Genetics of residual energy intake in Irish grazing dairy cows

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ABSTRACT

The objective of this study was to investigate the genetics of residual net energy intake (RNEI) in grazing Holstein-Friesian cows. RNEI was defined as net energy intake minus predicted net energy requirements using the unité fourragère lait (UFL) system. Net energy intake from grass and concentrate was estimated up to four times per lactation on 1,111 lactations from 463 cows on an experimental farm in Southern Ireland. Grass dry matter intake was estimated using the n-alkane technique. Lactation curves for milk, fat, protein, lactose and live weight were modeled with splines using weekly measures. A random regression was used to estimate residual, additive genetic and permanent environmental variances for RNEI and breeding values at Day 60 for each cow. Heritability for RNEI across lactation varied from 0.05 at 30 days in milk to 0.38 at 296 days in milk. Genetic parameters for RNEI obtained in this study are in agreement with those obtained under indoor conditions. Comparative performance between cows of low and high RNEI breeding value at Day 60 agrees with results obtained in beef cattle selected for high or low residual feed intake showing similar productivity but higher feed conversion efficiency in cows selected for low residual feed intake.

Keywords: residual energy intake; genetic parameters.

INTRODUCTION

The breeding goal of most breeding programs for the genetic improvement of dairy cattle is to increase farm profit. One way to maximise farm profit is to improve the genetic merit of the cows for feed conversion efficiency (FCE), which usually is expressed as the ratio of milk or milksolids produced to feed intake. In dairy cattle this measure can also be expressed as the energy produced in milk divided by the energy intake. There are two major problems with the genetic improvement of FCE in dairy cattle. Firstly, selection on ratio measures present inherent difficulties in constructing a selection index (Gunsett, 1986); two cows might have similar FCE but distinctly different feed intake and production. Secondly, FCE does not distinguish between the energy used for the separate functions of maintenance, lactation and body tissue gain (Veerkamp *et al*., 1995). Residual feed intake (RFI), defined as the difference between actual feed intake and that predicted on the basis of requirements for milk production, pregnancy and maintenance of live weight, was first proposed as an alternate measure of feed efficiency by Koch *et al*. (1963). Efficient animals eat less than expected and have a negative or low RFI, while inefficient animals eat more than expected and have a positive or high RFI.

Results in beef cattle have shown that selection for low RFI has the potential to increase the efficiency of the production system by reducing feed intake without changing the growth rate of the young animal, as well as having no effect on mature cow size or meat quality (Herd *et al*., 2004). Genetic gain for RFI in beef cattle can be achieved because it is moderately heritable (h^2 = 0.16 to 0.43; Herd *et al*., 2004). Estimates of heritability of RFI in dairy cattle range from 0.00 to 0.38 depending on the method used to estimate RFI and stage of lactation (Van Arendonk *et al.*, 1991; Ngwerume & Mao, 1992; Svendsen *et al*., 1993; Veerkamp *et al*., 1995). Estimates of the genetic correlation between RFI and feed intake is moderately positive whereas the genetic correlation between RFI and milk production in close to zero (Van Arendonk *et al.*, 1991) suggesting that more efficient animals tend to eat less. The estimates of these genetic parameters, however, originate from cows fed indoors predominantly on total mixed rations or ensiled forages. No study has attempted to estimate genetic parameters for RFI in grazing dairy cows, largely because accurate individual measures of feed intake are difficult to obtain.

The objective of this study was to investigate the genetics of residual net energy intake (RNEI) in grazing Holstein-Friesian cows. RNEI was defined as net energy intake minus predicted net energy requirements.

MATERIAL AND METHODS

Data

The data were collated from four separate studies (Buckley *et al*., 2000; Kennedy *et al*., 2003; Horan *et al*., 2006; McCarthy *et al*., 2007) carried out at the Curtins Research Farm of Moorepark Production Research Centre, Fermoy, Co. Cork, Ireland. These studies compared different strains of Holstein-Friesian cows on perennial ryegrass (*Lolium perenne*) pasture-based systems during 1995 to 2006.

A total of 1,111 lactations from 463 cows representing 96 sires were available for inclusion in the analyses. A description of the feeding systems are summarised by Berry *et al*. (2007). Animals within strain, at the start of lactation, were randomly assigned to feed systems differing in stocking rate, concentrate input, or both. Annual concentrate feeding level across studies varied from 325 to 1,452 kg per cow.

Individual milk yields were recorded daily, whereas milk fat, protein, and lactose concentrations were determined from successive evening and morning milk samples once per week using near infrared spectroscopy (Fos-let instrument, AS/N Foss Electric, Hillerød, Denmark). Live weight of each animal was recorded weekly using portable weighing scales and the Winweigh software package (Tru-Test Ltd., Auckland, New Zealand). Body condition score was recorded approximately every three weeks during the lactation on a 1 to 5 scale (1 = Emaciated, 5 = Obese) in increments of 0.25. Individual animal dry matter intake (DMI) was measured while at pasture when the diet consisted of exclusively pasture or pasture plus concentrate depending on feed system. Individual animal grass DMI was estimated using the n-alkane technique (Mayes *et al*., 1986) as modified by Dillon (1993). During each intake period, the cows were dosed twice daily after milking for 12 days with paper filters or bungs (Carl Roth GmbH and Co. KG, Karlesruhe, Germany) containing 500 mg of dotriacontane ($C_{32}H_{66}$) each. Fecal grab samples were collected twice daily from each cow immediately before or after milking in the last six days. The fecal samples from each cow for each 6-day period were bulked for analysis. After close observation of the grazing animal, herbage samples were collected manually to represent herbage grazed after both the morning and evening milkings on Day 6 to 11 of each measurement period. Number of daily measures of milk, live weight and are shown in Table 1.

Estimation of residual net energy intake

Phenotypic lactation curves for yields of milk, fat, protein and lactose, live weight, body condition score and net energy intake for each cow were modelled using cubic splines in the statistical software ASReml (Gilmour *et al*., 2002). Using predicted values for these traits, requirements of net energy for each day of the lactation were calculated using equations provided by Berry *et al*. (2006) according the French net energy system, in which 1 unité fourragère lait (UFL) is the net energy for lactation equivalent of 1 kg of standard air-dry barley (Jarrige et al., 1986) equivalent to 7.11 MJ net energy or 11.85 MJ metabolisable energy.

Residual net energy intake was then calculated as:

$RNEI = NEI - (NEM + NEL + NEP + \Delta NE) - 4.5 |\Delta LW|$ if liveweight change is positive;

$RNEI = NEI - (NEM + NEL + NEP + \Delta NE) + 3.5 |\Delta LW|$ if liveweight change is negative.

where NEI is the net energy intake from pasture and concentrate, NEM is the net energy requirements for maintenance including energy for activity, NEL is net energy requirements for milk production, NEP is net energy requirements for pregnancy, ΔNE is an adjustment of net energy intake for the proportion of concentrate in the diet and |ΔLW| is the absolute change in live weight. The following equations define the individual components of the above formula:

$NEI = (GDMI \times 1.02) + (CDMI \times 1.05)$; $\Delta NE = 6.3 PrC^2 + 0.002 NEI^2 - 0.017 NEI$;

$NEL = [(0.054 \times Fat) + (0.031 \times Protein) + (0.028 \times Lactose) - 0.015] \times$ kg milk;

$NEM = (1.4 + 0.6 \times (LW/ 100)) \times AA$;

NEP = 0.9, 1.6, 2.6 UFLs from days 180, 210 and 240 of gestation, respectively.

where GDMI is grass dry matter intake (kg/d), CDMI is concentrate dry matter intake (kg/d), PrC is proportion of concentrate in the diet, Fat is the concentration of fat in the milk (g fat/kg milk), Protein is the concentration of protein in the milk (g protein/kg milk), Lactose is the concentration of lactose in the milk (g lactose/kg milk), LW is the live weight of the cow (kg), AA is the activity allowance included as a modification for the Irish pasture based systems and assumed to be 1.2.

Concentration of net energy in concentrate was assumed as 1.05 UFL/kg dry matter, whereas concentrations net energy in grass (UFL/kg dry matter) were assumed as 1.01 for October, November, December and January; 1.06 for February and June, 1.09 for March, April and May; 1.03 for July; 0.97 for August; and 1.02 for September.

Estimation of heritability

A random regression was used to estimate variance components across lactations for RNEI and breeding values at Day 60 for each cow. Estimates of residual, additive genetic and permanent environmental variances for RNEI were obtained using ASReml (Gilmour *et al*., 2002) fitting a mixed random regression model of RNEI on days in milk (DIM). The model included the fixed effects of date of intake measure for each experiment and feed system group, the combination between year of experiment and experiment, parity (1 to 5) , age at calving nested within parity and a third order fixed regression on days in milk modelled using orthogonal Legendre polynomials across all the data and within each parity. The random effects included were a third order random regression for the additive genetic component and the permanent environmental component within parity and constant permanent environmental effect across parities. Residuals were assumed independently distributed with heterogeneous variance for each 50-day period, that is, 1 to 50 DIM, 51 to 100 DIM, 101 to 150 DIM, 151 to 200 DIM, 201 to 250 DIM, and 251 to 305 DIM. Statistical analysis and cows with breeding values above the mean (H_RNEI). Analyses of variances were carried out to detect significant differences between the two groups of cows for lactation yields of milk, solid-correct milk, fat, protein and lactose, live weight and condition at calving, live weight and condition change from Day 1 to Day 60, average LW and BCS during the lactation, total net energy intake and requirements and RNEI during the lactation. The model included the fixed effects of experiment, strain nested within experiment, feeding system within experiment, parity and RNEI group plus the random effects of cow and residual error. These analyses were performed using the MIXED procedure of SAS (2002).

RESULTS AND DISCUSSION

Descriptive statistics of the data used in this study are shown in Table 1. The amount of data used to estimate variance components for RNEI was limited by the number of observations with intake measures. The mean of RNEI for each day of the lactation was 1.4 with a large standard deviation. This means that estimates of net energy intake were, on average, higher than the predicted requirements but there was a large variation.

Estimates of additive genetic, permanent environmental, residual and phenotypic variances of daily RNEI at different days of the lactation and corresponding values of heritabilities and repeatabilities are presented in Table 2. Estimated residual variances were largest in early lactation and decreased almost consistently as the lactation progressed. Estimates of additive genetic variances were high at the start of the lactation, declined by Day 60 and started increasing again toward the end of the lactation. The variance for the permanent effect within lactation had a similar trend to the genetic variance, high values at the start and end of the lactation and lower values in the middle of the lactation. Estimates of heritability of daily RNEI ranged from 0.05 in early lactation to 0.38 in late lactation whereas estimates of repeatability ranged from 0.07 to 0.46.

The increase in the heritability after 270 days in milk should be looked at with caution, as few records of dry matter intake were available. The estimates of heritability for RNEI obtained in this study, in which pasture dry matter intake was estimated using the n-alkane technique, are within the range of heritabilities obtained from indoor experiments with cows fed total mix rations or conserved forages (Van Arendonk *et al.*, 1991; Ngwerume &

TABLE 1: Number of records, means, and standard deviations for daily yields of milk, fat, protein and lactose and measures live weight, body condition score (scale 1 – 5) and residual net energy intake in grazing dairy cows in Ireland. UFL = Unité fourragère lait.

Parameter	Number of records	Mean	Standard deviation
Milk yield (kg)	45,337	23.1	7.9
Fat yield (kg)	42,170	0.92	0.30
Protein yield (kg)	42,170	0.80	0.24
Lactose yield (kg)	42,170	1.08	0.38
Live weight (kg)	42,669	547	65
Body condition score	11,983	2.9	0.4
Total dry matter intake (kg)	3,552	18.2	3.2

TABLE 2: Additive genetic, permanent environment, residual and phenotypic variances, heritabilities (h^2) and repeatabilities (r) for residual net energy intake estimated at different days in milk in grazing dairy cows in Ireland. UFL = Unité fourragère lait.

Days in milk	Variance (square units of UFL's)					h^2	r
	Additive genetic	Permanent – within lactation	Permanent – across lactations	Residual	Phenotypic		
8	0.71	3.33	0.01	4.75	8.81	0.08	0.46
30	0.29	1.27	0.01	4.75	6.33	0.05	0.25
60	0.21	0.25	0.01	3.89	4.36	0.05	0.11
90	0.24	0.06	0.01	3.89	4.20	0.06	0.07
120	0.27	0.06	0.01	3.17	3.50	0.08	0.10
150	0.30	0.05	0.01	3.17	3.53	0.08	0.10
180	0.33	0.03	0.01	2.55	2.93	0.11	0.13
210	0.33	0.03	0.01	2.68	3.01	0.09	0.11
240	0.29	0.03	0.01	2.68	3.01	0.09	0.11
270	0.47	0.07	0.01	2.13	2.69	0.18	0.21
296	1.46	0.28	0.01	2.13	3.89	0.38	0.45

TABLE 3: Least squares means and standard errors (SEM) of milk production, live weight, body condition score (scale 1-5) and feed conversion efficiency and residual net energy intake for two groups of cows classified into low (L_RNEI) and high (H_RNEI) breeding value for residual net energy intake at Day 60 of the lactation. UFL = Unité fourragère lait.

Parameter	Breeding value		SEM	Significance
	L_RNEI	H_RNEI		
Breeding value for RNEI at Day 60	-0.2042	0.2705	0.008	***
Lactation length (d)	311.6	312.6	2.6	NS
Lactation yields				
Milk (kg)	7,047	6,980	141.3	NS
Solid-corrected milk (kg)	6,934	6,926	146.5	NS
Fat (kg)	278	278	6.1	NS
Protein (kg)	240	240	5.4	NS
Lactose (kg)	326	324	6.5	NS
Live weight at calving (kg)	575	579	6.7	NS
Live weight change from D 1 to D 60	-25	-23	6.6	NS
Average live weight (kg)	576	584	3.3	*
Body condition score at calving	3.20	3.18	0.05	NS
Body condition score change from Day 1 to Day 60	-0.33	-0.31	0.02	NS
Average body condition score	2.90	2.91	0.03	NS
Net energy intake (UFL)	6,311	6,608	97.1	***
Net energy requirements (UFL)	5430	5458	71.6	NS
Residual net energy intake (UFL)	864	1132	57.6	***
Solid-corrected milk/1000 UFL NE	1152	1079	18.8	***

Mao, 1992; Svendsen *et al*., 1993; Veerkamp *et al*., 1995).

The estimates of heritability and repeatability for dry matter intake reported by Berry *et al*. (2007) using the current data set and measurements of intakes from another grazing experiment carried out at Moorepark suggest that across diverse genotypes and feed systems, the n-alkane method of predicting grass dry matter intake is consistent across animals. Although repeatability statistics in that study did not indicate accuracy of prediction, the validation of n-alkanes as an accurate predictor of herbage intake has been discussed elsewhere (Dillon, 1991).

Comparative performance between cows of low and high RNEI breeding value at Day 60 of lactation is shown in Table 3. Compared to cows of low breeding value for RNEI, cows of high breeding value had similar total yields of milk, fat, protein and lactose and similar liveweight and condition score at calving and at Day 60 resulting in no significant differences in net energy requirements between the two groups. However, cows of low RNEI breeding value were significantly (P <0.013) lighter (576 vs 584 kg) and had significantly (P <0.001) less net energy intake (6311 vs 6608 UFLs) over the entire lactation resulting in higher feed conversion efficiency (1152 vs 1079 L of solids-corrected milk/1000 UFLs). These results agree with results obtained in beef cattle selected for high or low residual feed intake showing similar productivity but less feed intake resulting in higher feed conversion efficiency in cows selected for low residual feed intake. These results also give some insight on the genetic correlation between RFI, feed intake and feed conversion efficiency. In agreement with Koch *et al*. (1963), compared to cows of high breeding value for RNEI, cows of low breeding values for RNEI are more efficient because they eat less food to achieve the same levels of production. However in this study, the low RNEI breeding values cows were lighter than the high RNEI breeding values cows. These data also support current views that RFI is independent of milk production, but can be correlated with feed intake, feed conversion efficiency and average live weight.

CONCLUSIONS

This study attempted to quantify the genetic variation for RNEI in grazing Holstein-Friesian cows in Ireland. Estimates of heritability for RNEI were within the ranges reported from indoor experiments; estimates were low at the start of the lactation and moderate at the end of the lactation. Comparative performance between cows of low and high breeding values for RNEI provide some possible gains in feed conversion efficiency by creating cows that produce the same amount of solid-corrected milk with less dry matter intake.

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