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Metabolic feed efficiency – opportunities for selection in dairy cows

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ABSTRACT

A literature review and simulation study is presented to investigate the potential role of metabolic feed efficiency in dairy cattle breeding programmes. Metabolic efficiency is generally calculated as the difference between actual feed intake and expected feed requirements and as a result is a residual term, hence it is often referred to as residual feed intake (RFI). There is evidence of genetic variation in RFI in poultry, sheep and beef cattle. Heritability estimates in beef cattle are moderate (0.14 to 0.43). Heritability estimates in dairy cattle range from zero (no genetic variation) to moderate (0.38). RFI is positively genetically correlated with feed intake, so more efficient animals tend to eat less. Information is sparse, but suggests there is no genetic correlation between milk production and RFI. Genetic correlations between health and fertility traits and RFI in cattle have not been established, but evidence from mice and pigs suggests unfavourable correlations between RFI and fertility. Estimating the genetic relationships between RFI and health and fertility in dairy cattle is required. The identification of genetic markers that explain sizeable variation in RFI, or an easily measured correlated trait would be the preferred options to enable selection for RFI in dairy cattle, ideally breeding values for RFI would be estimated and included as part of a multiple-trait selection index.

Keywords: residual feed intake; dairy cattle; genetic variation.

INTRODUCTION

Feed conversion efficiency is an important trait as feed costs are a high proportion of total costs in all livestock production systems. Thus efficiency of production has been the focus of the genetic improvement programmes of most domestic livestock species. As a result of these efforts and due to concurrent improvements in management and feeding, milk yield and the efficiency of production of lean meat have changed substantially over the last 50 years. For example, van der Steen *et al.* (2005) reported that the amount of lean meat (kg/t of feed) in pigs has increased from 85 kg/t in the 1960s to 170 kg/t in 2005, which is a 100% increase. Similarly feed conversion ratio in broiler chickens has improved from 330 kg of meat per tonne of feed to 590 kg/t, which is a 77% improvement. In dairy cattle in New Zealand, the average amount of milk produced per lactation has increased by approximately 28% from 2923 litres in 1965/1966 to 3763 litres in 2005/2006, over the same period yield of milkfat has increased by 33%.

For dairy cows, output is commonly expressed as some form of measure of milk yield with no reference to the feed consumed (*e.g.* energy requirements for maintenance and production), however this may mean that efficient strains or breeds are overlooked in preference to high-yielding strains or breeds. For example, in experiments run in New Zealand, Ahlborn & Bryant (1992) demonstrated that while Holstein-Friesians yielded more than Jerseys; Jersey

farmlets were more efficient in terms of milksolids produced per hectare. Therefore, in order to fairly compare breeds that differ in size, some account needs to be made of the liveweight of the animal.

The introduction of across-breed genetic evaluation in New Zealand encouraged the adoption of an across-breed selection index based on profitability (Harris *et al.*, 1996) known as Breeding Worth (BW). Two relevant aspects of dairy farm profit that are included in the calculation of BW are feed costs and revenue from beef production, both requiring estimates of mature liveweight. The BW index is fundamentally composed of income minus costs, expressed per kg DM and is therefore a genetic measure of gross production efficiency. Selection on BW over the last 10 years has seen the rate of gain in milksolids relative to gain in liveweight more than double compared to the preceding 10 years (Harris *et al.*, 2007). So selection on BW has led to an improvement in the conversion of feed into milk in preference to maintenance.

The BW index effectively selects for animals that have high gross efficiencies, or those that are the most efficient converters of feed into milk. If BW captures most of the variation in gross efficiency, then a relevant question is whether there are remaining differences in efficiency that cannot be assigned to differences in production relative to size, or put another way, if there are genetic differences in underlying metabolic efficiency. Establishing if there are genetic differences in metabolic efficiency can be

estimated by calculating residual feed intake (RFI), which is the feed an animal consumes adjusted for the predicted energy requirements for maintenance, production and body condition score change. Thus, everything else being equal, more is produced from the same amount of feed.

The aim of the present study is to summarise genetic parameters for RFI in dairy cattle, use a simulated dataset to determine the size of experiment required to estimate the heritability of RFI and examine the possible role of RFI in future breeding programmes.

EVIDENCE FOR GENETIC VARIATION IN RFI

It has been demonstrated that there is genetic variation in RFI in species such as poultry, beef cattle and sheep (Arthur *et al.*, 2001a; Bordas & Minvielle, 1999; Cammack *et al.*, 2005). Divergent selection for RFI (single-trait selection) has been practised in poultry and in beef cattle. After 2.4 generations of selection, residual feed intake was -0.39 ± 0.17 and 0.64 ± 0.19 kg/day in low and high RFI beef cattle respectively, meaning that the low RFI line ate around 1kg/day less per day at the same liveweight and level of liveweight gain (Hegarty *et al.*, 2005). Since 2002, the BREEDPLAN genetic improvement system has estimated breeding values for RFI (Arthur *et al.*, 2005). The standard test of RFI for growing beef cattle in Australia involves a minimum 21-day adaptation to a concentrate diet and training period followed by a test period of at least 70-days duration (Exton, 2001). The test must meet these conditions in order for the results to be used for genetic evaluation purposes. Recent research in beef cattle has focussed on whether the length of the test can be reduced (Wang *et al.*, 2006) and determining whether there are physiological differences in low and high RFI animals (Nkrumah *et al.*, 2006).

RFI tests in beef cattle are generally conducted

in growing animals, so that the calculation of RFI requires measurements on intake, liveweight and liveweight change. In lactating dairy cattle the calculation of RFI is complicated by the dynamic changes in liveweight and body condition which occurring during the lactation cycle and which need to be accurately accounted for if RFI is to be determined.

Genetic variation in RFI in dairy cattle has been investigated with the research predominantly being done in Europe during the 1980s and 1990s. In most dairy studies Holstein Friesian cattle were used, although Svendsen *et al.* (1993), used dual-purpose Norwegian cattle. Difficulties in measuring individual animal intakes in grazing cattle mean that the majority of research into RFI has been conducted indoors with animals fed diets based on silage and concentrates through individual feeders where the amount of feed offered minus the amount of feed refused is calculated on a daily basis.

Table 1 summaries heritability estimates for RFI in beef and dairy cattle. The heritability estimates in all trials, except those of Arthur *et al.* (2001a; 2001b) are characterised by large standard errors around the mean, due to the small populations studied. Two of the dairy studies (Ngwerume & Mao, 1992; Svendsen *et al.*, 1993) failed to find evidence of genetic variation in RFI. Veerkamp *et al.* (1995) estimated that the heritability of RFI was 0.32, when RFI was calculated using a phenotypic adjustment of predicted energy requirements by fitting those traits used to predict energy requirements as covariates in a regression model, *e.g.* a simple model might be:

$$y = \mu + \beta_1 MY + \beta_2 FY + \beta_3 PY + \beta_4 LW + \beta_5 CS + RFI$$

where y is daily feed intake; μ is the overall mean (which accounts for fixed effects); MY is milk volume, FY is fat yield, PY is protein yield, LW is liveweight and CS is body condition score.

Table 1: Heritability estimates for residual feed intake in beef and dairy cattle.

Study	Animals used	No. of records	Heritability (s.e)
Beef			
Fan <i>et al.</i> (1995)	Postweaning Hereford and Angus bulls	534	0.14 (0.12)
Herd & Bishop (2000)	200-400 days of age, Hereford bulls	540	0.16 (0.08)
Arthur <i>et al.</i> (2001a)	Postweaning Angus	1180	0.39 (0.03)
Arthur <i>et al.</i> (2001b)	Growing Charolais bulls	1302	0.43 (0.04)
Dairy			
Korver <i>et al.</i> (1991)	Growing dairy heifers	417	0.22 (0.11)
Van Arendonk <i>et al.</i> (1991)	First 105 days, first lactation	360	0.19 (0.12)
Ngwerume and Mao (1992)	Whole lactation, mixed age	247	0.02
Svendsen <i>et al.</i> (1993)	Wks 2-12 of lactation, mixed age	353	0.00 (0.06)
Svendsen <i>et al.</i> (1993)	Wks 13-24 of lactation, mixed age	353	0.02 (0.08)
Veerkamp <i>et al.</i> (1995)	Up to 26 weeks of lactation, mixed age	377	0.32

Thus, RFI is what is generally considered to be the error term in a statistical model. Kennedy *et al.* (1993) argued that a phenotypic adjustment does not fully adjust for the genetic relationship between RFI and the traits used to predict energy requirements. To solve this problem, they suggested calculating RFI that is genetically independent of covariates fitted in the model using the genetic covariance matrix. When RFI was calculated using this approach by including partial genetic regressions of energy intake on milk energy yield, metabolic liveweight and liveweight change, the heritability was 0.05 (Veerkamp *et al.*, 1995). However, based on a simulation exercise where RFI was calculated from distributions of feed intake, liveweight and liveweight change, Veerkamp *et al.* (1995) concluded that this estimate was likely to be biased downwards. The method used to estimate RFI impacts on the heritability estimated, correctly accounting for traits that contribute to predicted intake, especially liveweight change, is of great importance. By not fully adjusting for predicted intake requirements, estimates for the heritability of RFI are inflated. However, Herd & Bishop (2000) suggested that using genetically adjusted RFI may result in ignoring real variation in the relationships between RFI and the traits used in the regression. The variability in the heritability estimates of RFI in the literature and the different methods used to calculate RFI make it difficult to determine whether genetic improvement of this trait is feasible. Therefore, there is still the need for further research to estimate whether genetic variation exists in RFI of dairy cattle

GENETIC CORRELATIONS WITH OTHER TRAITS

When considering genetic selection for a trait it is important to estimate genetic correlations with other traits of interest, as selection will simultaneously change two genetically correlated traits. RFI was positively genetically correlated with both feed intake and feed conversion ratio (feed intake divided by average daily liveweight gain) in the beef cattle studies of Arthur *et al.* (2001a; 2001b), with correlations above 0.65 in both trials. Phenotypic correlations were of a similar magnitude. Herd & Bishop (2000) reported phenotypic correlations of 0.64 and 0.70 between RFI and feed intake and feed conversion ratio, respectively, also in beef cattle.

In the Netherlands RFI was measured first in non-lactating, growing dairy heifers (Korver *et al.*, 1991) and then in the same animals as first lactation cows (Van Arendonk *et al.*, 1991). In

both the heifer and lactating cow trial RFI had a strong genetic correlation with feed intake, so that the less efficient animals (high RFI) had greater intakes, RFI was not correlated with body weight. The phenotypic correlation between RFI measured in growing heifers and RFI in cows in early lactation was low (0.07), but the genetic correlation was moderate to high (0.58), suggesting that selection on RFI in young stock would also improve RFI in lactating animals. The results obtained in studies of both beef and dairy cattle give similar genetic correlations between feed intake and RFI, these correlations suggest that selection solely for RFI would result in a decrease in feed intake.

Only two papers reported genetic correlations between milk traits and RFI. Genetic correlations between RFI and 105-day fat and protein-corrected milk, and 105-day milk yield were 0.02, indicating no relationship between milk production and RFI (Van Arendonk *et al.*, 1991). Veerkamp *et al.* (1995) reported that genetic correlations between RFI and milk, protein and lactose yields, and fat and protein percentage were between -0.08 and 0.04, except for RFI and fat percentage which was -0.31. The overall trend that emerges from these two studies is that the genetic relationship between milk traits and RFI appears to be close to zero. However, due to the small size of these studies, the genetic parameter and correlation estimates were subject to large standard errors. Before the introduction of RFI into a dairy cattle breeding scheme, the genetic correlations between RFI and milk traits would need to be estimated with a greater degree of accuracy.

Most selection indices for dairy cattle now include health (often mastitis, or somatic cell score) and fertility traits, recognising the contribution of these traits to the economic success of a typical dairy farm (Miglior *et al.*, 2005). There is a paucity of information on the genetic relationship between feed efficiency and reproduction and health traits. Negative energy balance (often considered as condition score loss) in early lactation has been the subject of intense phenotypic (and genetic) investigation, particularly in the area of fertility. Veerkamp (2002) argued that energy balance (EB) is numerically equivalent to RFI, where EB is considered to be the difference between energy inputs and energy outputs. If EB is equal to RFI, it would mean that animals that appear to be in more negative energy balance may in fact be more efficient. Similarly, if there is a small genetic component to RFI, then animals that may appear to be more efficient simply have more negative energy balance.

Genetically poorer energy balance has been demonstrated to result in poorer fertility in cattle (Pryce *et al.*, 2000). Distinguishing between RFI and EB is only possible if condition score and liveweight loss in early lactation is properly accounted for, otherwise there is a risk that selection for low RFI could select for animals that mobilise more body condition (more negative energy balance), with negative consequences for fertility. Genetic correlations between RFI and health and fertility traits are required to determine if this risk is real. None of the studies with dairy or beef cattle have investigated genetic correlations with health or fertility traits. In beef cattle the effect of divergent selection for RFI on maternal productivity traits was examined in 185 Angus cows over three mating seasons. The cows were the result of an average of 1.5 generations of divergent selection for RFI and differed by 0.8kg/day in estimated breeding values for RFI (Arthur *et al.*, 2005), which is approximately two genetic standard deviations (Arthur *et al.*, 2001). At the start of each mating season, rib-fat depths were greater in the high RFI line cows, but there was no difference between the lines in liveweight at any of four different times during the season. Weight of calf weaned per cow exposed to the bull and milk yield did not differ between the two lines and nor did pregnancy, calving or weaning rates.

EFFECTS OF SELECTION FOR RFI ON PHYSIOLOGICAL PROCESSES

Understanding whether there are underlying differences in physiological processes between high and low RFI animals is of interest. Feedlot efficiency, metabolic rate, methane production and energy partitioning was examined in calorimetry chambers in high, medium and low RFI beef steers ($n=27$), that were selected from an initial population of 306 animals with information on RFI (Nkrumah *et al.*, 2006). Daily heat production and energy retention were highly significantly associated with feedlot RFI. Heat production was 21% and 10% less in low RFI steers than in steers with high or medium RFI. The reverse was true for methane. Methane production was around 24% and 25% higher per kg of body weight in medium and high RFI steers than low RFI steers, the differences were significant, even though numbers of animals per group were small. In a larger experiment of 91 steers, Hegarty *et al.* (2005) reported 6% lower methane emissions in low RFI than high RFI steers. Methane production, expressed per unit of DMI was not different between the two lines, so the difference in methane production is most likely due to the lower DMI by

the low RFI animals. These results show that heat production is partly responsible for genetic variation between animals in RFI. Furthermore, selection for low RFI would lead to reduction in methane emissions per kg of body weight.

Mice selected for high heat loss for 15 generations also have significantly greater feed intake (per unit of metabolic liveweight), compared to control, or low heat loss lines (Nielsen *et al.*, 1997). Liveweight was unaffected by selection for heat loss, but body fat percentage was significantly lower in the high heat production line after 14 generations. Both ovulation rate and litter size were reduced in the low heat loss line, with a positive genetic correlation reported between heat loss and number of offspring born.

In pigs, selection for improved lean food conversion resulted in smaller litter size (Kerr & Cameron, 1995), but there was no significant difference in age at first oestrus (Cameron *et al.*, 1999). Feed intake in chickens is positively associated with egg number (Hagger, 1994). However, chickens selected for low RFI have better reproductive performance than animals selected for high RFI. After 18 generations of divergent selection the high RFI line had a lower proportion of motile spermatozoa and reduced hatchability, due to a higher proportion of unfertilized eggs (Morisson *et al.*, 1997). There were 17% less mitochondria in the spermatozoa from the high RFI line, which may have an impact on energy production and fertilization ability of the spermatozoa and therefore explain the differences in reproductive rates between the lines (Morisson *et al.*, 1997).

Based on the results reported in this section and the preceding section, it appears that there is evidence, in several species, of impaired reproductive performance by selecting for improved metabolic efficiency. As Veerkamp (2002) highlighted, the calculation of both RFI and energy balance are very similar, so failure to account for BCS change in calculating RFI may result in selection for negative energy balance and consequently unfavourable correlated responses in fertility (*e.g.* Pryce *et al.*, 2000). Heat loss appears to be one of the main differences between divergent lines in metabolic efficiency. If heat production is linked to important physiological functions, then there is a risk that selecting for reduced heat production will have undesirable effects. The relationship between low heat production and impaired reproductive performance is certainly worthy of further investigation.

INTEGRATION OF SELECTION FOR RFI INTO DAIRY BREEDING SCHEMES

Selection for RFI is now feasible in beef cattle. To our knowledge selecting for RFI in dairy cattle is not integrated directly in to any major dairy cattle breeding programme. One reason for the lack of adoption by the dairy industry may be the difficulty in integrating RFI measurements into existing breeding schemes. The cost and difficulty in measuring feed intake, particularly in pasture-based dairying, may mean it is not economically viable to include the RFI in dairy breeding schemes. It is necessary to determine the economic value for RFI for genetic evaluation purposes; the size of the economic value in addition to the amount of genetic variation would dictate the importance of RFI in the breeding objective and whether it is worthwhile including (*e.g.* its impact on sire rankings). Also, the major driver behind dairy cattle breeding schemes in the USA and Europe is selection of animals that are robust, using multiple-trait breeding goals, which include health, fertility and body condition score in addition to high production. There is insufficient experimental data on the relationship between these traits and RFI for the inclusion of RFI into breeding schemes at this point. However, assuming this information becomes available in the future there are two main options for the integration of RFI data into a dairy cattle breeding scheme.

One option would be to performance test all bulls in a progeny test scheme for RFI, or correlated traits and predict the RFI of their daughters. In the study of Nieuwhof *et al.* (1992), roughage intake, ME intake and gross feed efficiency were measured in young bulls in a progeny test programme and individual feed intakes were measured in female progeny of 38 sires identified as being either high or low for dry matter intake. Roughage intake in heifers was highly correlated with that in bulls (a genetic correlation of 0.77); in addition to this, RFI in heifers was genetically correlated to weight gain (-0.94) and gross feed efficiency (0.73) in growing bulls. Feed intake, and weight gain in bulls were positively correlated with RFI in lactating heifers (0.74 and 0.71). Gross feed efficiency in bulls was moderately to highly genetically correlated with fat and protein corrected milk production in early lactation (0.5). These correlations suggest that measuring RFI in bulls to predict RFI in their daughters is an option that should be further investigated.

Alternatively, RFI could be measured in the daughters of bulls in a progeny test scheme. Currently in New Zealand progeny testing is

carried out on dedicated commercial farms, which are not set up to measure RFI. Unless the technology to measure RFI easily in grazing animals on commercial farms becomes available it is difficult to envisage this being an option. An alternative would be to improve RFI by selection on a correlated trait, which is more easily and cheaply measured, such as IGF-1. Selection for animals with low IGF-1 results in animals with lower RFI, lower subcutaneous fat depth and increased growth (Moore *et al.*, 2005). Another option is to find genetic markers or QTL for RFI that explain a sufficient amount of genetic variation and then be able to select for RFI based on a genotype test, or as part of a genomic selection approach.

To evaluate the potential of including RFI as an additional trait in the BW index a large-scale experiment is required to estimate the heritability of RFI and genetic correlations with the existing traits that are included in the BW index. Undertaking an association based QTL study would allow one experiment to estimate the required genetic parameters and provide data for QTL mapping.

SIMULATION RESULTS

We have carried out a simulation study to determine the size of trial required to estimate the heritability of RFI, assuming the true heritability is between 0.1 and 0.3. These values were chosen, as they represent the range of estimates in the literature presented in Table 1. The true heritability was a predetermined value used in the simulation program. A simulated pedigree was generated that included 50 foundation sires with 5 sons and 5 grandsons each. Random normal distributions were generated for genetic and error variance for simulated animals in each generation, so every animal had an estimated breeding value and phenotypic value. Bulls were randomly selected from the grandson generation and mated to unselected cows, *e.g.* values for error and genetic terms were sampled from random normal distributions with a mean of zero. Phenotypic means were calculated for the simulated offspring of these matings. The resultant dataset and pedigree were analysed using ASReml (Gilmour *et al.*, 2002) to estimate genetic variation and heritability estimates. The simulations were repeated 10,000 times in order to calculate 95% confidence intervals about the mean heritability estimates. The results of the simulations are presented in Table 2. The larger the population studied the more likely it is that the estimated heritability will be closer to the true heritability.

Table 2: Results from a simulation to determine the stability of heritability estimates from various population sizes. Results are from 10,000 simulations of each scenario.

Cows	Sires	True Heritability	Mean Estimated Heritability	SE mean heritability	Not possible to estimate genetic variation (%)	95% CI
500	100	0.1	0.14	0.12	19.3	0 to 0.35
500	100	0.2	0.21	0.13	5	0 to 0.47
500	100	0.3	0.30	0.14	1.04	0.04 to 0.58
1000	200	0.1	0.11	0.08	9.36	0 to 0.27
1000	200	0.2	0.20	0.09	0.9	0.03 to 0.41
1000	200	0.3	0.30	0.10	0.08	0.11 to 0.50
2000	200	0.1	0.10	0.05	1.0	0 to 0.20
2000	200	0.2	0.20	0.06	0	0.1 to 0.31
2000	200	0.3	0.30	0.07	0	0.18 to 0.44
10000	100	0.1	0.10	0.02	0	0.06 to 0.14
10000	100	0.2	0.20	0.035	0	0.14 to 0.27
10000	100	0.3	0.30	0.05	0	0.21 to 0.40

Even with a population of 10,000 individuals the 95% confidence interval for a heritability of 0.2 is from 0.14 to 0.27. When very large numbers of observations were simulated and used to estimate genetic parameters many times, the mean heritability estimate will be close to the true value and the error around this estimate small. Conversely, when few observations are simulated, the mean heritability is often incorrect and the error associated with the mean heritability large.

CONCLUSION

This literature review has found evidence of genetic variation in RFI in dairy cattle. However, the size of this variation in the New Zealand dairy cattle population is as yet unknown and based on literature estimates could vary between nothing to moderate (0.38). Studies in beef cattle suggest that there are physiological differences between low and high lines for RFI including differences in heat and methane output; there is also evidence to suggest that metabolic efficiency is related to impaired reproductive function. Quantifying genetic correlations between RFI and health and fertility traits is important before embarking on selection programmes that incorporate RFI.

Genetic improvement of RFI should be as part of a multiple-trait selection index, which would require estimates of breeding values. However, the expense in measuring RFI in a large number of animals could be prohibitive. The identification of genetic markers that explain sizeable variation in RFI, or an easily measured correlated trait would be the best options to provide selection tools for RFI. If selection on RFI is to be considered by the New Zealand dairy industry the first step needs to be a large-scale trial to establish the heritability of RFI under pastoral farming conditions and to search for genetic markers for RFI.

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