	24.2	23.5	20.9
Legume silage	21.9	22.1	21.2	21.4	11.1	22.6	20.6	18.4
Wheat straw	4.97	5.04	5.19	—	3.79	1.94	4.82	—
Soybean hulls	—	28.9	—	30.5	—	10.6	—	32.1
Cottonseed, whole	—	—	—	—	7.45	9.07	—	9.22
Corn, ground	29.6	3.61	21.4	—	13.1	—	30.8	7.18
Corn, high moisture	—	—	8.28	8.16	21.5	11.0	—	—
Soybean meal	16.6	13.5	17.17	12.9	15.9	14.6	17.2	9.08
Fat supplement ³	—	—	—	—	—	2.51	—	—
Vitamin and mineral ⁴	2.03	2.06	2.06	2.09	2.02	2.05	2.08	2.08
Limestone	0.50	—	0.50	—	0.75	0.76	0.52	—
Sodium bicarbonate	0.51	0.52	0.49	0.50	0.75	0.76	0.51	0.51
Dicalcium phosphate	—	0.25	0.18	0.50	—	—	—	0.51
Nutrient, % of DM								
DM	53.9	53.6	55.9	55.7	55.8	51.7	49.5	52.2
NDF	27.2	43.9	25.9	39.4	25.1	32.8	27.6	44.2
Starch	30.1	12.2	30.3	15.5	32.5	16.1	28.2	11.8
CP	16.4	15.9	16.6	16.0	17.0	18.3	16.9	15.2
Ash	5.9	6.4	6.5	7.3	5.4	6.8	6.1	6.5
Ether extract	2.52	1.90	2.15	1.95	3.24	5.61	2.30	3.41
NE _L , ⁵ Mcal/kg	1.62	1.56	1.68	1.62	1.80	1.75	1.72	1.62
GE, ⁶ Mcal/kg	4.15	4.14	4.16	4.11	4.26	4.34	4.19	4.21

¹High (HI) and low (LO) starch diets fed to lactating cows during experiments 1, 2, 3, and 4 (n = 32, 25, 32, and 20, respectively).

²Nutrient composition was determined from feed ingredients sampled during the last 5 d of each 28-d treatment period.

³Fat supplement was enriched palmitic acid.

⁴Vitamin and mineral mix contained 34.1% dry ground shell corn, 25.6% white salt, 21.8% calcium carbonate, 9.1% Biofos (The Mosaic Co., Plymouth, MN), 3.9% magnesium oxide, 2% soybean oil, and <1% of each of the following: manganese sulfate, zinc sulfate, ferrous sulfate, copper sulfate, iodine, cobalt carbonate, vitamin E, vitamin A, vitamin D, and selenium.

⁵Mean apparent net energy concentration of diets, based on average cow performance. For each diet, DietNE_L = the average of (MilkE + 0.08 × MBW + ΔBodyE)/DMI for all cows on the diet, where MBW = metabolic BW (BW^{0.75}).

⁶Gross energy concentration, calculated from nutrient profile of individual feed ingredients, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0, Michigan State University, East Lansing): 4.20 kcal/g of carbohydrate, 5.65 kcal/g of CP, 9.50 kcal/g of FA estimated from ether extract, 3.95 kcal/g of sugar (Merrill and Watt, 1973).

analyzed for fat, true protein, lactose, SCC, and milk urea nitrogen with infrared spectroscopy (AOAC, 1990; method 972.160) by Michigan DHIA (Universal Lab Services, Lansing, MI). Body weight for each cow was recorded 3 (experiments 2, 3, and 4) or 5 (experiment 1) days per wk immediately after the morning milking. Body condition score was determined on a 5-point scale in 0.25 increments, where 1 = thin and 5 = fat, as described by Wildman et al. (1982) by 3 trained investigators and recorded for each cow at the beginning and end of each period.

Collection and analyses of diet ingredients were the same for all 4 experiments. During the last 5 d of experimental periods, samples of feed ingredients were obtained daily to determine the nutrient profile of the diets. All samples were frozen after collection until analysis. Samples were composited to obtain one sample per period and dried in a forced-air oven (135°C for >72 h) before grinding through a Wiley mill (1-mm screen; Arthur H. Thomas Co., Philadelphia, PA). The

reported nutrient and ingredient composition of diets was determined by the average composition of both periods for each experiment. For all experiments, the treatment diets for periods 1 and 2 were very similar (CV <8% for individual nutrient content).

Samples of feed were analyzed for CP, starch, NDF, ether extract, and ash. Crude protein was determined according to Hach et al. (1987). Starch was analyzed by an enzymatic method after gelatinization with sodium hydroxide (Karkalas, 1985); subsequently, glucose concentration was determined via glucose oxidase method (Glucose kit #510, Sigma Chemical Co., St. Louis, MO), and absorbance was measured with a micro-plate reader (SpectraMax 190, Molecular Devices Corp., Sunnyvale, CA). Neutral detergent fiber was determined according to Mertens (2002), and ether extract was determined using a modified Soxhlet apparatus (AOAC, 1990). Ash was determined after 5 h combustion at 500°C, and concentrations of nutrients are expressed as a percentage of DM.

Calculations

Milk energy output (**MilkE**; Mcal/d) for a cow was estimated by the following equation (NRC, 2001; from equations 2 to 15):

$$\text{MilkE} = 9.29 \times \text{fat (kg)} + 5.63 \times \text{true protein (kg)} + 3.95 \times \text{lactose (kg)},$$

where each component is based on the mean output of a cow during a 28-d treatment period. Metabolic BW for a cow (**MBW**) was estimated as $\text{BW}^{0.75}$, where BW was the mean BW for the cow during the 28-d treatment period. Mean daily BW change (**ΔBW**; kg) was calculated for each cow within a 28-d treatment period by linear regression after 2 iterations of outlier removal. After the first regression, records >3.5 SD were removed before the second regression was performed; records >3.5 SD were removed after the second regression before determining ΔBW, which was the slope from the third regression. Energy expended for body tissue gain (**ΔBodyE**; Mcal/d) was estimated by an equation derived from NRC (2001; Tables 2 to 5):

$$\Delta\text{BodyE} = (2.88 + 1.036 \times \text{BCS}) \times \Delta\text{BW},$$

where BCS is the average BCS for a cow during a 28-d treatment period. Energy partitioning was predicted based on observed performance:

$$\begin{aligned} \% \text{ to milk, maintenance, or body tissue} &= \text{MilkE}, 0.08 \\ &\times \text{MBW, or } \Delta\text{BodyE}/(\text{MilkE} + 0.08 \\ &\times \text{MBW} + \Delta\text{BodyE}) \times 100, \end{aligned}$$

where % to milk, maintenance, or body tissue is the percentage of apparent energy absorbed partitioned to milk production, maintenance requirement, or body tissue gain, respectively. As an indicator of frame size, an adjusted BW was calculated as $\text{adjusted BW} = \text{BW}/(0.137 \times \text{BCS} + 0.589)$. The adjustment offers an assessment of body size based on BW after making adjustments for BCS.

The milk:feed ratio for a cow during a period was determined as the average daily ECM yield [$\text{ECM} = 0.327 \times \text{milk (kg)} + 12.95 \times \text{fat (kg)} + 7.20 \times \text{protein (kg)}$; Tyrrell and Reid, 1965] over the average daily DMI. Gross energy efficiency, or the percent of energy consumed captured in milk and body tissue gain, was calculated as the average MilkE and ΔBodyE divided by the average gross energy intake during a 28-d treatment period. Individual feed nutrient analyses were used

to calculate the gross energy of each diet, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0, Michigan State University, East Lansing). Energy values for each nutrient were assigned according to Merrill and Watt (1973): 4.20 kcal/g of carbohydrate, 5.65 kcal/g of CP, 9.50 kcal/g of FA estimated from ether extract, 3.95 kcal/g of sugar, and 3.62 kcal/g of fermented acid.

To determine income over feed cost (**IOFC**), daily feed cost for each diet was calculated using economic values for commodities in the Midwestern United States in the fall of 2013. Commodity prices (\$/kg of DM) used were \$0.22/kg of corn silage, \$0.11/kg of legume silage, \$0.10/kg of wheat straw, \$0.22/kg of soybean hulls, \$0.41/kg of whole cottonseed, \$0.34/kg of ground corn, \$0.33/kg of high moisture corn, \$0.56/kg of soybean meal, \$1.55/kg of fat supplement, \$0.13/kg of vitamin and mineral mix, \$0.22/kg of limestone, \$0.22/kg of sodium bicarbonate, and \$0.45/kg of dicalcium phosphate. Milk income was determined for a cow based on individual production of protein (\$7.11/kg), fat (\$3.46/kg), lactose (\$0.87/kg), and milk (\$0.04/kg). Based on average production for all cows and the economic values for components, average milk price was determined to be \$17.47 per 45.4 kg. Gain of BW was assigned an economic value of \$1.78/kg, which was based on the value of a cull cow.

Apparent diet energy density (**DietNE_L**; Mcal/kg) was calculated for each cow as

$$\text{DietNE}_L = (\text{MilkE} + 0.08 \times \text{MBW} + \Delta\text{BodyE})/\text{DMI},$$

where MilkE, MBW, ΔBodyE, and DMI are based on individual cow performance when fed a diet; individual DietNE_L was averaged by diet (HI or LO) to determine the mean DietNE_L for each diet. Multiple of maintenance (**MM**) was calculated based on (1) production and (2) actual intake. Multiple of maintenance based on requirements for observed production was calculated as:

$$\begin{aligned} \text{MM}_R &= (\text{MilkE} + 0.08 \times \text{MBW} \\ &+ \Delta\text{BodyE})/(0.08 \times \text{MBW}). \end{aligned}$$

Multiple of maintenance based on actual intake was calculated as

$$\text{MM}_I = (\text{DMI} \times \text{diet energy density})/(0.08 \times \text{MBW}),$$

where diet energy density was the mean DietNE_L for each diet, as described above (1.7 and 1.6 Mcal of NE_L/kg for HI and LO diets, respectively).

Table 2. Pearson correlations for the repeatability of feed efficiency traits across high (HI) and low (LO) starch diets¹

Group ²	Trait ³					P-value ⁴				
	RFI	Milk: feed	Gross efficiency	IOFC	DMI	RFI	Milk: feed	Gross efficiency	IOFC	DMI
All cows	0.73	0.72	0.15	0.84	0.92	<0.01	<0.01	0.13	<0.01	<0.01
Primiparous	0.69	0.72	-0.19	0.89	0.72	<0.01	<0.01	0.22	<0.01	<0.01
Multiparous	0.74	0.73	0.30	0.78	0.87	<0.01	<0.01	0.02	<0.01	<0.01
Experiment 1	0.71	0.72	0.44	0.75	0.88	<0.01	<0.01	0.01	<0.01	<0.01
Experiment 2	0.81	0.74	0.16	0.94	0.97	<0.01	<0.01	0.46	<0.01	<0.01
Experiment 3	0.73	0.68	-0.17	0.83	0.95	<0.01	<0.01	0.35	<0.01	<0.01
Experiment 4	0.61	0.58	-0.55	0.88	0.93	<0.01	<0.01	0.01	<0.01	<0.01

¹Correlations are the relationships between animal performance when fed a HI diet and animal performance when fed a LO diet.

²Animals included for each analysis included all cows (n = 109), primiparous cows (n = 44), multiparous cows (n = 65), experiment 1 cows (n = 32), experiment 2 cows (n = 25), experiment 3 cows (n = 32), and experiment 4 cows (n = 20).

³RFI = residual feed intake, kg of DM/d; milk:feed = ECM per unit of feed; IOFC = income over feed cost, \$/d.

⁴P-values for repeatability correlations reported for animal groups.

Statistical Analysis

Dry matter intake for an individual cow during each 28-d treatment period was regressed as a function of major energy sinks using the GLM Procedure in SAS (version 9.3, SAS Institute Inc., Cary, NC). To define RFI, DMI was modeled as follows:

$$\begin{aligned} \text{DMI}_i = & \beta_0 + \beta_1 \times \text{MilkE}_i + \beta_2 \times \text{MBW}_i \\ & + \beta_3 \times \Delta\text{BodyE}_i + \text{Parity} + \text{Experiment} \\ & + \text{Cohort}(\text{Experiment}) \\ & + \text{Diet}(\text{Cohort} \times \text{Experiment}) + \epsilon_i, \end{aligned}$$

where DMI_i was the observed DMI, MilkE_i was the observed milk energy output, MBW_i was the average $\text{BW}^{0.75}$, and ΔBodyE_i was the estimated change in body energy, based on measured BW and BCS, for ith

cow. Parity (1 or 2+), experiment (1, 2, 3, or 4), cohort (1 or 2) nested within experiment, and diet (HI or LO) nested within cohort and experiment were fixed effects, where a cohort was a group of cows that received a diet in the same sequence (i.e., HI then LO or LO then HI). Residual feed intake was defined as the error term in the model (ϵ_i). To determine the number of animals that changed their efficiency ranking when they were switched from one diet to another, cows were grouped into high (**HRFI**), medium (**MRFI**), and low (**LRFI**) RFI groups. Cows >0.5 SD of the mean RFI for a cohort were classified as HRFI, cows <-0.5 SD were classified as LRFI, and those ± 0.5 SD were classified as MRFI. Weekly estimates of RFI for a cow were also computed using data collected during each week (8 wk per experiment) according to the model previously stated except the fixed effect of experimental week nested within cohort and experiment replaced the fixed effect of diet

Table 3. Pearson and Spearman correlations for the repeatability of weekly residual feed intake (RFI) across experimental week for cows (n = 109) fed high and low starch diets¹

Week ^{2,3}	1	2	3	4	5	6	7	8
1	1.00	0.66	0.66	0.54	0.48	0.59	0.38	0.42
2	0.62	1.00	0.75	0.69	0.60	0.61	0.54	0.54
3	0.64	0.67	1.00	0.66	0.68	0.63	0.48	0.55
4	0.54	0.66	0.65	1.00	0.61	0.64	0.61	0.61
5	0.49	0.55	0.64	0.62	1.00	0.73	0.62	0.57
6	0.53	0.54	0.59	0.61	0.70	1.00	0.63	0.67
7	0.37	0.51	0.50	0.63	0.64	0.62	1.00	0.67
8	0.44	0.54	0.54	0.57	0.53	0.66	0.64	1.00

¹Pearson correlation coefficients are above the diagonal; Spearman's correlation coefficients are below the diagonal. All correlation coefficients were highly significant ($P < 0.01$).

²Week of experiment. Diet change occurred after completion of wk 4, so all cows were fed the same diet (either high or low starch) for wk 1 through 4, and then the other diet for wk 5 through 8.

³Weekly RFI was estimated from performance of each cow for the specified week, with change in body energy being calculated using change in BW defined as the difference between average BW for the week minus the average BW for the previous week.

Table 4. Least squares means of performance and efficiency of cows (n = 109) fed high (HI) and low (LO) starch diets

Item ¹	Diet		SEM	P-value ²				
	HI	LO		Diet	Exp ³	Parity	Period (Exp)	Diet × Exp
Intake and production								
DMI, kg/d	25.7	25.2	0.24	0.09	<0.01	<0.01	0.80	0.21
Milk yield, kg/d	42.3	40.2	0.67	0.03	<0.01	<0.01	0.17	0.69
MilkE, Mcal/d	29.6	28.9	0.45	0.27	<0.01	<0.01	0.16	0.39
Milk fat, %	3.63	3.88	0.05	<0.01	<0.01	<0.01	0.76	<0.01
Milk protein, %	3.13	3.01	0.03	<0.01	<0.01	<0.01	0.05	0.99
BW and Δ Tissue								
MBW, kg ^{0.75}	131	130	0.92	0.77	0.02	<0.01	0.88	1.00
Δ BW, kg/d	0.63	0.35	0.05	<0.01	0.49	0.49	<0.01	0.12
Δ BCS, units/28 d	0.16	0.06	0.02	<0.01	0.53	<0.01	<0.01	0.01
Δ BodyE, Mcal/d	3.76	2.04	0.32	<0.01	0.41	0.35	<0.01	0.07
Energy partitioning ⁴								
% to milk	67.5	69.7	0.66	0.02	0.01	<0.01	<0.01	0.06
% to maintenance	24.2	25.8	0.35	<0.01	<0.01	<0.01	0.01	0.79
% to body tissue	8.30	4.48	0.74	<0.01	0.87	0.05	<0.01	0.13
Efficiency								
Milk:feed	1.66	1.65	0.02	0.80	<0.01	0.05	<0.01	0.04
Gross efficiency, %	31.0	29.1	0.39	<0.01	<0.01	0.45	<0.01	0.98
IOFC, \$/d	10.6	10.5	0.21	0.65	<0.01	<0.01	0.06	0.72
RFI, kg of DM/d	-0.01	0.03	0.15	0.86	0.99	0.83	1.00	0.99

¹MilkE = milk energy output; MBW = metabolic BW (BW^{0.75}); Δ BW = change in BW; Δ BCS = change in BCS per 28-d treatment period; Δ BodyE = change in body energy; milk:feed = ECM per unit of feed; IOFC = income over feed cost; RFI = residual feed intake.

²P-value associated with main effects of diet, experiment, parity, period nested within experiment, and the interaction between diet and experiment.

³Exp = experiment.

⁴Energy partitioning: % to milk = percent of apparently absorbed energy partitioned to milk production; % to maintenance = percent of apparently absorbed energy partitioned to maintenance; percent of apparently absorbed energy partitioned to body tissue gain.

Table 5. Pearson correlations of efficiency and performance with residual feed intake as determined from each 28-d treatment period¹

Item ²	Parity ³						Diet			
	All cows		Primiparous		Multiparous		HI		LO	
	r	P-value ⁴	r	P-value	r	P-value	r	P-value	r	P-value
Intake and production										
DMI, kg/d	0.38	<0.01	0.56	<0.01	0.54	<0.01	0.36	<0.01	0.40	<0.01
MilkE, Mcal/d	0.00	1.00	0.12	0.27	-0.03	0.72	-0.06	0.56	0.05	0.59
BW, BCS, and Δ Tissue										
MBW, kg ^{0.75}	0.00	1.00	-0.01	0.92	0.00	0.96	0.02	0.81	-0.02	0.80
BCS	-0.11	0.09	-0.10	0.33	-0.13	0.15	-0.06	0.57	-0.17	0.07
Δ BW, kg/d	0.00	0.95	0.20	0.06	-0.08	0.40	-0.09	0.37	0.11	0.24
Δ BodyE, Mcal/d	0.00	1.00	0.19	0.08	-0.08	0.37	-0.08	0.41	0.10	0.30
Energy partitioning ⁵										
% to milk	-0.01	0.89	-0.11	0.29	0.03	0.74	0.02	0.85	-0.04	0.67
% to body tissue	0.01	0.88	0.16	0.13	-0.06	0.50	-0.06	0.50	0.10	0.32
Efficiency										
Milk:feed	-0.39	<0.01	-0.34	<0.01	-0.40	<0.01	-0.45	<0.01	-0.32	<0.01
Gross efficiency, %	-0.35	<0.01	-0.14	0.19	-0.44	<0.01	-0.46	<0.01	-0.25	0.01
IOFC, \$/d	-0.13	0.05	-0.08	0.48	-0.17	0.05	-0.21	0.03	-0.06	0.54

¹Performance and efficiency of cows (n = 109) fed high (HI) and low (LO) starch diets. Two records per cow (1 for performance on HI diets and 1 for performance on LO diets) were included for all analyses except those that examine correlations within diet.

²MilkE = milk energy output; MBW = metabolic BW (BW^{0.75}); Δ BW = change in BW; Δ BodyE = change in body energy; milk:feed = ECM per unit of feed; IOFC = income over feed cost.

³Correlations including only primiparous cows (n = 44) or multiparous cows (n = 65).

⁴P-value associated with the preceding correlation of production and efficiency traits with residual feed intake.

⁵Energy partitioning: % to milk = percent of apparently absorbed energy partitioned to milk production; percent of apparently absorbed energy partitioned to body tissue gain.

nested within cohort and experiment. Weekly RFI estimates from wk 1, 2, 3, and 4 and wk 5, 6, 7, and 8 were used to determine within-diet repeatability of RFI.

To determine differences in performance between most efficient and least efficient animals, 11 cows with the lowest RFI (lowest 10%) and 11 cows with the highest RFI (highest 10%) for each diet (HI or LO) across all 4 experiments were compared with each other. The effect of efficiency status was determined using the GLM Procedure of SAS according to the model $Y_i = \mu + R_i + \varepsilon_i$, where μ is the overall mean, R_i is the fixed effect of efficiency group (i = efficient or inefficient), and ε_i is the residual error. The PDIF option was used to compare least squares means between the 2 efficiency groups. Production, efficiency, and energy partitioning responses to HI and LO diets were analyzed using the MIXED Procedure in SAS, with fixed effects of experiment, diet, parity, and period nested within experiment,

all interactions of fixed effects, and the random effect of cow nested within experiment and parity.

We determined repeatability for feed efficiency and performance traits with both intra- and interclass correlation coefficients. The intraclass correlation coefficient was calculated according to the following equation: $\sigma_b / (\sigma_b + \sigma_w)$, where σ_b is equal to the between-animal variance and σ_w is equal to the within-animal variance. The interclass correlation coefficient was determined using the CORR procedure of SAS. Pearson and Spearman correlation coefficients were obtained for the relationship between the trait of interest when cows were fed the HI diet and the same trait when cows were fed the LO diet. For correlations of traits with 28-d treatment period RFI, data from both treatments for each cow were used, so that the performance from both diets was included. Correlations and main effects were considered significant at $P < 0.05$ and trends at $P < 0.10$. Interac-

Figure 1. The relationship between residual feed intake (RFI) when cows were fed a low starch diet and a high starch diet ($y = -0.71x$; $R^2 = 0.53$). Each data point represents an individual cow ($n = 109$) and her performance when she was fed each diet. Open diamonds ($\diamond$) indicate experiment 1 primiparous cows ($n = 7$); closed diamonds ($\blacklozenge$) indicate experiment 1 multiparous cows ($n = 25$); open triangles ($\triangle$) indicate experiment 2 primiparous cows ($n = 10$); closed triangles ($\blacktriangle$) indicate experiment 2 multiparous cows ($n = 15$); open circles ($\circ$) indicate experiment 3 primiparous cows ($n = 16$); closed circles ($\bullet$) indicate experiment 3 multiparous cows ($n = 16$); open boxes ($\square$) indicate experiment 4 primiparous cows ($n = 11$); and closed boxes ($\blacksquare$) indicate experiment 4 multiparous cows ($n = 9$). Dotted lines represent ± 0.5 SD from the mean RFI for each diet.

tions were considered significant at $P < 0.10$ and trends at $P < 0.15$.

RESULTS

Repeatability of Feed Efficiency

In general, cows that were feed efficient (LRFI) within a production level when they were fed one diet were still efficient when they were fed the other diet. Pearson and Spearman correlation coefficients were similar for the repeatability of RFI, so only Pearson correlation coefficients are reported. The interclass correlation coefficients for the repeatability of RFI, milk:feed, IOFC, gross efficiency, and DMI across HI and LO diets are listed in Table 2. For all cows, RFI ($r = 0.73$; $P < 0.01$), milk:feed ($r = 0.72$; $P < 0.01$), IOFC ($r = 0.84$; $P < 0.01$), DMI ($r = 0.92$; $P < 0.01$), and MilKE ($r = 0.89$; $P < 0.01$) were repeatable across HI and LO diets for the 28-d treatment periods. The corresponding intraclass correlation coefficients for RFI, milk:feed, IOFC, DMI, and MilKE were 0.73, 0.72, 0.84, 0.89, and 0.88, respectively. However, the repeatabilities of gross feed efficiency (energy output as milk and body tissue gain as a proportion of gross energy intake) and Δ BodyE across diets were low ($r = 0.15$ and $r = -0.29$; $P = 0.13$ and $P < 0.01$, respectively). The corresponding intraclass correlation coefficients for gross efficiency and Δ BodyE were 0.09 and 0, respectively. Because we determined repeatability based on 2 measurements per cow (one measurement for the HI diet and one measurement for the LO diet), intra- and interclass correlation coefficients were similar; therefore, we define repeatability as the interclass correlation coefficient for the remainder of this paper unless otherwise specified. Figure 1 illustrates the relationship between RFI when cows were fed HI and LO diets. When diets were switched, 61 cows (56%) maintained their RFI group (HRFI, MRFI, or LRFI), and of the 48 cows that changed groups, only 4 cows changed from LRFI to HRFI or HRFI to LRFI. Repeatabilities of RFI, milk:feed, IOFC, and DMI were similar across experiments and parity. Residual feed intake was also repeatable across experimental week (Table 3). The average repeatability of weekly RFI within-diet (wk 1 through 4 and wk 5 through 8) was 0.65 and across diet (wk 1 through 4 compared with 5 through 8) was 0.56. Thus, across diet repeatability of weekly RFI was ~86% of within-diet repeatability.

Dry Matter Intake Model

Among the 4 experiments, partial regression coefficients for MilKE, MBW, and Δ BodyE for the model used to predict DMI ranged from 0.28 to 0.41, 0.02 to

0.13, and -0.03 to 0.11 , respectively. When animals from all experiments were included in the model, coefficients for MilKE, MBW, Δ BodyE, and parity 1 were 0.35, 0.09, 0.05, and -1.96 , respectively, and the model R^2 was 0.86. Milk energy output was always significant ($P < 0.01$), and MBW was significant for all models ($P < 0.01$) except for experiment 4 ($P = 0.46$), which was likely due to the greater parity effect in that experiment (55% primiparous). When parity was removed from the model, coefficients for MilKE, MBW, and Δ BodyE were 0.42, 0.13, and 0.04, respectively, and the model R^2 was 0.83. For our analysis, we used the full model, which included the fixed effect of parity.

Animal Performance

Table 4 shows performance and feed efficiency least squares means when cows were fed HI and LO diets. Gross feed efficiency was greater when cows were fed HI diets ($P < 0.01$) and DMI tended to be greater for HI diets ($P = 0.09$), but milk:feed and IOFC were not different between diets ($P = 0.80$ and $P = 0.65$, respectively). Milk yield was greater when cows were fed HI diets ($P = 0.03$), but MilKE was not affected by diet ($P = 0.27$). Milk fat concentration was reduced (3.88 vs. 3.63%; $P < 0.01$) and milk protein concentration was increased (3.01 vs. 3.13%; $P < 0.01$) when cows were fed HI diets. When compared with LO diets, HI diets increased gain in BW, BCS, and BodyE ($P < 0.01$). Cows partitioned a greater proportion of energy toward body tissue gain and less energy toward milk when fed HI diets ($P < 0.02$). A diet by experiment interaction was found for Δ BCS ($P = 0.01$), milk fat concentration ($P < 0.01$), milk:feed ($P = 0.04$), Δ BodyE ($P = 0.07$), and energy partitioned to milk ($P = 0.06$).

Production and RFI

Correlations between RFI and production and other measures of feed efficiency are listed in Table 5. Residual feed intake was not correlated with production and BW variables, which was expected because RFI was estimated based on observed performance. Income over feed cost, gross feed efficiency, and milk:feed correlated negatively with RFI ($r = -0.13$, $r = -0.35$, $r = -0.39$; $P = 0.05$, $P < 0.01$, and $P < 0.01$, respectively), though IOFC was not related to RFI when cows were fed LO diets ($r = -0.06$; $P = 0.54$). Multiple of maintenance based on requirements was not related to RFI ($r = 0.01$; $P = 0.87$), but MM_I correlated positively with RFI ($r = 0.47$; $P < 0.01$; data not shown). Body condition score tended to correlate negatively with RFI ($r = -0.11$, $P = 0.09$), but was not related to RFI when cows were fed HI diets ($r = -0.06$; $P = 0.57$). Im-

portantly, energy partitioning was not associated with RFI ($P > 0.80$), and MilkE, MBW, and Δ BodyE were also not related to RFI ($P = 1.0$). Figure 2 illustrates the relationship between daily feed cost and product value for HRFI, MRFI, and LRFI cows. The slopes for HRFI and LRFI cows were similar, but the y-intercept was smaller for LRFI cows, indicating a savings in feed cost of about \$0.80/d for the same amount of product produced regardless of level of production.

Most Efficient Versus Least Efficient Cows

No significant differences were observed for milk and component yields (data not shown), MilkE, MBW, adjusted BW, Δ BodyE, Δ BW, BCS, Δ BCS, or energy partitioning between the most feed efficient cows (10% lowest RFI; $n = 11$) and least feed efficient cows (10% highest RFI; $n = 11$; Table 6). When compared with the most efficient cows, DMI was greater for the least efficient cows when fed HI (29.6 vs. 25.4 kg/d; $P < 0.01$) and LO diets (28.8 vs. 23.0 kg/d; $P < 0.01$). The most efficient cows had significantly greater milk:feed when fed the HI (1.83 vs. 1.51; $P < 0.01$) and LO diets (1.71 vs. 1.49; $P = 0.01$). Gross feed efficiency was also greater for the most efficient cows when fed HI diets (34.2 vs. 27.5%; $P = 0.01$). Though only a weak trend, IOFC was greater for the most efficient cows when HI diets were fed (\$12.4 vs. \$10.4; $P = 0.15$), but was similar between the most efficient and least efficient cows when LO diets were fed (\$11; $P = 0.89$). When compared with the least efficient cows, the most efficient cows had lower daily feed cost for HI (\$7.1 vs. \$8.3; $P = 0.01$) and LO diets (\$5.7 vs. \$7.3; $P < 0.01$), but similar product output value (value of milk and body gain; $P > 0.20$).

DISCUSSION

We observed that RFI was repeatable across HI and LO diets, and that only 4 of 109 cows changed their efficiency ranking from HRFI to LRFI or vice versa. Differences between the HI and LO diets in each of the 4 studies were great enough to cause significant differences in milk yield and component concentrations, feed intake, BW gain, energy partitioning, or all 4. Thus, these findings provide support for the use of RFI as a tool to identify animals that eat less than others within a production level, independent of the type of diet fed. Although some re-ranking occurred when cows changed from one diet to the other, this re-ranking was minor, so that within a level of production, cows that eat less than contemporaries when fed a high starch diet should also consume less than contemporaries when fed a low starch diet. As expected, RFI was independent

of production and BW, and cows with low RFI ate less feed to produce the same amount of product as contemporaries.

Repeatability of RFI

The repeatability of RFI across diets in this study was greater than that shown for beef cattle during growing and finishing phases; however, our diets were not as different as the diets in those studies. Durunna et al. (2011) examined the repeatability of RFI in beef steers ($n = 181$) fed consecutive grower (80% concentrate) and finisher diets (100% concentrate) across growing and finishing periods. They determined that RFI was moderately repeatable ($r = 0.33$) and that 55% of the steers changed feed efficiency ranking (RFI > 0.5 SD, RFI < 0.5 SD, or RFI ± 0.5 SD) from period 1 to period 2 and 16% changed from high RFI to low RFI or vice versa. Kelly et al. (2010a,b) fed high forage diets to beef heifers in the growing period followed by high-concentrate diets during the finishing period and found RFI to be more repeatable ($r = 0.62$). One reason that the repeatability of RFI in our study was greater than in the studies of Kelly et al. (2010b) and Durunna et al. (2011) could be that their diets differed in % forage, whereas our HI and LO diets had similar % forage. Additionally, the cattle in both of those studies were at different stages of growth between measurement periods. Poor growth during the first period could have a compensatory effect of growth and efficiency in the second period, which could have also reduced repeatability.

Estimation of RFI across different periods may be more repeatable if measurements are obtained from periods when animals are in similar physiological states. The diets fed in the current study elicited quite different responses in milk yield and component concentrations, in addition to energy partitioning. Because changes in BW are difficult to quantify, shifting energy partitioning to BW gain might have been expected to introduce more error into the estimation of RFI when cows were fed HI diets. However, production differences and changes in energy partitioning observed between HI and LO diets in this study did not seem to affect the repeatability of RFI. Residual feed intake for each 28-d treatment period was highly repeatable ($r = 0.73$) across the diets, suggesting that our ability to identify the most efficient cows was not impeded by diets that altered performance and shifted energy partitioning. That weekly estimates of RFI were also repeatable within and across diet suggests that we were able to account for many of the production and BW changes that occurred from one week to the next that affect the calculation of RFI. Repeatability of weekly RFI was ex-

Figure 2. Relationship between daily feed cost and product value by residual feed intake (RFI) groups for cows fed high and low starch diets. Product value was determined by the sum of mean daily milk income and mean daily BW gain value. Milk income was determined for a cow based on individual production of protein (\$7.11/kg), fat (\$3.46/kg), lactose (\$0.87/kg), and milk (\$0.04/kg). Gain of BW was assigned an economic value of \$1.78/kg. Feed cost was determined using the following values for feeds (\$/kg of DM): \$0.22/kg of corn silage, \$0.11/kg of legume silage, \$0.10/kg of wheat straw, \$0.22/kg of soybean hulls, \$0.41/kg of whole cottonseed, \$0.34/kg of ground corn, \$0.33/kg of high moisture corn, \$0.56/kg of soybean meal, \$1.55/kg of fat supplement, \$0.13/kg of vitamin and mineral mix, \$0.22/kg of limestone, \$0.22/kg of sodium bicarbonate, and \$0.45/kg of dicalcium phosphate. High, low, and medium RFI groups were defined as $>$, $<$, or ± 0.5 SD of the mean RFI of each cohort, respectively. Animals in the high RFI group are denoted by $\blacklozenge$. Animals in the low RFI group are denoted by $\circ$. Animals in the medium RFI group are denoted by $\times$. The solid line is the regression line for the high RFI group ($y = 0.28x + 2.33$), the dashed line is the regression line for the medium RFI group, and the dotted line is the regression line for the low RFI group ($y = 0.28x + 1.52$).

pected to be lower than the repeatability of 28-d treatment period RFI because each period averaged data for 28 d and therefore had less measurement error. That RFI was not perfectly repeatable between HI and LO diets or across weeks within diet suggests that genotype by environment interactions may be important or that error is associated with the measurement of RFI from one week to another.

Repeatability of Other Efficiencies

Milk:feed was highly repeatable across diets for the current study, which was higher than the repeatability for gain:feed reported by Kelly et al. (2010b) and Durunna et al. (2011). The repeatability of IOFC across HI and LO diets also was high, suggesting that cows that are most profitable within a group will likely still be the most profitable even when expensive, high starch concentrates, such as corn grain, are replaced with cheaper nonforage fiber sources, such as soybean

hulls. We realize that feed prices change frequently and that corn prices in September 2014 were about half of what they were in 2013. In light of this, we reanalyzed IOFC data after changing concentrate ingredient prices to those of September 2014 (0.16, 0.16, 0.77, 0.28, and 0.47 \$/kg of DM for ground corn, high moisture corn, soybean meal, soybean hulls, and whole cottonseed, respectively). After adjusting concentrate prices, the repeatability of IOFC across diets was similar to the across diet repeatability of IOFC as determined from 2013 ingredient prices. Repeatability for DMI was 0.92, which is higher than results reported by Kelly et al. (2010b). The high repeatability of Milke ($r = 0.89$; $P < 0.01$; data not shown) may have played a role in determining the repeatability of DMI, as well as RFI and milk:feed because production drives DMI. The low repeatability of Δ BodyE suggests that much more error is associated with determining Δ BodyE, which may have influenced the low repeatability of gross feed efficiency. Reasons for such a low repeatability for gross

Table 6. Performance of the most efficient [lowest residual feed intake (RFI); $n = 11$] and least efficient cows (highest RFI; $n = 11$) fed high (HI) and low (LO) starch diets¹

Item ²	Diet							
	HI				LO			
	Most efficient	Least efficient	SE	<i>P</i> -value ³	Most efficient	Least efficient	SE	<i>P</i> -value
Intake and production								
DMI, kg/d	25.4	29.6	1.02	<0.01	23.0	28.8	1.06	<0.01
MilkE, Mcal/d	32.4	30.9	1.98	0.60	27.6	29.9	1.84	0.39
Feed cost, \$/d	7.13	8.30	0.30	0.01	5.66	7.31	0.31	<0.01
Product value, \$/d	20.7	19.7	1.17	0.56	16.7	18.8	1.16	0.22
BW, BCS, and Δ Tissue								
MBW, kg ^{0.75}	136	137	3.25	0.83	133	133	2.93	1.00
Adjusted BW, kg	714	734	27.7	0.62	699	714	24.6	0.67
BCS	2.90	2.74	0.16	0.48	2.84	2.68	0.13	0.42
Δ BW, kg/d	0.65	0.56	0.24	0.77	0.22	0.54	0.14	0.12
Δ BCS, units/28 d	0.15	0.17	0.08	0.83	0.04	0.17	0.06	0.18
Δ BodyE, Mcal/d	3.82	3.30	1.35	0.79	1.29	3.02	0.80	0.14
Energy partitioning ⁴								
% to milk	68.8	68.3	2.33	0.88	70.0	68.2	1.71	0.47
% to maintenance	23.4	25.1	1.44	0.42	27.6	25.1	1.26	0.17
% to body tissue	7.7	6.6	2.84	0.77	2.4	6.7	2.21	0.18
Efficiency								
Milk:feed	1.83	1.51	0.07	<0.01	1.71	1.49	0.05	0.01
Gross efficiency, %	34.2	27.5	1.66	0.01	30.0	27.2	1.27	0.14
IOFC, \$/d	12.4	10.4	0.94	0.15	10.7	10.5	0.86	0.89
RFI, kg of DM/d	-2.87	2.52	0.31	<0.01	-2.20	2.63	0.26	<0.01

¹Most efficient cows (lowest RFI; $n = 11$) and least efficient cows (highest RFI; $n = 11$) were selected based on their ranking among all cows ($n = 109$) for residual feed intake when fed high and low starch diets separately.

²MilkE = milk energy output; product value = daily income from milk and body gain; MBW = metabolic BW ($BW^{0.75}$); adjusted BW = BW adjusted to a BCS of 3, defined as $[BW/(0.137 \times BCS + 0.589)]$; Δ BW = change in BW; Δ BCS = change in BCS per 28-d period; Δ BodyE = change in body energy; milk:feed = ECM per unit of feed; IOFC = income over feed cost.

³*P*-value associated with differences in efficiency group (efficient or inefficient).

⁴Energy partitioning: % to milk = percent of apparently absorbed energy partitioned to milk production; % to maintenance = percent of apparently absorbed energy partitioned to maintenance; percent of apparently absorbed energy partitioned to body tissue gain.

feed efficiency are not clear. The repeatability of gross feed efficiency for cows that were fed the HI diet in period 1 followed by the LO diet in period 2 was 0.15 ($P = 0.27$). For cows fed the LO diet in period 1 followed by the HI diet in period 2, repeatability of gross efficiency was 0.24 ($P = 0.07$). These findings suggest that the sequence in which diets were fed did not significantly alter the repeatability of gross feed efficiency across HI and LO diets.

RFI and Performance

As expected, DMI correlated positively with RFI. These results are similar to other reports for beef and dairy animals (Castro Bulle et al., 2007; Kelly et al., 2010b; Green et al., 2013). Consistent with these results, the most feed efficient cows ($n = 11$) ate ~5 kg of DM/d less than the least efficient cows in our study. Similar to reports of negative correlations between RFI and gain:feed in beef cattle (Arthur et al., 2001; Castro Bulle et al., 2007; Kelly et al., 2010b), milk:feed cor-

related negatively with RFI; this was expected because cows with low RFI eat less than their cohorts to maintain a similar level of production, and this difference in DMI would increase milk:feed. Multiple of maintenance based on energy requirements was not related to RFI, but was highly correlated with both gross feed efficiency and milk:feed ($r = 0.8$ and $r = 0.7$, respectively; data not shown), confirming that RFI is independent of the dilution of maintenance, unlike milk:feed and gross feed efficiency. Residual feed intake quantifies efficiency within a production level and allows for the identification of animals that convert gross energy into NE more efficiently by reducing energetic losses in feces, urine, gas, and nonmaintenance heat and thus is independent of the dilution of maintenance when multiple of maintenance is calculated based on requirements for observed production (MM_R).

When compared with the least feed efficient cows based on RFI ($n = 11$), the most efficient cows ($n = 11$) had similar MilkE, MBW, Δ BW, Δ BodyE, Δ BCS, and average BCS for both HI and LO diets, and RFI was

not correlated with any of these traits, as was expected because the model used to derive RFI accounted for these variables. Energy partitioning was not different between efficiency groups and not correlated with RFI. Although each efficiency group contained only 11 animals, it is likely that these production traits would still be similar among the groups if more animals were considered due to the performance variables used in the calculation of RFI. Because body energy change is accounted for in the prediction of RFI, it is expected that cows with low RFI will not be any more likely to mobilize body tissue to support production than cows with high RFI. The independence of RFI from BW loss is important because excessive tissue mobilization can lead to negative energy balance, which is related to metabolic diseases and poor fertility (Butler et al., 1981; Collard et al., 2000). When BW change was included in the model to derive RFI, RFI was not associated with reproductive performance of beef cattle (Arthur et al., 2005; Basarab et al., 2007; Blair et al., 2013). However, more research needs to be conducted to determine if selection for RFI will influence fertility in dairy cattle.

Production Responses to High and Low Starch Diets

Similar to results shown by others (Ipharraguerre et al., 2002; Voelker and Allen, 2003; Ranathunga et al., 2010; Ferraretto et al., 2011; Weiss et al., 2011), feeding diets that differed in starch content in our study altered DMI, milk yield, milk component concentrations, Δ BW, and Δ BCS. We also observed differences in energy partitioning, with more energy partitioned to milk and less to body gain when cows were fed LO diets. We observed a significant interaction of diet and experiment for energy partitioned to milk because diets for experiments 3 and 4 resulted in large shifts in partitioning, but diets in experiments 1 and 2 did not significantly alter energy partitioning. The interaction of diet and experiment was also significant for Δ BCS and Δ BodyE, with cows in all experiments having greater Δ BCS and Δ BodyE when fed HI diets, but differences between diets were only significant for experiment 3 (Boerman et al., 2015a). One reason that differences were significant for experiment 3 and not experiments 1, 2, and 4 could be that the LO diet for experiment 3 was formulated by replacing starch with forage, nonforage fiber, and supplemental fat (Boerman et al., 2015a); in experiments 1 (Boerman et al., 2015b), 2, and 4, nonforage fiber replaced starch to formulate LO diets. Gross feed efficiency was greater when cows were fed HI diets, which could have been due to the greater energy content of HI diets or to increased lipogenesis that was observed for HI diets (as indicated by increased Δ BodyE and Δ BW), but similar MilkE for both diets.

RFI and Profitability

Because feed accounts for a large proportion of production costs, it is of interest whether RFI is related to profitability. Animals with low RFI consume less feed than contemporaries to yield the same amount of product, so theoretically these animals should cost less to feed on a daily basis. Our results suggest that low-RFI cows will be more profitable than high-RFI cows when the cost of all other maintenance factors for these animals (breeding, health, and so on) are held constant. However, because RFI was not strongly correlated with IOFC, our results indicate that profitability is mostly independent of RFI when using IOFC as an indicator of profit because RFI is independent of MM_R , and MM_R is a major determinant of profitability (VandeHaar and St-Pierre, 2006).

CONCLUSIONS

We conclude that RFI is repeatable across high and low starch diets fed to mid-lactation dairy cows. Our results suggest that cows that have low RFI when eating diets that are high in starch content, as is typical for the Midwestern United States, will also still have low RFI when consuming diets that are high in nonforage fiber sources, such as soybean hulls. Residual feed intake, unlike milk:feed and gross feed efficiency, is independent of multiple of maintenance on a requirement basis, so it will be useful for identifying efficient animals independent of the dilution of maintenance. Although IOFC may be independent of RFI, cows with low RFI will cost less to feed on a daily basis because DMI is lower for cows with low RFI.

ACKNOWLEDGMENTS

The authors acknowledge R. J. Tempelman, J. S. Liesman, D. G. Main, and C. L. Preseault (Michigan State University), as well as the staff of the Michigan State University Dairy Cattle Field Laboratory, for their assistance in this experiment. This project was supported by Agriculture and Food Research Initiative Competitive Grant no. 2011-68004-30340 from the USDA National Institute of Food and Agriculture (Washington, DC) and by Michigan State University AgBioResearch.

REFERENCES

- AOAC. 1990. Official Methods of Analysis. 15th ed. Association of Official Analytical Chemists, Gaithersburg, MD.
- Arthur, P. F., R. M. Herd, J. F. Wilkins, and J. A. Archer. 2005. Maternal productivity of Angus cows divergently selected for post-weaning residual feed intake. *Aust. J. Exp. Agric.* 45:985–993.

- Arthur, P. F., G. Renand, and D. Krauss. 2001. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. *Livest. Prod. Sci.* 68:131–139.
- 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.
- Blair, E. E., J. M. Bormann, D. W. Moser, and T. T. Marston. 2013. Relationship between residual feed intake and female reproductive measurements in heifers sired by high- or low- residual feed intake. *Prof. Anim. Sci.* 29:46–50.
- Boerman, J. P., S. B. Potts, M. J. VandeHaar, M. S. Allen, and A. L. Lock. 2015a. Milk production responses to a change in dietary starch concentration vary by production level in dairy cattle. *J. Dairy Sci.* 98:4698–4706. <http://dx.doi.org/10.3168/jds.2014-8999>.
- Boerman, J. P., S. B. Potts, M. J. VandeHaar, and A. L. Lock. 2015b. Effects of partly replacing dietary starch with fiber and fat on milk production and energy partitioning. *J. Dairy Sci.* <http://dx.doi.org/10.3168/jds.2015-9467>.
- Butler, W. R., R. W. Everett, and C. E. Coppock. 1981. The relationships between energy balance, milk production and ovulation in postpartum Holstein cows. *J. Anim. Sci.* 53:742–748.
- Castro Bulle, F. C. P., P. V. Paulino, A. C. Sanches, and R. D. Sainz. 2007. Growth, carcass quality, and protein and energy metabolism in beef cattle with different growth potentials and residual feed intakes. *J. Anim. Sci.* 85:928–936.
- Collard, B. L., P. J. Boettcher, J. C. M. Dekkers, D. Petitclerc, and L. R. Schaeffer. 2000. Relationships between energy balance and health traits of dairy cattle in early lactation. *J. Dairy Sci.* 83:2683–2690.
- Connor, E. E., J. L. Hutchison, H. D. Norman, K. M. Olson, C. P. van Tassell, J. M. Leith, and R. L. Baldwin VI. 2013. Use of residual feed intake in Holsteins during early lactation shows potential to improve feed efficiency through genetic selection. *J. Anim. Sci.* 91:3978–3988.
- Durunna, O. N., M. G. Colazo, D. J. Ambrose, D. McCartney, V. S. Baron, and J. A. Basarab. 2012. Evidence of residual feed intake reranking in crossbred replacement heifers. *J. Anim. Sci.* 90:734–741.
- Durunna, O. N., F. D. N. Mujibi, L. Goonewardene, E. K. Okine, J. A. Basarab, Z. Wang, and S. S. Moore. 2011. Feed efficiency differences and reranking in beef steers fed grower and finisher diets. *J. Anim. Sci.* 89:158–167.
- Ferraretto, L. F., R. D. Shaver, M. Espineira, H. Gencoglu, and S. J. Bertics. 2011. Influence of a reduced-starch diet with or without exogenous amylase on lactation performance by dairy cows. *J. Dairy Sci.* 94:1490–1499.
- Green, T. C., J. G. Jago, K. A. Macdonald, and G. C. Waghorn. 2013. Relationships between residual feed intake, average daily gain, and feeding behavior in growing dairy heifers. *J. Dairy Sci.* 96:3098–3107.
- Hach, C. C., B. K. Bowden, A. B. Kopelove, and S. V. Brayton. 1987. More powerful peroxide Kjeldahl digestion method. *J. Assoc. Off. Anal. Chem.* 70:783–787.
- Ipharraguerre, I. R., R. R. Ipharraguerre, and J. H. Clark. 2002. Performance of lactating dairy cows fed varying amounts of soyhulls as a replacement for corn grain. *J. Dairy Sci.* 85:2905–2912.
- Karkalas, J. 1985. An improved enzymatic method for the determination of native and modified starch. *J. Sci. Food Agric.* 36:1019–1027.
- Kelly, A. K., M. McGee, D. H. Crews, A. G. Fahey, A. R. Wylie, and D. A. Kenny. 2010a. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers. *J. Anim. Sci.* 88:109–123.
- Kelly, A. K., M. McGee, D. H. Crews, T. Sweeney, T. M. Boland, and D. A. Kenny. 2010b. 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.
- Macdonald, K. A., J. E. Pryce, R. J. Spelman, S. R. Davis, W. J. Wales, G. C. Waghorn, Y. J. Williams, L. C. Marett, and B. J. Hayes. 2014. Holstein-Friesian calves selected for divergence in residual feed intake during growth exhibited significant but reduced residual feed intake divergence in their first lactation. *J. Dairy Sci.* 97:1427–1435.
- Merrill, A. and B. Watt. 1973. Energy Value of Foods. USDA Agriculture Research Service, Agriculture Handbook 74. USDA, Washington, DC.
- Mertens, D. R. 2002. Gravimetric determination of amylase-treated neutral detergent fiber in feeds with refluxing in beakers or crucibles: Collaborative study. *J. AOAC Int.* 85:1217–1240.
- NRC. 2001. Nutrient Requirements of Dairy Cattle. 7th ed. Natl. Acad. Press, Washington, DC.
- Pryce, J. E., J. Arias, P. J. Bowman, S. R. Davis, K. A. Macdonald, G. C. Waghorn, W. J. Wales, Y. J. Williams, R. J. Spelman, and B. J. Hayes. 2012. Accuracy of genomic predictions of residual feed intake and 250-day body weight in growing heifers using 625,000 single nucleotide polymorphism markers. *J. Dairy Sci.* 95:2108–2119.
- Ranathunga, S. D., K. F. Kalscheur, A. R. Hippen, and D. J. Schingoethe. 2010. Replacement of starch from corn with nonforage fiber from distillers grains and soyhulls in diets of lactating dairy cows. *J. Dairy Sci.* 93:1086–1097.
- Tempelman, R. J., D. M. Spurlock, M. Coffey, R. F. Veerkamp, L. E. Armentano, K. A. Weigel, Y. de Haas, C. R. Staples, E. E. Connor, Y. Lu, and M. J. VandeHaar. 2015. Heterogeneity in genetic and nongenetic variation and energy sink relationships for residual feed intake across research stations and countries. *J. Dairy Sci.* 98:2013–2026.
- Tyrrell, H. F., and J. T. Reid. 1965. Prediction of the energy value of the milk. *J. Dairy Sci.* 48:1215–1223.
- van Arendonk, J. 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.
- VandeHaar, M. J., and N. St-Pierre. 2006. Major advances in nutrition: Relevance to the sustainability of the dairy industry. *J. Dairy Sci.* 89:1280–1291.
- Voelker, J. A., and M. S. Allen. 2003. Pelleted beet pulp substituted for high-moisture corn: 1. Effects on feed intake, chewing behavior, and milk production of lactating dairy cows. *J. Dairy Sci.* 86:3542–3552.
- Weiss, W. P., W. Steinberg, and M. A. Engstrom. 2011. Milk production and nutrient digestibility by dairy cows when fed exogenous amylase with coarsely ground dry corn. *J. Dairy Sci.* 94:2492–2499.
- Wildman, E. E., G. M. Jones, P. E. Wagner, R. L. Boman, H. F. Troutt, and T. N. Lesch. 1982. A dairy cow body condition scoring system and its relationship to selected production characteristics. *J. Dairy Sci.* 65:495–501.
- Williams, Y. J., J. E. Pryce, C. Grainger, W. J. Wales, N. Linden, M. Porker, and B. J. Hayes. 2011. Variation in residual feed intake in Holstein-Friesian dairy heifers in southern Australia. *J. Dairy Sci.* 94:4715–4725.