Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle

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Abstract

Variation in residual feed intake, that is, variation in feed intake in relation to liveweight (LW) and growth rate, was investigated using data from 540 progeny of 154 British Hereford sires, collected over ten 200-day postweaning performance tests conducted between 1979 and 1988. Residual feed intake (RFI) was calculated for each test as the difference between actual feed and expected feed intake predicted from a multiple regression of feed intake on metabolic mid-test LW and average daily gain (ADG). RFI was heritable (0.16, S.E. 0.08) and phenotypically and genetically independent of size and growth rate. RFI had favourable phenotypic and genetic correlations with feed conversion ratio (FCR) and estimated maintenance energy expenditure. It was negatively correlated with estimated lean content of the carcase (LEAN) and appeared to be genetically independent of mature cow LW (COWWT). RFI over the performance test was not affected by differences in pre-test rearing treatments, in contrast to start-of-test LW and end-of-test LW, and in some years, ADG and FCR. Selection against RFI has the potential to increase the efficiency of beef production by reducing feed intake without changing the growth rate of the young animal, or increasing mature cow size.

Keywords: Beef cattle; Selection; Efficiency; Residual feed intake

1. Introduction

The cost of feeding animals is a major determinant of profitability in livestock production enterprises. Traditionally selection for growth rate has received considerable emphasis in most breed improvement schemes. However its value to the improvement of enterprise efficiency and profitability of ruminant production systems has been questioned, since increased mature size is a direct consequence, resulting in an increased cost of maintaining breeding females (Barlow, 1984). Modelling work by Thompson and Barlow (1986) showed greater improvements in enterprise efficiency (lean output/food input) would result from improvement in feed conversion efficiency of the growing animal and reduction in feed intake of the mature dam, but at that time the evidence for genetic variation in either of these traits was equivocal. In their review of genetic parameter estimates for beef cattle, Koots et al. (1994b) re-
ported that the weighted mean genetic correlations for feed conversion ratio (FCR) with growth rate and size were highly negative. These correlations indicate that selection to reduce FCR and improve efficiency would be accompanied by an increase in growth rate, and presumably in mature cow size. That this would indeed occur was demonstrated by Mrode et al. (1990b) who reported that selection to reduce lean FCR resulted in a correlated increase in cow size.

Recent research has shown that there is genetic variation in the feed eaten by young growing beef cattle beyond that explained by the size and growth rate of the cattle (Archer et al., 1998). This variation in feed intake net of expected requirements based on size and growth is measured as residual feed intake (RFI). RFI is calculated as the difference between actual feed intake by an animal and its expected feed intake based on its size and growth rate. Selection to reduce RFI offers to reduce feed intake, without compromising growth performance, and thereby to improve the profitability of beef production. Evidence demonstrating genetic variation in RFI in beef cattle was reviewed by Arthur et al. (1998). Notable in this review were the small number of published estimates of the heritability for this trait and the relatively small datasets upon which they were based. Arthur et al. (1998) concluded there remained a need for more information about this trait and its relationship with other important production traits, including maternal traits and mature cow efficiency.

In principle, central testing of cattle for performance traits permits accurate comparison of animals from different herds, under uniform conditions (Simm, 1983). However, accuracy of central testing may be reduced due to environmental variation arising from differences in rearing pre-test. Simm (1983) reviewed several reports of negative environmental correlations between pre-test growth rate and growth rate on test, whereas genetic correlations are positive. He concluded that the combination of these two effects often leads to low or negative correlations, indicating some degree of compensatory growth on test. Simm (1983) showed that differences in pre-test growth due to rearing treatments and between year environmental variation can influence liveweight (LW) at the start of postweaning testing, and subsequent LW-gain, feed intake and FCR, but did not examine the effect on RFI. If young cattle are to be evaluated for selection on RFI measured over a postweaning performance test, then the influence of pre-test growth on RFI over the performance test needs to be assessed.

The purpose of this study was to establish whether there exists genetic variation in RFI in young British Hereford bulls during postweaning performance testing, and to determine the phenotypic and genetic correlations of RFI, growth rate and FCR with some key production traits, including mature cow size. A second objective was to investigate the effect of pre-test rearing treatments on variation in RFI and other production traits measured over the subsequent performance test.

2. Materials and methods

2.1. Source of data

The data analysed were collected during the course of a selection experiment in Hereford cattle run by the Roslin Institute (formerly the Institute of Animal Physiology and Genetics Research; Mrode et al., 1990a). Briefly, a foundation herd of 227 Hereford cows were purchased from 62 pedigree herds from all sections of the Hereford Herd Book: Horned, Polled and British Hereford. During 1978–79 the females were mated, largely by artificial insemination, to 48 bulls from a variety of sources. After the initial two years, the herd was closed and females randomly allocated to two selection lines.

The data consisted of performance measurements on 542 bull calves taken over 10 years, from 1979 to 1988, and bimonthly weight records taken on the cow herd. In years 1 to 6 of the experiment, bulls were assigned to one of three rearing treatments: weaning at birth (after getting colostrum) and artificial rearing to 84 days of age, or weaning at 84 days, or weaning at 168 days of age. After year 6, all bull calves were weaned at about 84 days of age. After 84 days of age (the two early weaning treatment groups), or 168 days, the bulls were introduced to the test diet and trained to use individual Calan–Broadbent electronic feed gates. From approximately 200 to approximately 400 days of age, LW and feed intake were recorded at 30-day intervals on each bull calf. During this performance test the cattle were offered a complete grass/barley pelleted diet offered
ad libitum with a small quantity of hay to stimulate ruminination. Carcase lean content (LEAN) was predicted at the end of test for each animal from backfat thickness measured by ultrasound scanning at the 10th and 13th ribs and the third lumbar vertebrae. LEAN was standardised each year to have a mean of 0.60 and a coefficient of variation of 0.04. Detailed descriptions of the husbandry and selection methods are given by Simm (1983) and Mrode et al. (1990a).

In the selection experiment, the traits selected for were lean growth rate (LGR; growth rate to 400 days × predicted carcase lean content) and lean feed conversion ratio [LFCR; feed intake/(weight gain × predicted carcase lean content)] from 200 to 400 days. Both LGR and LFCR were scaled by a constant predicted killing out proportion of 0.577, estimated from bulls slaughtered in the initial years of the experiment. Responses to selection on these traits, as well as the components traits of birth weight, predicted LEAN, growth rate to 400 days, feed intake and FCR have been presented by Mrode et al. (1990a,b).

2.2. Derivation of traits

The performance test data for LW and feed intake measurements were precorrected to 200 days of age at the start of the test and 400 days of age at the end of the test. This was not done by Mrode et al. (1990a,b). The traits of LGR, LFCR, FCR, feed intake (FI), 200-day weight (W200), 400-day weight (W400) and 200 to 400-day daily weight gain (ADG) were then calculated for each animal. Also calculated was average metabolic weight (MBW) as the mean of W200 and W400, raised to 0.75.

Bishop (1992) also derived traits to describe the energy required for the deposition of fat and protein in the body of the growing animal, for maintenance energy expenditure, and for maintenance energy expenditure per unit metabolic LW. Maintenance energy expenditure (MAINT) of growing animals was defined as the difference between total metabolisable energy (ME) intake and the amount of ME required for growth. The ME required for growth (DEP) was calculated using allometric equations describing the costs of protein and fat accretion, and assumed standard efficiencies for fat and protein deposition. Full derivations for MAINT and DEP are given in Bishop (1992). Maintenance energy expenditure per kg of metabolic body weight (MBBW) was calculated as MAINT divided by MBW.

Residual feed intake for each animal was calculated as the difference between actual feed intake over the 200-day performance test, less their expected feed intake over the test. For each of the 10 performance tests, FI was regressed on MBW and ADG (Proc REG; SAS Institute, 1989), and RFIReg for each animal was calculated as the residual from the multiple regression. The distributions of RFIReg and its component traits (FI, MBW and ADG) for each performance test were checked for normality (Proc UNIVARIATE; SAS Institute, 1989). Feed intakes by calves born in year 9 of the experiment were not normally distributed (P < 0.05). The FI by two bull calves were judged to be abnormally low, being more than three standard deviations below the mean FI for their test group. Data for these two animals were not subsequently used. Results for 540 bull calves, from 154 sires, are presented in this report, compared to 542 calves by Bishop (1992).

Although RFIReg is phenotypically independent of size and growth rate, Kennedy et al. (1993) showed that under some circumstances it may be genetically correlated with these same traits. Residual feed intake was therefore also calculated from the phenotypic (RFIphen) or genetic (RFIgen) variances and covariances obtained from multivariate analyses for FI, MBW and ADG. These calculations assumed constant relationships between the component traits across years whereas the calculation of RFIReg allowed these relationships to vary from year to year.

To investigate if there was association between postweaning test performance and cow size, the LW of the dam at just over 4.5 years of age (COWWT) was used as an estimate of her mature size. This weight was taken after all the four-year-old cows had weaned their calves. Weight records were available for 331 cows, some of whom may have had more than one bull-calf performance tested. The mean weight of the cows was 498±59 kg (SD).

2.3. Data analysis

Heritabilities, and phenotypic (rph) and genetic correlations (rg) for all traits were estimated within multivariate analyses by ASREML (Gilmour et al., 1996; version 28 February 1998), fitting an animal
model along with the fixed effects of birth year (10 levels), rearing treatment (three levels), age of dam (10 levels) and selection line (three levels: two selected lines plus an unselected control line). Although the data had been collected on animals previously selected on the basis of LGR and LFCR, Bishop (1992) showed this to produce little bias in the genetic variances and covariances estimated for the traits he studied. For this reason, in this study it was judged sufficient to include only LFCR in the trivariate analyses of the other traits. As only males were performance tested, no animals had both performance and cow traits available. Calculation of phenotypic correlations for COWWT with performance test traits was therefore not possible.

Differences in test performance, resulting as a consequence of the three different pre-test nutritional treatments (i.e., ages of weaning), were analysed using a general linear model (GLM) procedure (Proc GLM; SAS Institute, 1989). Data for 339 calves from years 1 to 6 of the selection experiment was used, as in later years all calves were weaned at the same age (84 days). The traits analysed were W200 as a measure of pre-test growth rate, and FI, ADG, W400, LEAN, FCR, LFCR and RFI \text{Reg} measured for the 200-day performance tests. The GLM model included the fixed effects of year (1 to 6), rearing treatment (birth, 84 or 168 days of age), and line (control, LGR, LFCR), fitted sequentially. The interaction of test year with rearing treatment was also included in the model. In years 1 and 2, calves were not assigned to selection lines, and in year 3, all calves were assigned to either the LGR or LFCR lines. This meant that the design was unbalanced and results were therefore calculated as least-squares means.

### 3. Results

#### 3.1. Performance test results

The phenotypic and genetic correlations between FI and MBW (0.67 ± 0.03 (S.E.) and 0.89 ± 0.08, respectively), and between FI and ADG (0.47 ± 0.04 and 0.70 ± 0.14) were medium to high, but less than one, indicating that there was both phenotypic and genetic variation in the relationship between FI and growth performance. RFI \text{Reg} had a heritability of 0.16 ± 0.08 and was phenotypically independent of size and growth (i.e., \( r_p \) with W200, W400, MBW and ADG were all zero; Table 1). RFI \text{Reg} was genetically independent of ADG, but the genetic correlations with size (i.e., \( r_g \) with W200, W400 and MBW) were not so close to zero, even though not statistically different from it. The large standard errors were due to the small size of the dataset as well as the lowheritabilities of the component traits. RFI \text{Reg} was positively correlated with FCR and LFCR, both phenotypically and genetically, such that lower RFI \text{Reg} was associated with improved FCR and LFCR (Table 1). RFI \text{Reg} was negatively associated with LEAN and LGR, implying that superior residual feed intake was accompanied by a greater proportion of lean in the weight gain and final carcase of the calves. RFI \text{Reg} was phenotypically

### Table 1

<table>
<thead>
<tr>
<th>Trait</th>
<th>Mean (SD)</th>
<th>( h^2 ) (S.E.)</th>
<th>( r_p ) (S.E.)</th>
<th>( r_g ) (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>W200 (kg)</td>
<td>166 (30)</td>
<td>0.23 (0.08)</td>
<td>0.00 (0.04)</td>
<td>0.34 (0.34)</td>
</tr>
<tr>
<td>FI (kg/200 d)</td>
<td>1458 (176)</td>
<td>0.31 (0.08)</td>
<td>0.70 (0.02)</td>
<td>0.64 (0.16)</td>
</tr>
<tr>
<td>ADG (kg/d)</td>
<td>1.21 (0.18)</td>
<td>0.38 (0.10)</td>
<td>-0.01 (0.05)</td>
<td>0.09 (0.29)</td>
</tr>
<tr>
<td>MBW (kg)</td>
<td>69.2 (50.6)</td>
<td>0.36 (0.09)</td>
<td>-0.01 (0.04)</td>
<td>0.22 (0.29)</td>
</tr>
<tr>
<td>W400 (kg)</td>
<td>408 (41)</td>
<td>0.42 (0.10)</td>
<td>-0.01 (0.04)</td>
<td>0.15 (0.28)</td>
</tr>
<tr>
<td>LEAN (kg/kg)</td>
<td>0.600 (0.024)</td>
<td>0.49 (0.11)</td>
<td>-0.22 (0.04)</td>
<td>-0.43 (0.23)</td>
</tr>
<tr>
<td>LGR (kg/d)</td>
<td>0.32 (0.04)</td>
<td>0.47 (0.10)</td>
<td>-0.33 (0.04)</td>
<td>-0.47 (0.17)</td>
</tr>
<tr>
<td>FCR (kg/kg)</td>
<td>6.14 (1.07)</td>
<td>0.17 (0.09)</td>
<td>0.61 (0.04)</td>
<td>0.70 (0.17)</td>
</tr>
<tr>
<td>LFCR (kg/kg)</td>
<td>17.76 (3.24)</td>
<td>0.26 (0.09)</td>
<td>0.63 (0.05)</td>
<td>0.72 (0.22)</td>
</tr>
<tr>
<td>DEP (MJ ME)</td>
<td>5327 (818)</td>
<td>0.36 (0.10)</td>
<td>0.06 (0.04)</td>
<td>0.27 (0.18)</td>
</tr>
<tr>
<td>MAINT (MJ ME)</td>
<td>9083 (1821)</td>
<td>0.23 (0.08)</td>
<td>0.77 (0.13)</td>
<td>0.77 (0.18)</td>
</tr>
</tbody>
</table>
| MMBW (kJ/kg kg/d) | 655 (118) | 0.14 (0.08) | 0.93 (0.06) |}
independent of feed energy required for gain of lean and fat (DEP), although the genetic correlation was not so close to zero, even though not statistically different from it. RFI
\textsubscript{Reg} was highly correlated, both phenotypically and genetically, with variation in feed energy attributed to maintenance (MAINT) and to maintenance energy expenditure per unit MBW (MMBW).

RFI
\textsubscript{Reg} (calculated phenotypically for each test) had a high phenotypic correlation with RFI\textsubscript{Phe} and RFI\textsubscript{Gen} (0.88 ± 0.01 and 0.73 ± 0.02 respectively), but the correlations were less than unity implying that RFI
\textsubscript{Reg} was phenotypically a different trait than RFI\textsubscript{Phe} and RFI\textsubscript{Gen}. The genetic correlation of RFI
\textsubscript{Reg} with RFI\textsubscript{Phe} (0.75 ± 0.14) was also less than unity, although not statistically different from it. The genetic correlation of RFI
\textsubscript{Reg} with RFI\textsubscript{Gen} (0.47 ± 0.24) was considerably less than unity, implying that they were genetically different traits. This was unexpected as our preliminary calculations based on expectations from the (co)variance components indicated all these correlations should have been greater than 0.95. Two assumptions used in the calculation of RFI\textsubscript{Phe} and RFI\textsubscript{Gen} were that the component traits (FI, MBW and ADG) were normally distributed, and that the regression coefficients for FI with MBW and ADG were constant across years. With respect to the first assumption, FI and MBW for the 540 calves were normally distributed ($P > 0.05$) but ADG was not ($P < 0.01$). To check the second assumption, the relationships of FI to MBW and ADG across years were examined in a GLM, with the interactions of MBW with year, and ADG with year, fitted after year, MBW and ADG. The interaction of MBW with year was not significant ($P > 0.2$), indicating that the regression coefficients for the relationship of FI with MBW were similar across years. However, the interaction of ADG with year was significant at $P = 0.08$. Examination of regression indicated that in years 2 and 6 these coefficients differed from those in the other years. Thus the two assumptions used to calculate RFI\textsubscript{Phe} and RFI\textsubscript{Gen} appeared to have been violated. Finally, although the three measures of residual feed intake (RFI
\textsubscript{Reg}, RFI\textsubscript{Phe} and RFI\textsubscript{Gen}) all had means of zero, only RFI
\textsubscript{Reg} had a normal distribution for all 540 calves. The distributions for RFI\textsubscript{Phe} and RFI\textsubscript{Gen} were skewed towards numerical more positive values, with median values of 8.5 and 19.7 kg/200 d, co-efficients of skewness equal to $-0.25$ and $-0.50$, and Shapiro–Wilk statistics (Proc Univariate; SAS Institute, 1989) of 0.98 and 0.97, indicative of non-normality ($P < 0.05$ and $P < 0.01$), respectively.

### 3.2. Associations with cow size

There was genetic variation in estimated mature cow size (COWWT) as evidenced by its heritability of $0.69 ± 0.11$. Even though estimated from a small dataset this value is close to the weighted mean heritability for mature cow weight of 0.50 calculated from 24 published estimates by Koots et al. (1994a). Although estimated with a rather large standard error, COWWT appeared to be genetically independent of RFI
\textsubscript{Reg} measured during the postweaning performance test ($r_e = -0.09 ± 0.26$). The genetic correlations between growth traits (ADG, W400 and LGR) and COWWT were all positive ($0.40 ± 0.18, 0.40 ± 0.16$ and $0.43 ± 0.16$, respectively). The genetic correlations between measures of feed conversion efficiency (FCR and LFCR) and COWWT were less than zero, although not significantly different from it ($-0.29 ± 0.24$ and $-0.23 ± 0.22$, respectively).

### 3.3. Effect of pre-test weaning treatments

The different rearing treatments resulted in different pre-test growth rates, as indicated by the significantly lighter LW at the start of the performance test (W200) of the artificially-reared bulls, compared to the calves weaned at 84 and 168 days (Table 2). Across the six years (i.e., six tests) these differences in start-of-test LW were associated with a lower FI during the subsequent 200-day performance test and final LW (W400), and lean growth rate from birth to 400 days of age (LGR), but not with differences in ADG, LEAN, FCR, LFCR or RFI. However, there were significant year-by-rearing interactions such that in some years there were differences in ADG, FCR and LFCR between rearing-treatment groups. In years 2 and 5, the 184-day weaned calves had a slower ADG, and a higher FCR, during the test, than either the calves weaned at birth or 86 days. In year 5, LFCR was also worst for the 184-day weaned
Table 2
Least-squares means (S.E.s) for performance test results of bull calves weaned at birth, 84 or 168 days of age during the first six years of the selection experiment

<table>
<thead>
<tr>
<th>Birth</th>
<th>Rearing treatment</th>
<th>Interaction of rearing × test year</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>84 days</td>
<td>168 days</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W200</td>
<td>162 (4)</td>
<td>179 (2)</td>
</tr>
<tr>
<td>ADG</td>
<td>1.11 (0.03)</td>
<td>1.13 (0.01)</td>
</tr>
<tr>
<td>FI</td>
<td>1474 (30)</td>
<td>1520 (15)</td>
</tr>
<tr>
<td>W400</td>
<td>385 (7)</td>
<td>405 (3)</td>
</tr>
<tr>
<td>LEAN</td>
<td>0.606 (0.005)</td>
<td>0.603 (0.003)</td>
</tr>
<tr>
<td>LGR</td>
<td>0.307 (0.006)*</td>
<td>0.322 (0.003)*</td>
</tr>
<tr>
<td>FCR</td>
<td>6.66 (0.14)</td>
<td>6.77 (0.07)</td>
</tr>
<tr>
<td>LFCR</td>
<td>19.1 (0.5)</td>
<td>19.5 (0.2)</td>
</tr>
<tr>
<td>RFI_{Reg}</td>
<td>1 (22)</td>
<td>-12 (11)</td>
</tr>
</tbody>
</table>

Means within a row with different superscripts differ (P < 0.05). ***P < 0.001; *P < 0.05; ns P > 0.05.

calves. The faster growth, and better FCR, of the artificially-reared calves in years 2 and 5 was evidence that compensatory gain in LW occurred during their 200-day test in these two years. Feed efficiency, as measured by RFI_{Reg}, was unaffected each year (i.e., over each test) by differences in rearing treatment and pre-test growth rate.

4. Discussion

This study has shown that in young British Hereford bulls there exists both phenotypic and genetic variation in feed intake that is independent of size and growth rate. Therefore it should be possible to implement genetic selection to reduce feed intake without compromising growth, and to thereby improve the profitability of beef production. The genetic correlations of performance test traits with mature cow size had rather large standard errors because of the small size of the dataset. However estimates of the genetic correlation of FCR with cow size are scant (only one reported in the review by Koots et al., 1994b), and that for RFI with cow size reported here appears to be the first published estimate of this correlation. Even if treated as preliminary, the genetic correlation reported here indicates that RFI_{Reg} was genetically independent of estimated cow mature size (COWWT), and therefore, selection against RFI has the potential to improve feed efficiency in the young animal without increasing the size of the cow. This is an important advantage over selection for growth rate, LGR or LFCR. In this study these three traits were genetically correlated with COWWT indicating that selection to improve these traits would be accompanied by an increase in cow size. Selection for growth rate has been repeatedly associated with an increase in cow size and its benefit to whole herd productivity has been seriously questioned (Barlow, 1984). Within the current selection experiment, selection for LGR and LFCR were both shown to produce correlated increases in cow LW (Mrode et al., 1990b).

Our estimate of the heritability for RFI_{Reg} (0.16) is modest and similar to five other estimates reported in the review by Arthur et al. (1998), but low compared to the estimate of 0.46 reported for British-breed cattle by Archer et al. (1998). In both studies, the phenotypic variances (V_p) of two components traits of RFI_{Reg} (ADG and MMBW) are of similar magnitude, both in absolute size and relative to mean for each trait (Table 3). The V_p of the third component trait, FI, is larger in this study and contributes to the V_p for RFI_{Reg} which in this study was much larger than that in the Australian study. The corresponding genetic variances for RFI_{Reg} are not so different (1601 and 2182 kg, or 1.1- and 1.7-times the respective mean feed intakes). Rather it is the environmental variances in RFI_{Reg} that differ most between the two studies, being much larger in this study compared to the Australian study (8555
Table 3
Means and phenotypic variances ($V_p$) for RFI, and its components traits measured over postweaning performance tests with British cattle

<table>
<thead>
<tr>
<th>Trait</th>
<th>This study</th>
<th>Archer et al. (1998)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>$V_p$</td>
</tr>
<tr>
<td>FI (kg)</td>
<td>1458</td>
<td>20 560</td>
</tr>
<tr>
<td>MMBW (kg)</td>
<td>69.2</td>
<td>23.6</td>
</tr>
<tr>
<td>ADG (kg/d)</td>
<td>1.21</td>
<td>0.021</td>
</tr>
<tr>
<td>RFI (kg)</td>
<td>0</td>
<td>10 156</td>
</tr>
</tbody>
</table>

* Using the mean for FI.

and 2561 kg, or 5.9- and 2.0-times their mean feed intakes, respectively. This is presumably due to the tighter relationships between FI, and MMBW and ADG, and hence lower range in residuals (i.e., $RFI_{reg}$) in the Australian postweaning performance tests compared to those in this study. One explanation for this could be less measurement error in the more recently conducted Australian experiment. The $R^2$ values for multiple regressions for the seven Australian tests are typically 70% or higher (unpublished data) compared to a mean of 54% (range 39% to 65%) for the $R^2$ values over the 10 tests in this study. Had the environmental variance for RFI in this study been lower and similar to that in the Australian study, then the differences in heritabilities would not have been so large.

In this study variation in RFI was associated with variation in measures of body composition and of maintenance energy expenditure. The phenotypic and genetic correlations of RFI with LEAN and LGR were both low indicating that selection against RFI might slightly increase carcase leanness. This is in agreement with the observed small reduction in subcutaneous-fat thickness reported by Richardson et al. (1998) in response to a single generation of selection against RFI. However, variation in LEAN explained little additional variation in FI beyond that explained by MBW and ADG. In the GLM described above that was used to examine the relationship between FI, and MBW and ADG, over the 10 years of testing, the latter two traits and their interactions with year explained 68% of the variation in FI. Adding LEAN to this model explained only an additional 1.5% of the variation in FI. LEAN is a measure of carcase leanness, largely dependent on measurement of subcutaneous fat depths, and may be poorly related to differences in whole-body chemical composition. The full importance of variation in body composition to variation in RFI remains to be determined.

Our assumption that the feed energy requirements for protein and fat accretion (DEP) can be determined from allometric equations is in agreement with Veerkamp and Emmans (1995) who could find no conclusive evidence in dairy cows for variation in the partial efficiencies for conversion of substrate to product. In defining the maintenance energy expenditure (MAINT) of the young animals in this study as feed energy intake surplus to the requirements for DEP, we have included in MAINT sources of variation in feed intake recognised by Veerkamp and Emmans (1995) as being distinct from $k_m$: the partial efficiency of maintenance. These include differences in mobilisation of tissues to meet energy requirements, differences in partitioning of substrate to lean and fat compartments, and, perhaps, differences in activity. We calculated both RFI and MAINT as that feed intake surplus to expected requirements based on regression with MBW and ADG (for $RFI_{reg}$) or from allometric equations (MAINT) and it is, therefore, not surprising that they are phenotypically and genetically very similar traits. Both traits would have included unexplained variation in feed intake due to these sources. The high phenotypic and genetic correlations between $RFI_{reg}$ and MAINT and MMBW suggest that selection against RFI should favour those animals with lower maintenance energy expenditures. This should lead to improvement in the apparent efficiency of maintenance but without compromise to growth performance.

Residual feed intake calculated from phenotypic (co)variances ($RFI_{Phen}$) should be similar to $RFI_{reg}$ calculated using the conventional regression method used in this study, and the close homology of the two
was supported by the recent results of Archer et al. (1998). Archer et al. (1998) also reported a very high correlation between RFI\textsubscript{phen} and RFI\textsubscript{gen} and led to the conclusion that selection for RFI\textsubscript{gen} (RFI calculated to be genetically independent of production) would give similar results to selection for RFI\textsubscript{reg}. However, in this study the genetic correlation of RFI\textsubscript{reg} with RFI\textsubscript{gen} was considerably less than unity, implying that they were genetically different traits. This may have been due to two of the assumptions used in the calculation of RFI\textsubscript{gen}: that the component traits (FI, MBW and ADG) were normally-distributed, and that the regression coefficients for FI with MBW and ADG were constant across years, having been violated. The calculation of RFI\textsubscript{reg} allowed these regression relationships to vary across year. Whilst RFI\textsubscript{reg} may under some circumstances be genetically correlated with production (Kennedy et al., 1993), use of RFI\textsubscript{gen} (and assuming constant relationships across years) may be ignoring real variation in these relationships. An alternative approach that could be investigated on larger datasets may be to fix the genetic variances and covariances and allow environmental covariances to vary between years, and then use the parameters to calculate RFI which differs between years. Clearly, the choice of traits to be included in a selection program to improve feed efficiency will require further consideration.

Pre-test environmental variation in the form of different ages of weaning was shown to affect phenotypic performance during the subsequent post-weaning test. Rearing treatment affected pre-test growth as measured by W200, but it also affected LGR, FI and W400, and in some years also affected LW gain over the test, LEAN, FCR and LFCR. RFI was unaffected by differences in rearing treatment and may therefore be less influenced by pre-test environmental variation than the other performance traits routinely measured on beef cattle. Current genetic evaluation schemes require that animals are evaluated within contemporary groups and that the test environments are linked by common sires. This is to remove environmental variation due to differences in management of groups, and between tests. These procedures improve the accuracy of the genetic evaluation and ranking of animals but these environmental effects can still affect the phenotypic ranking of animals. Thus there remains an argument favouring standardisation of the pre-test preparation (i.e., growth) of cattle to ensure a fairer phenotypic comparison over the subsequent test. The lack of effect of pre-test environment on RFI implies that it may be more robust across farms or environments than the other growth or efficiency traits measured.

This study has shown that selection against RFI has the potential to improve FCR in the young growing animal, to improve the efficiency of maintenance energy expenditure, and to avoid increasing the size of the cow. These are key responses to improvement in enterprise efficiency (Thompson and Barlow, 1986). RFI appeared to be less influenced by pre-test environmental variation than was LW, growth rate and other measures of efficiency during the postweaning performance tests on beef cattle.

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