# Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls

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**ABSTRACT:** No genetic parameters for performance and feed efficiency traits are available for Irish performance-tested bulls. The objective of this study was to determine the phenotypic and genetic variation for feed intake, BW, ADG, and measures of feed efficiency including feed conversion ratio (FCR), relative growth rate, Kleiber ratio, residual BW gain (RG), and residual feed intake (RFI). Observations were available on up to 2,605 bulls for each trait from one test station across 24 yr; breeds included in the analyses were Aberdeen Angus (AN), Charolais (CH), Hereford, Limousin (LI), and Simmental. The test period was at least 70 d. Bulls were individually offered concentrates ad libitum, with a restricted forage allowance. Differences in performance and feed efficiency existed among breeds. For example, AN, on average, ate 0.04 kg of DM/d more than CH but had ADG of 0.14 kg/d less over the 70-d test period. Results showed LI and CH were the most efficient breeds when efficiency was defined as FCR or RFI. When animals were partitioned into groups based on high, medium, or low RFI, the low RFI (i.e., most efficient) group were also the more efficient as defined by RG and FCR. The low RFI group had the same ADG as the medium group and a greater ADG ($P < 0.01$) than the high group (1.67 vs. 1.66 and 1.63 kg/d); yet they ate 0.67 kg of DM/d less ($P < 0.001$) than the medium RFI group and 1.22 kg of DM/d less ($P < 0.001$) than the high RFI (i.e., least efficient) group. Genetic parameters for all performance and efficiency measures were estimated across breeds using linear animal mixed models; heritability estimates for feed efficiency traits ranged from 0.28 ± 0.06 (RG) to 0.45 ± 0.06 (RFI). An additional series of analyses included a maternal component in the model; maternal heritability estimates for feed efficiency traits ranged from 0.05 ± 0.03 (RG) to 0.11 ± 0.05 (relative growth rate). Genetic correlations between most of the different feed efficiency measures were strong. Results from this study indicate significant genetic differences in performance and some measures of feed efficiency among performance-tested beef bulls.

**Key words:** beef cattle, feed efficiency, genetic parameter, maternal variance, residual feed intake



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## INTRODUCTION

Profitability in beef herds is a function of revenues and costs of which feed is the largest variable cost (Arthur et al., 2004). Traditionally, beef breeding programs have focused on outputs, due mainly to the routine availability of phenotypic data on outputs or correlated traits. However, approximately 65 to 75% of total dietary energy intake in beef cows is used solely for body maintenance (Ferrell and Jenkins, 1985; Montano-Bermudez et al., 1990), whereas the beef cow breeding herd uses 65 to 85% of the energy required in beef production systems (Montano-Bermudez et al., 1990). Therefore, the efficiency of converting feed into saleable product is of increasing importance.

Feed conversion ratio (**FCR**) was traditionally the most commonly used measure to quantify feed efficiency in beef cattle (Berry, 2008) and is generally defined as feed intake per unit ADG. However, net feed efficiency measures, such as residual feed intake (**RFI**), are increasing in popularity as a measure of feed efficiency in cattle (Berry, 2008) since it was first suggested for use in cattle by Koch et al. (1963). Residual feed intake is defined as the difference between actual and predicted feed intake, with negative or decreased values desirable. Similarly, residual BW gain (**RG**) is defined as the difference between actual and predicted daily BW gain, with greater or positive values desirable. Previous heri-

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tability estimates for FCR and RFI in beef cattle range from 0.17 to 0.46 (Herd and Bishop, 2000; Arthur et al., 2001a; Schenkel et al., 2004) and from 0.14 to 0.58 (Fan et al., 1995; Liu et al., 1998; Crews et al., 2003), respectively, which suggests that there is scope for genetic improvement in both traits. However, genetic parameters are population-specific, and estimates of genetic correlations with other important traits such as ADG and BW are vital to ensure no unfavorable correlated responses to genetic selection on feed efficiency.

No genetic parameters for feed efficiency traits are currently available for beef cattle in Ireland, and thus, the objective of this study was to quantify the genetic variation in traits related to feed efficiency in performance-tested pedigree beef bulls fed an energy dense diet and to estimate phenotypic and genetic correlations among these different measures of feed efficiency, as well as other economically relevant performance traits such as intake, BW, and ADG.

## MATERIALS AND METHODS

Data used were obtained from a preexisting database; hence, it was not necessary to secure animal care and use committee approval in advance of conducting this study.

### *Data*

Records were available on 3,545 bulls from the national beef bull performance test center at Tully, Kildare, Ireland, from September 1983 to February 2007, inclusive. Bulls entering the performance test station are currently selected by the Irish Cattle Breeding Federation as well as the respective breed societies. Before the Irish Cattle Breeding Federation took over the management of the test station in 2002, a Department of Agriculture-appointed station manager had charge of the selection process in conjunction with the breed societies. Selection of bulls for performance testing was based on several factors including breed, genetic merit, pedigree, and age.

Bulls were performance tested at the center in, on average, 3 separate groups annually, hereafter referred to as batches. Once in the test center, bulls were assigned to pens based on breed and BW at entry. Indoor pens (20 m wide by 30 m long) were bedded with peat moss, and bulls also had access to an adjacent outdoor pen (20 m wide by 30 m long). The outdoor pen was bedded with woodchip post-2002 to reduce the amount of peat usage and to encourage bulls to spend more time outdoors. Depending on the total numbers of bulls at the test center per year, the numbers of bulls per pen varied from 2 to 5. No information was available on which pen each animal was housed. Duration of the test period varied from 82 to 225 d. All bulls had free access to clean water.

The beginning of the test was set when all bulls had entered the performance center and had acclimatized to the facilities and diet. Initial BW was then recorded and subsequently every 14 d from the start of test with the exception of between 1995 and 2005 when bulls were weighed at 21-d intervals. The diet offered was composed of concentrates and a restricted forage (hay/lucerne) allowance. A Calan Broadbent gate system was used for recording individual animal intake (American Calan, Northwood, NH). On entering the test station, bulls were started on 4.5 to 6 kg of concentrate. Concentrate allowance was increased on a daily basis by 10% in excess of the intake of the previous day until reaching ad libitum. Once ad libitum levels were reached, concentrate intake (**CI**) was recorded, on a fresh-weight basis. Across all years, fresh concentrate was offered daily from Monday through Friday. Forage allowance was offered daily Monday through Sunday. Bulls were offered a 2-d allocation of concentrate on Saturday to facilitate a reduction in labor requirements on Sunday.

Forage was offered on an individual basis at a daily rate of 1.5 kg (fresh weight) per animal as a source of roughage to maintain healthy rumen function. No refusals were weighed. Because forage offered over the years remained the same for all animals, its effect on CI was not taken into consideration in this study. Concentrate refusals of each bull were weighed 1 d each week and subtracted from the cumulative feed offered the previous 7 d to obtain total concentrate fresh weight consumed over this time period. Although CI was therefore calculated weekly, only data on CI averaged over a 14-d period were available across the years 1983 to 1991, whereas CI averaged over a 21-d period was available from 1992 to 2005. From 2006 to 2007, however, average weekly CI was available for inclusion in the analysis.

Composition and DM of the concentrate offered before 1992 was not available. Between 1992 and 2007, two different concentrates were used. The concentrate offered between September 1992 and September 2002 had a DM of 875 g/kg and an estimated ME concentration of 12.1 MJ/kg of DM. The concentrate offered from October 2002 to February 2007 had a DM of 860 g/kg and an estimated ME concentration of 14.5 MJ/kg of DM. The forage was assumed to have a constant DM concentration of 850 g/kg and a ME concentration of 8.6 MJ/kg of DM throughout the years 1992 to 2007.

### *Data Editing*

Data from bulls not on test for at least 96 d (n = 202) were discarded. Concentrate intake and BW records in the last 70 d of the test period were retained because this is deemed to be a sufficiently long enough test period to accurately quantify RFI (Archer et al., 1997; Archer and Bergh, 2000) as well as ensuring minimal loss of bulls from this edit. This will be subsequently referred to as the test period. Additionally, the most recent BW record before the 70-d cut-off was also kept if it was within 92 d of the end of test. All bulls had to have at least 4 BW and CI records during the 70-d test period. A total of 3,167 bulls remained after these edits. Bulls younger than 160 d (n = 38) and older than 360 d (n = 28) on entry to the station were omitted, as were bulls younger than 330 d (n = 85) and older than 480 d (n = 46) at the end of the test. Data on bulls that could not be clearly allocated to a contemporary group or batch (n = 45) were discarded. Only Aberdeen Angus (**AN**), Charolais (**CH**), Hereford (**HE**), Limousin (**LI**), and Simmental (**SI**) breeds were included due to the small number of bulls (n = 245) from other breeds. Bulls with no pedigree information (n = 11) were discarded for the genetic analysis but included in the phenotypic analysis. Nonpurebred bulls (n = 14) were discarded. Data for a further 50 bulls were discarded due to abnormal growth rates described in more detail further on.

Due to the unavailability of diet composition and DM before September 1992, 2 separate data sets were generated: 1) all bulls (n = 2,605); and 2) bulls with records post-September 1992 (n = 2,102) when information on diet composition was available. The first data set was used in the genetic analysis, whereas the second data set was used in the phenotypic analysis as described later.

### *Performance Traits*

Pretest ADG was estimated by dividing the BW of each bull on entry into the test station less birth weight, by its age at entry into the test station. Birth weight is not routinely recorded in Ireland and was therefore not available for any of the bulls in this study. The following estimates of birth weights (Beef Improvement Federation, 1990) were used: AN = 31 kg, CH = 39 kg, HE = 36 kg, LI = 37 kg, and SI = 39 kg. Average daily gain during the test period for each bull was calculated by fitting a linear regression through all BW observations of each bull. The proportion of variation in bull BW explained by the linear regression varied from 0.36 to 0.99. As previously mentioned, data for 50 bulls were removed due to abnormal growth rates defined as r-squares of the regression being <0.90. Mid-test BW was represented as BW 35 d before the end of the test which was estimated from the intercept and slope of the regression line. Similarly mid-test metabolic BW (i.e., $BW^{0.75}$) was estimated from the intercept and slope of the regression line after fitting a linear regression through all metabolic BW observations. Mean daily CI was calculated as the arithmetic mean daily intake of concentrate, on a fresh basis, across the test period. Mean daily DMI was calculated as the sum of the mean daily CI on a DM basis and the daily DMI of forage; because of the unavailability of diet composition pre-1992, DMI was only available on the 2,102 bulls tested after 1992. Average daily ME intake (**MEI**; MJ/kg DM) was also calculated using concentrate DMI and forage DMI multiplied by their respective ME concentrations.

Feed conversion ratio was calculated as average intake (DMI or CI depending on the data set) divided by ADG. Relative growth rate (**RGR**) and Kleiber ratio (**KR**) were computed as follows:

$$\text{RGR} = 100 \times [\log_e(\text{end BW}) - \log_e(\text{start BW})]/\text{d on test};$$

$$\text{KR} = \text{ADG}/\text{mid-test BW}^{0.75}.$$

Residual feed intake was assumed to represent the residuals from a multiple regression model regressing MEI on ADG and $BW^{0.75}$ with batch included as a contemporary group effect; this multiple regression model explained 72% of the variation in MEI. The regression coefficient for ADG and $BW^{0.75}$ was 18.5 and 1.01, respectively. Similarly, RG was assumed to represent the residuals from a multiple regression model regressing ADG on MEI and $BW^{0.75}$ with batch included as a contemporary group effect in the model; this multiple regression model explained 51% of the variation in ADG. The regression coefficients for MEI and $BW^{0.75}$ were 0.01 and −0.001, respectively. When estimating genetic parameters, to increase the number of bulls in the data set and thus facilitate a more precise estimation of (co) variance components, data with missing diet DM and ME values were included. So, CI was used in the calculation of RFI and RG for the genetic analysis rather than MEI.

### *Statistical Analysis*

Factors that significantly affected each of the performance and efficiency traits were determined using linear models in GLM procedure (SAS Inst. Inc., Cary, NC) on the 2,102 bulls with diet information post-1992. Factors tested for significance in the statistical models were batch (n = 84), breed of bull (n = 5), dam lactation number (1, 2, 3 to 4, ≥5, and missing), and age of the bull at the end of test (continuous variable). Nonlinear associations with age at the end of the test as well as a 2-way interaction between age at the end of the test and breed were also tested. The 2,102 bulls with information on diet composition post-1992 were split evenly, within breed, into 3 groups: high, medium, and low RFI. Animals were also split into 3 even groups based on RG. Least squares means for performance and other efficiency measures were determined for the different RFI and RG groups, across breeds.

Repeatability of DMI and BW was calculated using a mixed model where the random effect of animal (n = 2,102) was included in the model along with the significant fixed effects. On average, there were 5 DMI records and 5 BW records per bull included in this analysis. Correlations among BW measures as well as among DMI measures at different weeks of test were also calculated.

**Table 1.** Overall mean and least squares means for BW, growth, and efficiency traits across the different breeds

| Trait | Mean, n = 2,102 | Breed[1] | | | | | SE[2] | *P*-value[3] |
|---|---|---|---|---|---|---|---|---|
| | | AN, n = 75 | CH, n = 521 | HE, n = 115 | LI, n = 850 | SI, n = 541 | | |
| Start age, d | 309 | 309[ab] | 309[a] | 309[a] | 309[a] | 309[b] | 0.09 | <0.001 |
| Final age, d | 389 | 383[a] | 389[ab] | 391[b] | 390[b] | 386[a] | 1.04 | <0.01 |
| Start BW, kg | 476 | 454[a] | 502[b] | 451[a] | 447[a] | 508[c] | 2.08 | 0.04 |
| Final BW, kg | 608 | 583[ac] | 641[b] | 587[a] | 572[c] | 644[b] | 2.30 | <0.01 |
| DMI, kg/d | 10.7 | 11.4[ad] | 11.0[b] | 11.2[ab] | 9.8[c] | 11.6[d] | 0.04 | <0.001 |
| ME intake, MJ/d | 132.3 | 142.2[a] | 135.3[b] | 138.2[c] | 121.2[d] | 143.8[a] | 0.60 | <0.001 |
| Mid-test BW, kg | 552 | 528[ac] | 581[b] | 528[a] | 518[c] | 586[b] | 2.17 | 0.01 |
| Metabolic BW, kg | 113.6 | 109.8[ac] | 118.1[b] | 109.9[a] | 108.3[c] | 118.8[b] | 0.33 | <0.01 |
| ADG, kg/d | 1.65 | 1.60[a] | 1.74[b] | 1.69[c] | 1.56[a] | 1.70[c] | 0.01 | <0.01 |
| Pretest ADG, kg/d | 1.41 | 1.34[a] | 1.49[b] | 1.33[a] | 1.32[a] | 1.52[c] | 0.01 | <0.001 |
| Feed conversion ratio | 6.75 | 7.40[a] | 6.57[b] | 6.82[c] | 6.46[b] | 7.19[a] | 0.04 | 0.03 |
| Relative growth rate | 0.14 | 0.14[a] | 0.14[a] | 0.14[b] | 0.14[a] | 0.13[c] | 0.001 | 0.21 |
| Kleiber ratio | 0.015 | 0.015[ac] | 0.015[a] | 0.015[b] | 0.014[c] | 0.014[c] | 0.0001 | 0.13 |
| Residual BW gain, kg/d | 0.00 | −0.14[a] | 0.07[b] | −0.02[cd] | 0.001[c] | −0.04[d] | 0.01 | 0.05 |
| Residual feed intake, MJ/d | 0.00 | 14.66[b] | −3.26[a] | 8.88[c] | −4.05[a] | 5.35[d] | 0.39 | <0.001 |

[a–d]Least squares means within a row with different superscripts differ ($P < 0.05$).
[1]AN = Aberdeen Angus; CH = Charolais; HE = Hereford; LI = Limousin; SI = Simmental.
[2]Pooled SE.
[3]Significance of the breed effect.

Phenotypic and genetic (co)variance components among traits were estimated, within and across breeds, using an animal model in ASREML (Gilmour et al., 2007). A sire model was also tested, but although (co) variance parameter estimates were similar to those calculated using the animal model, SE estimated using the sire model were greater. A total of 2,605 bulls were included in the across-breed analysis. Because diet composition was not available on all bulls, CI and variables using CI in their calculation were expressed on a fresh-weight basis. After testing the relevant fixed effects on the larger sized data set, the fixed effects included in the model were the same as those that had a significant effect on the respective trait in the previous phenotypic analyses using the fixed effects model. Animal was included as a random effect, and average genetic relationship among bulls was accounted for by tracing both sides of the pedigree back 4 generations. The pedigree file consisted of 11,428 animals. In an additional series of analyses, dam of the bull was included as a random effect, and relationships among dams was also accounted for using the relationship matrix. A covariance between the direct genetic and maternal genetic effect was also fitted. The significance of the maternal component was determined using the Akaike information criterion on nested models that did not include a maternal effect, compared with a model that included a maternal variance component and covariance with the direct genetic effect. In the present data set, 61% of the total number of herds (total number of herds = 630) contributed only 1 animal to the test station. A further 15% of the total number of herds contributed only 2 animals, and another 7% contributed only 3 animals. Therefore herd was not included as a random effect. Similarly, of the 2,104 dams represented in the data set, 84% had only 1 son in the data set, whereas a further 12% had only 2 sons. Therefore, a dam permanent environmental effect was not fitted in the model.

## RESULTS

Repeatability for BW and DMI across the 2,102 bulls, with information on the composition of the diet offered, was 0.95 and 0.33, respectively. Mean RFI across breeds was 0.00 MJ/d; the SD for RFI was 9.91 MJ/d. There was no difference ($P > 0.05$) between individual breeds in the average age of bulls on entry to the performance test station. Limousin bulls had the least mean DMI (9.8 kg/d; Table 1) and had a tendency ($P < 0.11$) to have the least BW (518 kg) and FCR (6.46) as well as the best (i.e., more negative) RFI (−4.05 MJ/d). When using RFI and FCR as measures of feed efficiency, LI and CH were the most efficient ($P < 0.001$) breeds (using RG as a measure, CH proved to be the most efficient), whereas AN was the least efficient. Although ADG was similar between AN (1.60 kg/d) and LI (1.56 kg/d), AN consumed more ($P < 0.001$; 11.4 kg of DM/d vs. 9.8 kg of DM/d). In comparison with CH, AN were 53 kg lighter; however, they consumed 7.40 kg of DM per kg of daily BW gain compared with CH that ate 6.57 kg of DM per kg of daily BW gain.

Significance of effects included in the model as well as the proportion of variation in the dependent variable explained by the chosen model are presented in Table 2. For all traits, batch was significant ($P < 0.001$), although it did not have any effect ($P > 0.05$) on RFI and RG because batch was included in the model for the calculation of these traits. Apart from KR and RGR, breed was significant ($P \leq 0.05$) for all traits. With the exception of ADG and RFI, age had a significant ($P \leq 0.05$) effect on all variables, whereas parity of dam had a significant effect on DMI ($P = 0.01$), BW ($P <$

**Table 2.** Significance of the effect of different fixed effects on BW, growth, and efficiency traits as well as the proportion of variation in each trait ($R^2$) explained by the multiple regression model

| Trait | Batch | Breed | Dam parity | Linear effect of final age | Quadratic effect of final age | $R^2$ |
|---|---|---|---|---|---|---|
| DMI, kg/d | <0.001 | <0.001 | 0.01 | <0.001 | 0.001 | 0.50 |
| ME, MJ/d | <0.001 | <0.001 | 0.11 | <0.001 | 0.01 | 0.60 |
| Mid-test BW, kg | <0.001 | 0.01 | <0.001 | <0.001 | <0.001 | 0.62 |
| Metabolic BW, kg | <0.001 | <0.01 | <0.001 | <0.001 | <0.001 | 0.62 |
| ADG, kg/d | <0.001 | <0.01 | 0.35 | 0.72 | 0.73 | 0.40 |
| Pretest ADG, kg/d | <0.001 | <0.001 | 0.001 | <0.001 | <0.001 | 0.38 |
| Feed conversion ratio | <0.001 | 0.03 | 0.04 | <0.001 | 0.01 | 0.46 |
| Relative growth rate | <0.001 | 0.21 | 0.12 | <0.001 | <0.001 | 0.41 |
| Kleiber ratio | <0.001 | 0.13 | 0.28 | <0.001 | 0.001 | 0.38 |
| Residual BW gain, kg/d | —[1] | 0.05 | 0.31 | 0.05 | 0.12 | 0.07 |
| Residual feed intake, MJ/d | —[1] | <0.001 | 0.81 | 0.89 | 0.81 | 0.30 |

[1]Batch was included as a contemporary group effect when calculating residual BW gain and residual feed intake and was, therefore, not included in the model.

0.001), pretest ADG ($P = 0.001$), and FCR ($P < 0.05$), which is presented in Table 3. As predicted from the model, progeny from parity 1 and 2 dams ate less ($P < 0.05$) and were lighter ($P < 0.05$) than progeny from other parity dams. Dry matter intake, BW, and FCR increased at a decreasing rate with age, whereas KR and RGR decreased at a decreasing rate with age. The developed multiple regression model explained 50% of the variation in DMI and 62% in BW. The proportion of variation in the feed efficiency traits explained by the multiple regression model varied from 7% (RG) to 46% (FCR).

The performance of bulls separated into groups based on RFI is summarized in Table 4. Bulls in the low RFI group (i.e., the more efficient bulls) consumed less feed ($P < 0.001$) and were on average 11 kg heavier ($P < 0.05$) at mid-test than those in the less efficient group and, additionally, had a greater ($P < 0.01$) ADG (1.67 vs. 1.63 kg/d) than the high RFI group. Low RFI bulls were superior ($P < 0.001$) to the other 2 RFI groups for FCR and RG. There was little or no difference ($P > 0.05$) between the 3 groups for KR and RGR.

The performance of bulls separated into groups based on RG is summarized in Table 5. The more efficient, high RG group had a slightly greater ($P < 0.05$) DMI than the medium and low RG groups (10.8 vs. 10.7 and 10.6 kg/d) along with the greatest ADG (1.89 vs. 1.66 and 1.41 kg/d) and proved to be the most efficient in all other measures of efficiency in this study: FCR, RGR, KR, and RFI. Unlike RFI, the more efficient RG group had the least pretest ADG.

### *(Co)Variance Components*

When the only random effect included in the model other than the residual component was the additive genetic effect of the animal, the heritability for the feed efficiency-related traits varied from 0.28 to 0.45 (Table 6); heritability estimates for CI, BW, MWT, and ADG varied from 0.30 to 0.69. However, a maternal heritability estimate in excess of 2-fold greater than its SE was evident for CI, BW, pretest ADG, RGR, and RFI; maternal heritability estimates for these traits varied from 0.09 to 0.24. When a maternal genetic component was also included in the model, the direct heritability estimate decreased from 0.49 to 0.38 (CI), 0.69 to 0.42 (BW), 0.71 to 0.41 (pretest ADG), 0.33 to 0.22 (RGR), and 0.45 to 0.37 (RFI). Heritability estimates within breed were similar to those estimated across breeds albeit with larger SE in the former. Heritability estimates

**Table 3.** Least squares means for traits where parity had a significant effect (Table 2) for animals (n = 2,102) with dams of differing parities

| | Parity[1] | | | | | |
|---|---|---|---|---|---|---|
| Trait | 1, n = 306 | 2, n = 395 | 3–4, n = 558 | ≥5, n = 819 | SE[2] | *P*-value[3] |
| DMI, kg/d | 10.6[a] | 10.6[a] | 10.7[b] | 10.8[b] | 0.04 | 0.01 |
| Mid-test BW, kg | 545[a] | 546[ab] | 554[b] | 556[b] | 0.28 | <0.001 |
| Metabolic BW, kg | 112.5[a] | 112.7[ab] | 113.9[b] | 114.2[b] | 0.33 | <0.001 |
| Pretest ADG, kg/d | 1.40[a] | 1.40[ab] | 1.43[ab] | 1.43[b] | 0.01 | 0.001 |
| Feed conversion ratio | 6.78[a] | 6.60[b] | 6.74[a] | 6.75[a] | 0.04 | <0.05 |

[a,b]Least squares means within a row with different superscripts differ ($P < 0.05$).
[1]Animals that had dams with missing parities; n = 24 were omitted.
[2]Pooled SE.
[3]Significance of the group effect.

**Table 4.** Least squares means for age, BW, growth, and efficiency traits for animals (n = 2,102) ranked high, medium, and low for residual feed intake

| Trait | Residual feed intake group[1] Low | Medium | High | SE[2] | *P*-value[3] |
|---|---|---|---|---|---|
| Residual feed intake, MJ/d | −8.96[a] | 0.20[b] | 8.75[c] | 0.75 | <0.001 |
| Start age, d | 309 | 309 | 309 | 0.07 | 0.21 |
| Final age, d | 390[a] | 388[b] | 388[b] | 0.86 | <0.05 |
| Start BW, kg | 481[a] | 476[a] | 471[b] | 1.75 | <0.001 |
| Final BW, kg | 614[a] | 609[a] | 602[b] | 1.93 | <0.001 |
| DMI, kg/d | 10.1[a] | 10.7[b] | 11.3[c] | 0.03 | <0.001 |
| ME intake, MJ/d | 124.4[a] | 132.7[b] | 139.7[c] | 0.40 | <0.001 |
| Mid-test BW, kg | 557[a] | 552[a] | 546[b] | 1.78 | <0.001 |
| Metabolic BW, kg | 114.4[a] | 113.6[a] | 112.7[b] | 0.28 | <0.001 |
| ADG, kg/d | 1.67[a] | 1.66[a] | 1.63[b] | 0.01 | <0.01 |
| Pretest ADG, kg/d | 1.44[a] | 1.42[b] | 1.40[b] | 0.01 | <0.001 |
| Feed conversion ratio | 6.25[a] | 6.70[b] | 7.24[c] | 0.03 | <0.001 |
| Relative growth rate | 0.13 | 0.14 | 0.14 | 0.0008 | 0.45 |
| Kleiber ratio | 0.015 | 0.015 | 0.015 | 0.0001 | 0.44 |
| Residual BW gain, kg/d | 0.08[a] | 0.01[b] | −0.09[c] | 0.008 | <0.001 |

[a–c]Least squares means within a row with different superscripts differ ($P < 0.05$).
[1]Residual feed intake group derived by dividing the data set equally into groups based on residual feed intake.
[2]Pooled SE.
[3]Significance of the group effect.

for RFI within breed varied from 0.23 (LI) to 0.55 (CH); SE varied from 0.09 (LI) to 0.58 (AN). Heritability estimates for RG within breed varied from 0.11 (CH) to 0.27 (SI); SE varied from 0.08 (LI) to 0.49 (AN). It was also investigated if heritability estimates for RFI differed across the 3 different time periods (1983 to 1991, 1992 to 2005, and 2006 to 2007). Standard errors were large, but the results suggested that heritabilities did not differ significantly ($P > 0.05$) between the different periods. The different heritabilities estimated were 0.58 ± 0.14 (1983 to 1991), 0.58 ± 0.08 (1992 to 2005), and 0.32 ± 0.22 (2006 to 2007). The covariances between the genetic and maternal genetic components were positive, although none significantly differed from zero.

The phenotypic and genetic correlations among the different traits measured are summarized in Table 7. The genetic correlations between the traits measured were in general stronger than the respective phenotypic correlations. The absolute phenotypic correlations between the 5 different measures of feed efficiency varied

**Table 5.** Least squares means for age, BW, growth, and efficiency traits for animals (n = 2,102) ranked high, medium, and low for residual BW gain

| Trait | Residual BW gain group[1] High | Medium | Low | SE[2] | *P*-value[3] |
|---|---|---|---|---|---|
| Residual BW gain, kg/d | 0.22[a] | 0.01[b] | −0.23[c] | 0.0048 | <0.001 |
| Entry age, d | 230[a] | 230[ab] | 229[b] | 0.20 | 0.06 |
| Start age, d | 309 | 309 | 309 | 0.07 | 0.63 |
| Final age, d | 388[a] | 388[b] | 390[b] | 0.86 | <0.05 |
| Start BW, kg | 468[a] | 474[b] | 486[c] | 1.69 | <0.001 |
| Final BW, kg | 619[a] | 607[b] | 600[c] | 1.87 | <0.001 |
| DMI, kg/d | 10.8[a] | 10.7[b] | 10.6[b] | 0.04 | <0.001 |
| ME, MJ/d | 133.4[a] | 132.4[b] | 130.9[c] | 0.40 | <0.001 |
| Midtest BW, kg | 554 | 550 | 551 | 1.79 | 0.31 |
| Metabolic BW, kg | 113.9 | 113.3 | 113.5 | 0.28 | 0.32 |
| ADG, kg/d | 1.89[a] | 1.66[b] | 1.41[b] | 0.01 | <0.001 |
| Pretest ADG, kg/d | 1.39[a] | 1.41[b] | 1.45[c] | 0.01 | <0.001 |
| Feed conversion ratio | 5.87[a] | 6.59[b] | 7.72[c] | 0.02 | <0.001 |
| Relative growth rate | 0.15[a] | 0.14[b] | 0.12[c] | 0.001 | <0.001 |
| Kleiber ratio | 0.017 | 0.015 | 0.013 | 0.00005 | 0.13 |
| Residual feed intake, MJ/d | −3.51[a] | 0.23[b] | 3.10[c] | 0.31 | <0.001 |

[a–c]Least squares means with a row with different superscripts differ ($P < 0.05$).
[1]Residual BW gain group derived by dividing the data set equally into groups based on residual BW gain.
[2]Pooled SE.
[3]Significance of the group effect.

**Table 6.** Genetic SD, direct heritability ($h^2$), direct heritability when a maternal genetic component is also included in the model ($h^2_{direct}$), maternal heritability ($h^2_{maternal}$), and the correlation between the direct and maternal components ($r_{mat,dir}$) for concentrate intake, BW, growth, and efficiency traits[1]

| | | Direct[2] | Direct and maternal[3] | | |
|---|---|---|---|---|---|
| Trait | $\sigma_{genetic}$ | $h^2$ | $h^2_{direct}$ | $h^2_{maternal}$ | $r_{mat,dir}$ |
| Concentrate intake, kg/d | 0.79 | 0.49 (0.06) | 0.38 (0.07) | 0.10 (0.04)[4] | 0.15 (0.34) |
| Mid-test BW, kg | 40.31 | 0.69 (0.07) | 0.42 (0.07) | 0.22 (0.04)[4] | 0.11 (0.23) |
| Metabolic BW, kg | 6.25 | 0.69 (0.07) | 0.43 (0.07) | 0.21 (0.04)[4] | 0.07 (0.23) |
| ADG, kg/d | 0.13 | 0.30 (0.06) | 0.27 (0.06) | 0.03 (0.03) | 0.26 (0.88) |
| Pretest ADG, kg/d | 0.13 | 0.71 (0.07) | 0.41 (0.07) | 0.24 (0.04)[4] | 0.04 (0.21) |
| Feed conversion ratio | 0.05 | 0.30 (0.06) | 0.23 (0.06) | 0.07 (0.04) | 0.32 (0.61) |
| Relative growth rate | 0.52 | 0.33 (0.06) | 0.22 (0.06) | 0.11 (0.04)[4] | 0.03 (0.33) |
| Kleiber ratio | 0.01 | 0.31 (0.06) | 0.24 (0.06) | 0.06 (0.03) | 0.08 (0.42) |
| Residual BW gain, kg/d | 0.01 | 0.28 (0.06) | 0.24 (0.06) | 0.05 (0.03) | 0.38 (0.70) |
| Residual feed intake, kg/d | 0.11 | 0.45 (0.06) | 0.37 (0.07) | 0.09 (0.04)[4] | 0.82 (0.82) |

[1]Associated SE are presented in parentheses.
[2]Heritability estimated with direct effect.
[3]Heritabilities were estimated with a direct and maternal component in the model but with no covariance fitted.
[4]Inclusion of a maternal genetic variance with the additive direct genetic effect significantly ($P < 0.001$) improved the model fit.

from 0.01 (RFI and KR) to 0.97 (RGR and KR); the corresponding absolute genetic correlations varied from 0.15 (RFI and KR) to 0.96 (RGR and KR). However, the correlations between the different feed efficiency measures were not always positive, due mainly to the differences in trait definition. Genetic correlations between RFI and both MWT and ADG were not different ($P > 0.05$) from zero, whereas the phenotypic correlations were zero. Similarly, genetic correlations between RG and both MWT and CI were not different ($P > 0.05$) from zero, whereas phenotypic correlations were zero. Genetic correlations between RG and other measures of feed efficiency were all moderate to strong, ranging from −0.89 (FCR) to 0.76 (KR). Phenotypic and genetic correlations within breed were generally similar and of the same sign to those reported across breed with the exception of only the genetic correlation between RFI and RGR, which was −0.28 ± 0.30 in LI.

## DISCUSSION

Tightening profit margins in Irish beef herds necessitate the evaluation of traits related to input costs such as feed efficiency. Results from this study clearly identified significant genetic variation in feed efficiency traits as evidenced by significant breed effects and heritability estimates. Furthermore, the moderate genetic correlations among most measures of feed efficiency suggest they are measuring similar, albeit not identical, attributes of the animal.

It is acknowledged by the authors that, in some cases in this study, the frequency of BW measurements over the feed intake measurement period for each animal might be very close to critical levels now accepted for accurate estimation of ADG and in turn the RFI trait (Archer et al., 1997). However, the authors are confident that sufficient steps (described in the Materials and Methods) were taken to accurately estimate RFI and its component traits. The proportion of variation in BW measures explained by a linear regression was large (>0.90), indicating that animals were growing linearly at a relatively constant rate. Furthermore, we are encouraged by the fact that heritabilities calculated for these traits are consistent with previously documented estimates (Arthur et al., 2001b; Schenkel et al., 2004).

The range in age of the bulls used in the present study is similar to most previous international studies (Archer et al., 1997; Archer and Bergh, 2000; Liu et al., 2000). The observed mean FCR of 6.75 in this study was also similar to that estimated, using the same definition, by Liu et al. (2000; FCR = 6.76) and Nkrumah et al. (2007; FCR = 7.29). Population means for RGR and KR in this study also corroborate previously published estimates in performance-tested French CH bulls (Arthur et al., 2001b) and hybrid Canadian cattle (Nkrumah et al., 2004).

The ranking of the breeds for FCR and ADG in the present study support the results of Chewning et al. (1990) in their analysis of 2,007 performance-tested bulls, although no LI animals were included in their study. The ranking of the breeds for ADG in the present study also corroborates the findings of Schenkel et al. (2004), although their ranking of breeds for FCR was slightly different, with AN ranking better than SI. Consistent with the results of the present study, Schenkel et al. (2004), in their analysis of 2,284 performance-tested bulls in Canada of the same breeds, reported that LI had better RFI, whereas AN had the worst. Therefore, the results from this study corroborate results from most other studies in that the LI and CH breeds appear to be the most efficient, whereas AN are the least efficient. Ranking does, however, depend on the definition of feed efficiency as well as the representation of the breed by the animals included in the different studies.

**Table 7.** Phenotypic[1] (below the diagonal) and genetic (above the diagonal with SE in parentheses) correlations among BW, growth, and efficiency traits

| Trait | Concentrate intake, kg/d | Mid-test BW, kg | Metabolic BW, kg | ADG, kg/d | Pretest ADG, kg/d | Feed conversion ratio | Residual feed intake, kg/d | Residual BW gain, kg/d | Relative growth rate, kg/d | Kleiber ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| Concentrate intake, kg/d | | 0.70 (0.05) | 0.73 (0.09) | 0.55 (0.09) | 0.66 (0.11) | 0.38 (0.11) | 0.59 (0.13) | −0.03 (0.13) | −0.08 (0.12) | 0.03 (0.24) |
| Mid-test BW, kg | 0.59 | | 1.00 (0.00) | 0.38 (0.10) | 0.98 (0.004) | 0.34 (0.11) | −0.18 (0.09) | 0.07 (0.12) | −0.54 (0.09) | −0.34 (0.11) |
| Metabolic BW, kg | 0.59 | 1.00 | | 0.37 (0.10) | 0.99 (0.004) | 0.35 (0.11) | −0.17 (0.09) | 0.06 (0.12) | −0.55 (0.08) | −0.34 (0.11) |
| ADG, kg/d | 0.38 | 0.34 | 0.34 | | 0.19 (0.11) | −0.53 (0.10) | 0.01 (0.13) | 0.82 (0.05) | 0.56 (0.09) | 0.75 (0.06) |
| Pretest ADG, kg/d | 0.53 | 0.77 | 0.77 | 0.13 | | 0.47 (0.09) | −0.19 (0.09) | −0.10 (0.12) | −0.69 (0.06) | −0.51 (0.09) |
| Feed conversion ratio | 0.34 | 0.12 | 0.12 | −0.71 | 0.27 | | 0.48 (0.10) | −0.89 (0.03) | −0.69 (0.07) | −0.75 (0.06) |
| Residual feed intake, kg/d | 0.58 | −0.001 | 0.00 | 0.00 | 0.03 | 0.41 | | −0.46 (0.11) | 0.21 (0.12) | 0.15 (0.13) |
| Residual BW gain, kg/d | 0.00 | 0.001 | 0.00 | 0.70 | −0.11 | −0.71 | −0.40 | | 0.61 (0.08) | 0.76 (0.06) |
| Relative growth rate, kg/d | −0.03 | −0.35 | −0.36 | 0.73 | −0.43 | −0.76 | 0.02 | 0.65 | | 0.96 (0.01) |
| Kleiber ratio | 0.09 | −0.20 | −0.21 | 0.84 | −0.30 | −0.80 | 0.01 | 0.72 | 0.97 | |

[1]SE of the phenotypic correlations were all <0.02.

The trends in performance among the different RFI groups in this study are consistent with the findings of previous studies (Basarab et al., 2003; Richardson and Herd, 2004; Baker et al., 2006) that also partitioned animals into groups based on their RFI. Low RFI bulls in the present study consumed on average 6% less than those in the medium RFI group and 11% less than high RFI bulls. Baker et al. (2006) documented no difference in ADG between 3 groups generated based on RFI, as well as no differences in RGR or KR, which reflects the lack of a phenotypic correlation with RFI as observed in the present study. When animals in the present study were divided into groups based on RG, the high, supposedly more efficient group, had the greatest ADG and a slightly greater DMI despite no difference in BW. However, the high RG group had a lighter starting BW and greater ending BW, implying that compensatory growth could be a reason behind the superior RG of these animals. It is interesting to note, however, that there was no difference among the RFI or RG groups in the age of the animals at the beginning of the test. The high RG group also had superior efficiency based on other measures estimated. Differences observed in MWT and ADG among animals in different RFI groups is attributable to the fact that RFI was estimated across breeds but animals were categorized into high, medium, and low RFI within breed. A similar conclusion was observed for differences in MEI among RG groups.

Most studies that evaluated animal performance in performance test stations (Archer and Bergh, 2000), experimental feedlots (Chewning et al., 1990; Herd and Bishop, 2000), or commercial feedlot type systems (Hicks et al., 1990) adjust for fixed effects such as contemporary group (Nkrumah et al., 2004), number of days on test (Archer and Bergh, 2000), sex (Nkrumah et al., 2004), birth year (Herd and Bishop, 2000), age (Chewning et al., 1990; Nkrumah et al., 2004; Hoque et al., 2008), BW at the beginning of the test (Archer and Bergh, 2000), breed (Chewning et al., 1990; Liu et al., 2000; Nkrumah et al., 2004), and selection line (Herd and Bishop, 2000) in their statistical model. Due probably to a lack of pedigree recording (Archer and Bergh, 2000), few studies (Herd and Bishop, 2000; Liu et al., 2000; Nkrumah et al., 2004; Hoque et al., 2008) have attempted to quantify the effect of age of dam on the feed efficiency of the progeny. Nkrumah et al. (2004) included age of dam as a linear covariate in their model when analyzing the effect of RFI group on measures of growth, feed intake, energetic efficiency, and ultrasound measurements; they did not, however, report the effect of dam age on performance. Liu et al. (2000) classified dam age into 5 classes but also did not report the effect of dam age on the variables analyzed. Furthermore, Herd and Bishop (2000) did not report the effect of age of dam on animal performance, although they did report correlations with cow BW. In the present study, dam parity was associated with DMI, BW, and FCR; the progeny of older parity animals consumed more feed and were heavier, whereas progeny of second parity dams had better FCR than animals from a first parity dam or a third parity or older dam. The heavier BW in progeny of older parity dams is likely due to the greater milk yield of older cows (Clutter and Nielsen, 1987), which, on average, would have also increased DMI given the positive correlation between BW and CI. The lack of an association between dam parity and RFI agrees with the conclusions of Nkrumah et al. (2004) who reported that RFI may be a robust indicator of feed efficiency because it is apparently less affected by pretest environmental factors such as age of dam. The phenotypic correlation between pretest ADG and RFI in the present study was 0.03.

## *Genetic Parameters*

Heritability estimates for CI, BW, and ADG are within the ranges of heritability estimates reported previously for feed intake (0.31 to 0.44; Herd and Bishop, 2000; Schenkel et al., 2004), BW or metabolic BW (0.35 to 0.37; Herd and Bishop, 2000; Arthur et al., 2001a; Schenkel et al., 2004), and ADG (0.34 to 0.38; Herd and Bishop, 2000; Arthur et al., 2001a; Schenkel et al., 2004). Previous studies in beef cattle reported heritability estimates ranging from 0.17 to 0.46 for FCR (Herd and Bishop, 2000; Arthur et al., 2001a; Schenkel et al., 2004), from 0.18 to 0.43 for RFI (Robinson and Oddy, 2004; Schenkel et al., 2004), and from 0.31 to 0.52 for KR (Bergh et al., 1992; Arthur et al., 2001b); heritability estimates reported in the present study are in general agreement with these previous estimates. The significant genetic variance and heritability for the traits investigated in the present study suggest that selection for these traits would be effective if sufficient data were available for genetic evaluation.

Most previous studies did not attempt to estimate maternal genetic variance for the different traits. With the exception of CI, BW, pretest ADG, RGR, and RFI there was no significant improvement in the fit of the model to the data by including a maternal component in addition to the animal additive genetic effect. Significant maternal genetic variance for BW in suckled or recently weaned calves has been documented elsewhere (e.g., Splan et al., 2002), whereas maternal variance components for feed intake or feed efficiency traits have not been estimated or have been found to have no significant effect (Hoque et al., 2007). It is, however, difficult in the present study to disentangle the effect of dam from the effect of herd of origin on performance; in the present study 58% of bulls originated from herds that entered 2 or less bulls into the performance test station for a given batch. The largest maternal heritability estimate was for pretest ADG (0.24), which probably includes some element of herd management, although the effect of dam milk-yield on ADG in suckling calves is well documented (McGee et al., 2005). A sire model was also fitted to the data. Heritability estimates were similar to those calculated using the animal model but with larger SE. For example, heritabilities derived from using the sire model for RFI, RG, and ADG were 0.37 (0.08), 0.36 (0.10), and 0.31 (0.07), respectively.

The moderate to strong genetic correlations between some of the different measures of feed efficiency traits agree with previous studies (Herd and Bishop, 2000; Arthur et al., 2001a). Nevertheless, the absolute genetic correlations among the other measures of feed efficiency were not all one, suggesting they are not under identical genetic influence. However, besides the correlations between RGR and KR and RFI, the moderate to strong correlations among the feed efficiency measures suggest that selection for any of the measures of feed efficiency examined in this study will, on average, improve all measures of feed efficiency despite not all measures requiring observations for feed intake (i.e., KR and RGR). However, RGR and KR, 2 measures of feed efficiency that do not require observations on feed intake, were almost genetically identical, but were not correlated with RFI. This indicates that indirect selection for RFI using measures such as RGR and KR will not be beneficial and may be attributable to the lack of a correlation between RGR and KR and feed intake. The negative correlation between some measures of feed efficiency is an artifact of the definition of the trait; for example, small or negative RFI and FCR are more desirable, whereas positive RGR, KR, and RG are more desirable. Residual BW gain, another net efficiency trait, was moderately to strongly genetically correlated with all measures of efficiency, which suggests that using RG as a selection criterion will have a desired effect on all other feed efficiency measures. Like RG, FCR has a similar range of genetic correlations with other measures of efficiency, but the fact that RG is genetically independent of feed intake and BW indicates its suitability as selection criteria.

The negative genetic correlation between FCR and ADG ($-0.53$) suggests that selection for reduced (i.e., better) FCR will result in faster growing animals, whereas the positive correlation between FCR and BW (0.34), which agrees with the estimate of 0.24 from Arthur et al. (2001b), suggests that animals will not get heavier over time from selecting for less FCR. This is in contrast to the genetic correlation between FCR and MWT reported by Robinson and Oddy (2004; $-0.62 \pm 0.18$) and the estimate presented by Hoque et al. (2006; $-0.57 \pm 0.25$). However, the genetic correlation between FCR and BW may differ with age of the animal. Bergh et al. (1992) estimated genetic correlations between FCR (defined as the reciprocal of the definition of FCR used in the present study) and BW of $-0.31 \pm 0.48$, $-0.40 \pm 0.49$, and $0.25 \pm 0.59$ for animals at 205, 260, and 400 d of age, respectively. In conclusion, significant differences in performance and some measures of feed efficiency existed among breeds, which was substantiated by the moderate and significant heritability estimates for the performance and feed efficiency traits evaluated in the present study.

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