Residual feed intake of lactating Holstein-Friesian cows predicted from high-density genotypes and phenotyping of growing heifers

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ABSTRACT

A genomic prediction for residual feed intake (RFI) developed in growing dairy heifers (RFI_{gro}) was used to predict and test breeding values for RFI in lactating cows (RFI_{lac}) from an independent, industry population. A selection of 3,359 cows, in their third or fourth lactation during the study, of above average genetic merit for milk production, and identified as at least 15/16ths Holstein-Friesian breed, were selected for genotyping from commercial dairy herds. Genotyping was carried out using the bovine SNP50 BeadChip (Illumina Inc., San Diego, CA) on DNA extracted from ear-punch tissue. After quality control criteria were applied, genotypes were imputed to the 624,930 single nucleotide polymorphisms used in the growth study. Using these data, genomically estimated breeding values (GEBV) for RFI_{gro} were calculated in the selected cow population based on a genomic prediction for RFI_{gro} estimated in an independent group of growing heifers. Cows were ranked by GEBV and the top and bottom 310 identified for possible purchase. Purchased cows ($n = 214$) were relocated to research facilities and intake and body weight (BW) measurements were undertaken in 99 “high” and 98 “low” RFI_{gro} animals in 4 consecutive groups [(beginning at $d 61 \pm 1.0$ standard error (SE), 91 ± 0.5 SE, 145 ± 1.3 SE, and 191 ± 1.5 SE d in milk, respectively)] to measure RFI during lactation (RFI_{lac}). Each group of ~50 cows (~25 high and ~25 low RFI_{gro}) was in a feed intake facility for 35 d, fed pasture-alfalfa cubes ad libitum, milked twice daily, and weighed every 2 to 3 d. Milk composition was determined 3 times weekly. Body weight change and BW at trial mid-point were estimated by regression of pre- and posttrial BW measurements. Residual feed intake in lactating cows was estimated from a linear model including BW, BW change, and milk component yield (as MJ/d); RFI_{lac} differed consistently between the high and low selection classes, with the overall means for RFI_{lac} being

+0.32 and –0.31 kg of dry matter (DM) per day for the high and low classes, respectively. Further, we found evidence of sire differences for RFI_{lac}, with one sire, in particular, being highly represented in the low RFI_{gro} class, having a mean RFI_{lac} of –0.83 kg of DM per day in 47 daughters. In conclusion, genomic prediction of RFI_{gro} based on RFI measured during growth will discriminate for RFI_{lac} in an independent group of lactating cows.

Key words: residual feed intake, genomic selection, dairy, feed conversion efficiency

INTRODUCTION

Feed conversion efficiency is an important component of profitable dairying and applies both to the feed costs of rearing as well as productive performance. Lifetime feed requirements per unit of milk production decline as the number of lactations increase. Further, within a lactation (or during growth), as productivity increases, feed conversion efficiency increases as the fixed costs of maintenance energy requirements become a smaller proportion of total energy requirements and intake.

Residual feed intake (RFI) is a component of feed conversion efficiency, being the difference between actual and predicted intake. This measure of efficiency has been well studied in growing beef animals (and non-ruminants) but much less so in dairy cattle. It is more difficult to quantify RFI accurately in lactating, relative to growing, cattle because feed intake is higher and quantification of energy requirements and utilization is problematic when, at some stages of lactation, cows can be in significant negative energy balance. Nevertheless, several reports describe successful measurement of RFI in lactating (Korver et al., 1991; van Arendonk et al., 1991; Ngwerume and Mao, 1992; Nieuwhof et al., 1992; Svendsen et al., 1993; Veerkamp et al., 1995) and growing (Nieuwhof et al., 1992; Williams et al., 2011; Waghorn et al., 2012) dairy cattle.

The physiological basis of RFI is not well understood (see Herd and Arthur, 2009 for review). The causative mechanism may be as simple as the relative proportions of visceral mass to carcass mass, given the relatively

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high metabolic activity of the former (Ferrell, 1988). Alternatively, a general change in metabolism may occur, such as that associated with ion pumps or protein turnover (Herd and Arthur, 2009) that might affect heat production relative to tissue deposition. In both cases, the required quantity of feed energy for maintenance, production, or both may differ from a predicted average for a group or population. Certainly, it can be envisaged that a difference in RFI associated with a difference in maintenance energy could be sustained and measured in both growth and lactation, albeit with more difficulty in lactation. In support of this assertion, genetic and phenotypic variation in maintenance energy requirements in young Hereford bulls was also closely associated with RFI (Herd and Bishop, 2000).

In both beef and dairy animals, RFI is a heritable trait (see reviews by Herd et al., 2003; Berry, 2008; Berry and Crowley, 2013). Estimates of heritability are relatively repeatable at different phases of the growth curve (Kelly et al., 2010) and in both growing and lactating dairy cattle (Nieuwhof et al., 1992). Further, there does not appear to be a strong interaction of RFI with diet used during testing. For example, steers that performed well on high-quality, pelleted rations appeared to maintain superior performance on pasture (Herd et al., 2002).

The relationship between RFI measured during growth (RFI_{gro}) and RFI measured during lactation (RFI_{lac}) has not been well established. Groups of cows selected for RFI_{gro} showed divergence for RFI_{lac} on diets of lucerne and pasture cubes with or without supplement of wheat grain (Macdonald et al., 2014). A moderate genetic correlation between RFI_{gro} and RFI_{lac} has been reported ($r = 0.58$; Nieuwhof et al., 1992). One study linked RFI_{lac} during lactation to RFI_{gro} during growth in beef animals (Arthur et al., 1999). Cows that had a low RFI at weaning appeared to require less feed as mature lactating animals, and cow performance was not compromised. Other work has demonstrated moderate repeatability of RFI at different stages of the growth phase, again in beef cattle (Archer et al., 2002). All of these data indicate that RFI may be a lifetime trait.

The experiment described here is the third in a series to examine RFI in Holstein-Friesian dairy cattle. The first experiment determined RFI at 6 to 9 mo of age (Williams et al., 2011; Pryce et al., 2012; Waghorn et al., 2012) and developed a genomic prediction for RFI. The second experiment examined RFI in the first lactation for 183 cows previously identified during growth to be extreme for high or low RFI (Macdonald et al., 2014). The current experiment used the genomically estimated breeding values (**GEBV**) developed for RFI_{gro} in heifers to predict GEBV for RFI_{gro} in an independent

data set of 3,359 cows selected from the general industry population in New Zealand and measure the RFI_{lac} in the predicted extremes. The hypothesis was that genomic markers generated from divergence in RFI_{gro} for growth in Holstein-Friesian heifers would enable identification of mature Holstein-Friesian cows with divergence in RFI_{lac} .

MATERIALS AND METHODS

Animals

Cows ($n = 3,359$), born in 2005 or 2006 (lactations 3 and 4 at the time of testing) and at least 15/16ths Holstein-Friesian, were identified in 224 commercial dairy herds in the South Auckland and Taranaki regions of New Zealand. Ear tissue samples were taken by an ear-punch and DNA extracted as described previously (Pryce et al., 2012).

Genotyping was undertaken with the Bovine SNP50 BeadChip (Illumina Inc., San Diego, CA), which assayed approximately 54,000 SNP. Quality control was applied to the data in a similar manner to that described by Pryce et al. (2012). The genotypes were imputed (using Beagle software: Browning and Browning, 2009) to the 624,930 SNP used in Pryce et al. (2012) derived from the high-density bovine SNP chip (Illumina Inc.), and the combined information from the New Zealand-Australian heifers as the reference data set.

Using the imputed genotype data, GEBV were calculated for RFI_{gro} based on the SNP estimates that were generated from the BayesA model that was presented by Pryce et al. (2012). Briefly, using the estimated SNP effects, a vector of GEBV was calculated for the 3,359 cows: $\text{GEBV} = \mathbf{X}\mathbf{u}$, where $\mathbf{X}$ is a matrix of the cows' genotypes and $\mathbf{u}$ is the vector of SNP effects estimated by the BayesMulti method (Pryce et al., 2012). Correlation of measured RFI with GEBV was 0.31 in the New Zealand heifer data set (Pryce et al., 2012). Animals were ranked by GEBV and the top and bottom 310 identified for possible purchase from 159 farms. After animal health checks (for Johne's disease, enzootic bovine leukemia, mastitis, and bovine viral diarrhoea), 214 of these animals, ranked in the top or bottom 10% for GEBV for RFI_{gro} , were purchased from 112 farms (maximum of 3 cows from any 1 farm) and relocated to the research farm in May 2011, at the end of their third or fourth lactation. Genetic merit for lactation traits (breeding worth) was 95 (± 3 SE) and 99 (± 4 SE) for the low and high RFI_{gro} cows, respectively. This compares with the New Zealand average for Holstein-Friesian cattle in 2010 of 72 (Dairy NZ/LIC, 2010). These cows were tested for RFI during the lactation beginning in spring (July/August) 2011.

The trial was undertaken on the Taranaki Agricultural Research Station Trust research farm near Hawera (39°61'S, 174°31'E) in Taranaki, New Zealand. Cows grazed on a diet of ryegrass and white clover pasture, without additional supplement, typical of a commercial farm, at a stocking rate of 3.25 cows/ha. Calving of the trial cows took place over a 7-wk period beginning on July 11, 2011. Median calving date was August 6, 2011. Cows were transferred to the feed intake facility for 1 of 4 consecutive trials to determine RFI_{lac} .

This trial was approved by the Ruakura Animal Ethics Committee, Hamilton, New Zealand.

Measurement of RFI

The pens in which the calf growth measurements had been made (Waghorn et al., 2012) were modified to allow up to 13 lactating cows continuous access to 7 feed bins. For each trial, approximately 50 cows were allocated across 4 rows of pens, 7 feed bins per row, balanced within row for RFI_{gro} class. On average, each cow spent 5 h/d at the feed bins for a total cow-occupancy of 12 to 13 h per bin per day, with up to 3 h used for cleaning and milking in each 24-h period. This observation and the very high intakes recorded (Table 1) indicate that DMI were not restricted. Individual DMI were measured using an automated feed intake system (Gallagher Animal Management Systems, Hamilton, New Zealand) that recorded all feeding bouts (Waghorn et al., 2012). At the morning milking, manure was removed from the bedding area and feed bins were refilled. The complete bedding area was cleaned out and wood chips replaced with clean material as required (Waghorn et al., 2012). Shade cloth provided protection from wind and sun.

A total of 204 cows were used in groups of 52, 52, 52, and 48 for trials 1, 2, 3, and 4, respectively. Cows were grouped to maximize DIM for each trial by mean calving dates of July 19, August 2, August 17, and August 21 for trials 1, 2, 3, and 4, respectively. All cows in trial 1 completed the 35 d in the pens. In trial 2, 3 cows were removed due to mastitis and 1 because of low milk production. In trial 3, 2 cows were removed because of mastitis; in trial 4, 1 had blood in her milk and was withdrawn. In total, 197 cows completed the study; of the cows removed, 4 were from the high RFI_{gro} class and 3 from the low RFI_{gro} class. With so few cows from any individual farm, farm of origin was not factored into the allocation of cows to trials.

Group 1 was on trial from September 19 to October 24, 2011; group 2 from November 7 to December 12, 2011; group 3 from January 10 to February 20, 2012; and group 4 from February 29 to April 9, 2012. Mean DIM were 61 (1.0 SE), 91 (0.5 SE), 145 (1.3 SE), and

Table 1. Milk component yields, mean BW at mid-trial, BW change $BW\Delta$, daily DMI, and residual feed intake (RFI) during lactation (RFI_{lac}) for cows classified according to GEBV (high or low) for RFI during growth (RFI_{gro}) in each of 4 trial groups over a lactation¹

Item	September				November				January				April				Overall mean ²	
	61 (1.0) DIM		91 (0.5) DIM		145 (1.3) DIM		191 (1.5) DIM		227 (1.3) DIM		245 (1.3) DIM		271 (1.5) DIM		291 (1.5) DIM		Overall mean ²	
	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High
No. of cows	26	26	24	22	26	24	22	22	26	24	22	27	22	27	22	27	98	99
Fat, kg/d	0.84 (0.01)	0.84 (0.02)	0.76 (0.01)	0.76 (0.01)	0.70 (0.01)	0.66 (0.02)	0.66 (0.02)	0.66 (0.02)	0.70 (0.01)	0.66 (0.02)	0.69 (0.02)	0.64 (0.02)	0.69 (0.02)	0.64 (0.02)	0.75 (0.02)	0.72 (0.01)**	0.75	0.72
Protein, kg/d	0.68 (0.01)	0.70 (0.01)	0.68 (0.01)	0.65 (0.02)	0.60 (0.01)	0.60 (0.01)	0.60 (0.02)	0.60 (0.02)	0.60 (0.01)	0.60 (0.02)	0.57 (0.01)	0.54 (0.01)	0.57 (0.01)	0.54 (0.01)	0.64 (0.02)	0.62 (0.01) ^{NS}	0.64	0.62
Lactose, kg/d	0.93 (0.02)	0.93 (0.02)	0.89 (0.02)	0.85 (0.02)	0.74 (0.02)	0.71 (0.02)	0.71 (0.02)	0.71 (0.02)	0.74 (0.02)	0.71 (0.02)	0.66 (0.02)	0.58 (0.02)	0.66 (0.02)	0.58 (0.02)	0.80 (0.02)*	0.77 (0.02) ^{NS}	0.80	0.77
BW, kg	485 (7)	476 (7)	506 (7)	502 (8)	540 (8)	534 (9)	534 (9)	534 (9)	540 (8)	534 (9)	528 (9)	533 (7)	528 (9)	533 (7)	514 (5)	511 (5.6) ^{NS}	514	511
$BW\Delta$, kg/d	0.53 (0.03)	0.48 (0.02)	0.18 (0.03)	0.19 (0.03)	0.12 (0.02)	0.16 (0.03)	0.16 (0.03)	0.16 (0.03)	0.12 (0.02)	0.16 (0.03)	0.15 (0.02)	0.25 (0.04)	0.15 (0.02)	0.25 (0.04)	0.24 (0.02) ^{NS}	0.27 (0.02) ^{NS}	0.24	0.27
DMI, kg/d	24.3 (0.3)	25.1 (0.4)	25.3 (0.4)	25.5 (0.4)	24.2 (0.4)	24.9 (0.6)	24.9 (0.6)	24.9 (0.6)	24.2 (0.4)	24.9 (0.6)	24.5 (0.5)	24.6 (0.3)	24.5 (0.5)	24.6 (0.3)	25.0 (0.2) ^{NS}	25.6 (0.2) ^{NS}	25.0	25.6
RFI_{lac} , kg of DM/d	-0.34 (0.21)	0.34 (0.28)	-0.22 (0.23)	0.24 (0.26)	-0.49 (0.30)	0.53 (0.34)	0.53 (0.34)	0.53 (0.34)	-0.49 (0.30)	0.53 (0.34)	-0.22 (0.36)	0.18 (0.20)	-0.22 (0.36)	0.18 (0.20)	-0.33 (0.34)	0.19 (0.27) ^{NS}	-0.33	0.34

¹Data in parentheses are standard errors of the mean.

²Statistical significance of difference of overall least squares means (after fitting trial and farm of origin) are shown.

³SED = standard error of the difference.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

191(1.5 SE), at the start of each trial for groups 1 to 4, respectively. They were fed pasture and alfalfa cubes (approximately 40:60 ratio at 90% DM, 28-mm chop length) supplied by MultiCube Stockfeed (Yarrawinga, Victoria, Australia) with 184 g of CP/kg of DM and an OM digestibility of 62.9%. Cows were given access to the cubes for 4 d before entering the feed intake facilities. The cows were in the pens for 35 d with a 3-d adaptation period. Water was freely available, as was trace mineralized salt in a block (Dominion Salt Ltd., Mount Maunganui, New Zealand).

Intake data for individual animals were validated to exclude daily intakes that differed by 20% (or more) from 3 previous daily means. Very high intakes (>20 kg in an individual feeding bout) were checked, as well as eating rate measurements exceeding 1 kg/5 min, or negative values. Bin weights and animal tag numbers were recorded continuously when cows were accessing the cubes, so intake, time, and duration of eating were recorded.

Cows were weighed 3 times weekly for 2 to 3 wk before and after each trial and during the 35 d that cows were in the pens. Change in BW was made on the basis of regression of the pre-and posttrial BW measurements (6 to 9 of each) on time because of a pronounced effect of the diet on gut-fill (approximately 40 kg). This effect rapidly diminished (2–3 d) when cows resumed grazing. The BW at mid-trial was calculated from this fitted line on the day corresponding to the mid-point of the measurement period, for each cow.

Milk yields were measured using in-line milk meters (Westphalia Surge, GEA Farm Technologies GmbH, Bönen, Germany) at morning and afternoon milkings each day. Composite a.m.-p.m. milk samples (in proportion to yield at each milking) were taken 3 times weekly and analyzed for fat, protein, and lactose by Fourier transform infrared spectroscopy (FT120, Foss Electric, Hillerød, Denmark).

Calculation of RFI_{lac}

Residual feed intake during lactation was calculated within each of the 4 trial groups as the residual term from a linear model fitted to DMI (kg/d) that included daily mean milk energy output (MJ/d), metabolic BW ($BW^{0.75}$; kg) at trial mid-point, and BW change ($BW\Delta$; kg/d). Milk energy output was calculated as the sum of fat, protein, and lactose yields converted to megajoules using 38.1, 24.5, and 16.5 as conversion factors per kilogram of each milk component (Primary Industries Standing Committee, 2007). We observed no effect of pen row on RFI_{lac} measures:

$$DMI = \mu + [\text{fat (MJ)} + \text{protein (MJ)} + \text{lactose (MJ)}] + BW^{0.75} + BW\Delta + RFI_{lac}.$$

Partial regression coefficients for this model are shown in Table 2.

Analysis of variance was used to test differences between high and low RFI_{gro} classes. Data were analyzed by ANOVA with trial number, efficiency class, and interactions included as fixed effects, and farm of origin included as a random effect for calculation of overall means in Tables 1 and 3.

RESULTS

Estimation of GEBV for RFI_{gro} produced a normal distribution of RFI for the 3,359 animals that were tested in commercial herds. From these, the selection process for the extremes produced 2 classes of cows (Figure 1) with a mean difference of GEBV for RFI_{gro} of 2.2 kg of DM/d (low RFI_{gro} : -1.44 ± 0.03 , high RFI_{gro} : 0.76 ± 0.01). After purchase of cows in the “tails” of the GEBV distribution, the low and high RFI classes for cows had an average ranking for GEBV of 113 (range

Table 2. Partial regression coefficients for the parameters used to calculate residual feed intake (RFI) in each trial¹

Trial	Partial regression coefficient ²			
	$BW\Delta$, kg/d	$BW^{0.75}$, kg	Milk energy output, MJ/d	Intercept, kg of DM/d
September	−4.15 (1.77)*	0.11 (0.04)*	0.15 (0.04)***	6.17 (3.54)
November	1.11 (1.50)	0.07 (0.03)*	0.19 (0.04)***	6.12 (3.62)
January	0.15 (1.92)	0.23 (0.04)***	0.08 (0.05)	−5.43 (4.96)
April	0.98 (1.132)	0.13 (0.03)***	0.13 (0.03)***	3.18 (3.81)
Overall	−0.32 (0.076)	0.14 (0.02)***	0.13 (0.02)***	2.77 (2.02)

¹Overall data were obtained after fitting trial to the model shown in Materials and Methods.

² $BW\Delta$ = BW change across each trial; $BW^{0.75}$ = metabolic BW. Milk energy output was calculated as the sum of fat, protein, and lactose yields.

* $P < 0.05$; *** $P < 0.001$.

Table 3. Milk yield and composition (SEM in parentheses) in each residual feed intake during growth (RFI_{gro}) class (low or high) within each trial group¹

Item	September		November		January		April		Overall mean	
	Low	High	Low	High	Low	High	Low	High	Low	High
Milk yield, kg/d	19.3 (0.48)	19.5 (0.44)	18.2 (0.46)	17.3 (0.44)	15.7 (0.41)	15.2 (0.47)	13.7 (0.44)	12.4 (0.43)	16.7	16.1
Fat, %	4.39 (0.10)	4.30 (0.07)	4.25 (0.10)	4.44 (0.08)	4.50 (0.11)	4.36 (0.09)	5.10 (0.14)	5.26 (0.14)	4.56	4.60
Protein, %	3.56 (0.05)	3.58 (0.04)	3.75 (0.06)	3.80 (0.04)	3.88 (0.06)	3.97 (0.04)	4.23 (0.09)	4.39 (0.07)	3.86	3.93
Lactose, %	4.79 (0.02)	4.78 (0.02)	4.89 (0.02)	4.90 (0.02)	4.72 (0.03)	4.68 (0.03)	4.78 (0.04)	4.68 (0.03)	4.79	4.76
									0.30 ^{NS}	0.07 ^{NS}
									0.04*	0.02 ^{NS}

¹Group sizes are shown in Table 1. Overall means are LSM after fitting RFI_{gro} class and trial as fixed effects and farm of origin as a random effect.

²SED = standard error of the difference.

* $P < 0.05$; NS = $P > 0.05$.

6–219) and 3,243 (range 3,067–3,358), respectively. Within selection classes, phenotypic RFI_{lac} and GEBV for RFI_{gro} were correlated (see legend to Figure 1) with values of $r = 0.36$ and $r = 0.28$ for low and high classes, respectively. Thus, GEBV for RFI_{gro}, estimated from a data set generated with growing heifers), explained 8 to 13% of the phenotypic variation in RFI_{lac}.

On average, the classes of cows selected by genomic prediction of RFI_{gro} differed in mean RFI_{lac} by 0.67 kg of DM/d (high RFI_{gro} class: 0.34, low RFI_{gro} class: -0.33 , $P < 0.01$; Table 1). Moreover, this difference was apparent in each of the 4 trial groups, tested over the lactation, ranging from a low of 0.40 kg of DM/d in late lactation (191 DIM) to a high of 1.02 kg of DM/d in the trial group beginning evaluation at 145 DIM. Trial group had no significant effect on RFI_{lac} and we observed no significant difference in DMI between RFI_{gro} classes (Table 1).

Fitting the model for RFI calculation revealed significant associations of BW and milk energy output with daily DMI, whereas effects of BW change were only significant in trial 1 (Table 2). Variation in partial regression coefficients among trials (Table 2) was probably due to variation in the strength of correlations among traits within the individual trials.

Overall, we observed no significant effect of trial ($P < 0.05$) on RFI_{lac}. The R^2 for DMI was 0.43 when fitted for milk energy yield, BW, BWΔ, and trial group. Addition of RFI_{gro} class increased this to $R^2 = 0.47$, and the RFI_{gro} class effect was statistically significant ($P < 0.01$). Thus, by using the genomic prediction based on RFI_{gro} in an independent group of heifers, it was possible to identify animals with high and low RFI_{lac} in lactation, differing in RFI_{lac} by an average of 0.67 kg of DM per day.

The first of the 4 trial groups began intake measurements when mean DIM was 61 d, beyond the expected period of rapid tissue mobilization and negative energy balance in early lactation. Indeed, animals in this group had the highest weight gains of any of the trial groups (Table 1). Dry matter intakes were consistently high in all treatment groups, at close to 5% of BW. These high intakes were also associated with higher rumen and gut fill, related to the change of diet. This was apparent when the animals were on trial and necessitated calculation of BW change on the basis of pre- and post-trial BW measurements. The frequency of these latter measures was increased to thrice weekly in trials 3 and 4 to improve the estimation of BW change over the trial periods. Similar BW changes related to gut-fill were observed in the study of Macdonald et al. (2014) with lactating cows fed a similar diet.

We found small differences in milk component yields between the high and low selection classes (Table 1)

Figure 1. Distribution of (a) residual feed intake (RFI) during lactation (RFI_{lac}; kg of DM/d) and (b) genomically estimated breeding values (GEBV) for RFI in cows selected from commercial herds based on genomic prediction of RFI during growth (RFI_{gro}). High ($n = 98$) and low ($n = 99$) RFI_{gro} classification was based on a GEBV prediction derived during growth in an independent group of growing heifers (Pryce et al., 2012). These animals represent the extremes for RFI_{gro} GEBV (within the top and bottom 10%, respectively) selected from a population of 3,359 cows identified in commercial herds. Within-class correlations of RFI_{lac} and GEBV for RFI_{gro} were $r = 0.36$ and $r = 0.28$ for low and high RFI_{gro} classes, respectively. Color version available in the online PDF.

but although fat and lactose yields showed statistically significant differences in favor of the low RFI_{gro} class, the size of the effect was very small. Milk yield and composition did not differ between the high and low RFI_{gro} selections except for a small but significant ($P < 0.05$) overall difference in milk protein percentage between the RFI classes, with the low RFI_{gro} class being 0.07% lower, overall (Table 3).

Thirty-one sires were represented in the selected animals, with only 4 sires represented in both selection classes (see legend to Figure 2). The low RFI_{gro} class included 64 daughters from 2 sires, and the high RFI_{gro} class included 46 daughters from 3 sires (Figure 2). The remaining sires were represented by 7 or fewer daughters. In particular, sire 5 represented by 47 daughters that were exclusively in the “low” group had, on average, an RFI_{lac} of -0.83 ± 0.21 kg of DM/d. In the high group, sire 16, with 7 daughters and a mean RFI_{lac} of 0.90 ± 0.41 , was among the sires with the least efficient daughters. Sires 9 (4 high, 3 low), 14 (15 high, 1 low), 18 (1 high, 1 low), and 23 (5 high, 6 low) had daughters in both RFI_{gro} classes.

The effect of farm of origin was explored by ANOVA within trials and in the overall data set. In each trial, fewer than 25% of the cows were present with another animal from the same farm and we observed no consistent improvement in the fit for RFI or any of the milk or BW traits within trials, likely because of this lack of power. However, fitting farm as a random effect in the overall means did improve the statistical significance of the differences in fat and lactose yield traits between RFI_{gro} classes and gave a small increase (0.04) in the RFI_{lac} differential.

DISCUSSION

The data presented here demonstrate that genomic prediction of genetic merit for RFI_{gro}, based on measurements taken during the growth phase of dairy heifers, is also capable of discriminating for RFI_{lac} in an independent group of lactating dairy cattle drawn from the same industry population. The data also showed a relatively consistent difference across lactation in RFI_{lac}. Other work with the growing heifers demonstrated that those animals that were extreme for RFI_{gro}, also maintained a differential in RFI_{lac} (Macdonald et al., 2014). The observed difference (0.96 kg of DM per day) between the extreme classes was similar to that seen in the current experiment.

Data for RFI in dairy cattle are few compared with RFI determinations in growing beef animals. Nevertheless, several studies have reported moderate heritabilities for RFI in growing dairy heifers ($h^2 = 0.22$; Korver et al., 1991) and in lactating heifers ($h^2 = 0.19$; van Ar-

Figure 2. Mean residual feed intake (RFI) of sire daughter groups ranked within high and low RFI_{gro} (RFI during growth) selection classes. Error bars are standard errors of the mean. Thirty-one sires were represented in the overall trial, with 17 sires in the low RFI_{gro} class and 18 in the high class. Four sires were represented in both RFI_{gro} classes. These were (paired, high and low, respectively) 15 and 17, 11 and 9, 2 and 7, and 4 and 16. Sires ranked 5 and 12 in the low class had 47 and 17 daughters, respectively. In the high RFI_{gro} class, sires ranked 5, 7, and 10 had 10, 15, and 21 daughters, respectively. All remaining sires were represented by 7 daughters or fewer within an RFI_{gro} class. Sire 5 (low RFI_{gro}), with 47 daughters, gave the most reliable estimate of RFI_{lac} in this data set, with a mean of -0.83 ± 0.21 kg of DM/d.

endonk et al., 1991). Nieuwhof et al. (1992) examined genetic aspects of feed efficiency in dairy bulls, as well as growing and lactating heifers, and reported a high genetic correlation of RFI measured during growth with RFI measured in lactation ($r = 0.58$). However, the study of Ngwerume and Mao (1992), with dairy heifers, reported heritability for RFI_{gro} close to zero. In beef animals, estimates of heritability for RFI during growth range from 0.16 to 0.43 (Herd et al., 2003; Arthur et al., 2010).

Archer et al. (2002) demonstrated a strong genetic correlation ($r_g = 0.98$) between intake-related traits (including RFI) measured from shortly after weaning to maturity in beef animals, indicating that the same processes regulating the expression of feed intake-related traits operate in both growing and mature animals. The phenotypic correlation between RFI measured at 8 to 10 mo and again in mature animals was lower ($r = 0.40$). Arthur et al. (2001) found a high genetic

correlation between RFI measured at 9 to 14 mo of age with a repeat measure at 14 to 19 mo. Several reports have indicated low to moderate repeatability of RFI in steers and heifers (Kelly et al., 2010; Durunna et al., 2011, 2012). Collectively, all the data, including this study, indicate that RFI is a lifelong trait, albeit with some environmental modulation depending upon age and physiological state.

Each selection class had some bias toward 1 or 2 sires (see legend to Figure 2), which were distributed relatively evenly across the 4 trial groups. Almost half of the daughters in the low RFI_{gro} class were sired by 1 bull (sire 5) whose daughters ($n = 47$) had an average RFI_{lac} for lactation of -0.83 ± 0.19 kg of DM. Conversely, RFI_{lac} for sire 16, with 7 daughters in the high RFI_{gro} class, was 0.89 ± 0.43 kg of DM/d. The level of difference in RFI seen among sires in this experiment, albeit with very limited data, suggests there may be merit in testing dairy sires for RFI during the growth

phase, a practice already applied to sires in the beef industry.

Eleven sires were common to both the growth (Pryce et al., 2012) and lactation data sets but the data were insufficient to examine any relationship between RFI measured in growth and lactation within sires. The sire most represented in the RFI_{lac} data set (low sire 5, $n = 47$) was not a sire of the animals used in the growth data set reported by Pryce et al. (2012). The bias toward a few sires might suggest that genomic selection is choosing low or high RFI families.

Improved accuracy (and genetic progress) for RFI might be obtained if causative mutations contributing to RFI variation were identified. Genetic variations that have been putatively identified to affect RFI in beef cattle (Sherman et al., 2009) do not appear to be associated with RFI in dairy animals in New Zealand (Littlejohn et al., 2012). A genome-wide association (GWAS) analysis indicated that *NCOA2* (nuclear receptor coactivator 2) variants on BTA14 might be linked to RFI measured during growth (Pryce et al., 2012) but this has not been confirmed. Others have examined markers on BTA14 that were predictive for RFI in crossbred steers (Lindholm-Perry et al., 2012). The most significant of these was in a different chromosomal location close to a major growth QTL (Karim et al., 2011). However, association of SNP in this location with RFI was not significant in the current study population (Littlejohn et al., 2012). Bolormaa et al. (2011) identified many SNP associated with RFI in beef breeds but with only limited crossover of statistically significant SNP between breeds.

In a GWAS study of RFI in several beef breeds, Barndse et al. (2007) also found many SNP associated with RFI, with a bias toward SNP in or close to genes regulating cellular energy metabolism. In addition, there was some indication that the microRNA profile might be involved in regulation of RFI, based on a comparison of SNP associations among feed efficiency and carcass traits. Testing of 138 markers in growing heifers in New Zealand did not replicate any of the associations seen in the beef study (Littlejohn et al., 2012).

Measurements of RFI relevant to New Zealand dairy animals should, ideally, be undertaken in grazing animals. However, the difficulty of accurately measuring intake in a grazing situation or even to measure pasture intake accurately in stall-feeding systems compromises accurate RFI measurement on pasture diets. Nevertheless, in one Irish study, estimates of heritability for RFI of 0.05 to 0.38 were determined using alkanes as markers of intake (Lopez-Villalobos et al., 2008). Herd et al. (1998) showed a relationship between RFI measured in calves on pelleted rations and the efficiency of the cow-

calf unit in mature animals at pasture. Arthur et al. (1999) reported that females that were more efficient, when tested after weaning, also required less feed as mature cows; they found no adverse correlations between low RFI and cow performance.

The choice of a pasture-alfalfa cube in our study was made to achieve a high-roughage diet that could be readily handled and fed in automatic feeders, and enable accurate measurement of DMI. We observed a substantial increase in intake on this diet, relative to pasture, associated with a marked increase in gut fill, reflected in the BW measures. This "fill effect" was rapidly (3 d) lost upon return to grazing after the trial. Although this complicated, it did not preclude measurement of BW and BW change, both of which were estimated by regression using BW data generated before and after the trial period in the pens. Nevertheless, the extremely high daily intakes of alfalfa-pasture cubes, approaching 50 g/kg of BW, were an unusual feature of this study. Pasture intakes with ad libitum feeding (grazing) with cows in New Zealand are usually well below 40 g/kg of BW (Kolver, 2003).

Milk energy output declined by about 25% over the 4 trials but there was no corresponding increase in BW gain, although DMI were similar. Indeed, in trial 1 at the highest milk energy output, BW gain was greatest. We can only speculate that some combination of change in digestibility and the composition of tissue gain were responsible for these observations.

The accuracy of GEBV estimation for RFI depends on its heritability, the number of animals studied, the level of linkage disequilibrium between the markers and the QTL, and the distribution of QTL effects across the genome. Increasing the accuracy of estimation will potentially increase the rate of genetic gain. Currently, the studies of Mujibi et al. (2011), Pryce et al. (2012), and Zeng et al. (2012) have all estimated RFI with relatively low accuracy compared with the accuracy with which, for example, milk traits can be predicted. Accuracies of prediction of true breeding value for RFI_{gro} were 0.31 and 0.37 in data sets generated in growing heifers in New Zealand and Australia, respectively (Pryce et al., 2012) and 0.32 for a similar Canadian data set with crossbred beef animals (Zeng et al., 2012). Accuracy of prediction was similarly low in another study with crossbred beef animals where admixture of the (small) study population appeared to be restricting accuracy of the genomic prediction (Mujibi et al., 2011).

In this study, GEBV for RFI in growth accounted for only 8 to 13% of the variance in RFI in lactation. Nevertheless, when study numbers can be increased or causal variations are identified, we expect that the accuracy of RFI prediction will improve.

CONCLUSIONS

This study has made a significant advance, confirming that genomic prediction of RFI_{gro} can be used to capture the efficiency benefits associated with RFI_{lac} in dairy cattle. Genomic predictions for RFI, developed from feed intake measurements in young growing dairy heifers, successfully identified dairy cows on commercial farms that were divergent for RFI in lactation. Although the difference in intake between RFI_{gro} classes was relatively small at ~ 0.67 kg of DM/d, the greater feed conversion efficiency of low RFI animals can lead to significant improvements in productivity over the lifetime of a dairy cow. Further, we found evidence that some sires produce daughters that are more efficient than those produced by other sires. Accurate sire ranking for RFI will help improve feed conversion efficiency in dairy cattle. Improvement in the accuracy of prediction will be the focus of future work.

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