Genetic associations between feed efficiency measured in a performance test station and performance of growing cattle in commercial beef herds

J. J. Crowley, R. D. Evans, N. Mc Hugh, T. Pabiou, D. A. Kenny, M. McGee, D. H. Crews, Jr. and D. P. Berry

The online version of this article, along with updated information and services, is located on the World Wide Web at:

http://jas.fass.org/content/89/11/3382

Genetic associations between feed efficiency measured in a performance test station and performance of growing cattle in commercial beef herds

J. J. Crowley,*†‡ R. D. Evans,§ N. Mc Hugh,*† T. Pabiou,§ D. A. Kenny,† M. McGee,‡ D. H. Crews Jr.,# and D. P. Berry*[1]

*Animal and Grassland Research and Innovation Centre, Teagasc, Moorepark, Fermoy, Co. Cork, Ireland; †School of Agriculture, Food Science and Veterinary Medicine, College of Life Sciences, University College Dublin, Belfield, Dublin 4, Ireland; ‡Grange Animal & Grassland Research and Innovation Centre, Teagasc, Dunsany, Co. Meath, Ireland; §Irish Cattle Breeding Federation, Bandon, Co. Cork, Ireland; and #Department of Animal Sciences, Colorado State University, Fort Collins 80523-1171

ABSTRACT: Interest in selection for improved feed efficiency is increasing, but before any steps are taken toward selecting for feed efficiency, correlations with other economically important traits must first be quantified. The objective of this study was to quantify the genetic associations between feed efficiency measured during performance testing and linear type traits, BW, live animal value, and carcass traits recorded in commercial herds. Feed efficiency data were available on 2,605 bulls from 1 performance test station. There were between 10,384 and 93,442 performance records on type traits, BW, animal value, or carcass traits from 17,225 commercial herds. (Co)variance components were estimated using linear mixed animal models. Genetic correlations between the muscular type traits in commercial animals and feed conversion ratio (-0.33 to -0.25), residual feed intake (RFI; -0.33 to -0.22), and residual BW gain (RG; 0.24 to 0.27) suggest that selection for improved feed efficiency should increase muscling. This is further evidenced by the genetic correlations between carcass conformation of commercial animals and feed conversion ratio (-0.46), RFI (-0.37), and residual BW gain (0.35) measured in performance-tested animals. Furthermore, the genetic correlations between RFI and both ultrasonic fat depth and carcass fat score (0.39 and 0.33, respectively) indicated that selection for improved RFI will result in leaner animals. It can be concluded from the genetic correlations estimated in this study that selection for feed efficiency will have no unfavorable effects on the performance traits measured in this study and will actually lead to an improvement in performance for some traits, such as muscularity, animal price, and carcass conformation. Conversely, this suggests that genetic selection for traits such as carcass quality, muscling traits, and animal value might also be indirectly selecting for more efficient animals.

Key words: beef cattle, carcass, feed efficiency, genetic, muscularity, skeletal

INTRODUCTION

There is increasing interest in improving feed efficiency in cattle through improvements to animal management and genetics (Berry, 2008). Significant genetic variation in feed efficiency has been reported by using data from performance test stations (Liu et al., 2000; Arthur et al., 2001b; Crowley et al., 2010). However, the correlated response in performance (e.g., carcass traits) in commercial herds to selection on animal performance, including feed efficiency, in performance test stations is less well investigated. This is especially true where differences in production systems exist between commercial farms and performance test stations. For example, in Ireland, performance-tested bulls are fed a high-energy concentrate diet (Crowley et al., 2010), whereas on commercial farms, grazed or ensiled grass constitutes the basal diet of cattle (Keane, 2005).

Furthermore, genetic selection on feed efficiency by using traditional methods of genetic evaluation is limited by routine access to the necessary phenotypes, such as feed intake. Indirect selection using routinely recorded, heritable traits that are genetically correlated with feed intake could provide useful information to increase the accuracy of selection when using multitrait genetic analyses. Linear type traits are routinely recorded in

3382

many countries as part of national breeding programs. Some of these traits, especially skeletal measures associated with body size, may be genetically correlated with feed intake or efficiency. However, information is lacking on whether such associations exist.

The objective of this study was to quantify the genetic associations between a range of definitions of feed efficiency and other performance traits measured during performance testing and linear type traits, BW, animal value, and carcass traits recorded in commercial herds.

MATERIALS AND METHODS

All data used in the present study 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. The data in the present study originated from 2 main sources: 1) data from the national performance test station, and 2) data from national commercial herds.

Performance Test Animals

The performance testing procedures are described in detail by Crowley et al. (2010). Concentrate intake (**CI**) and BW 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, inclusively. Bulls were performance tested at the center in, on average, 3 separate groups annually, hereafter referred to as "batches." Duration of the test period varied from 82 to 225 d.

Initial BW was recorded on entry and, subsequently, every 14 d from the start of test, with the exception of the years between 1995 and 2005, when bulls were weighed at 21-d intervals. The diet offered consisted of concentrates and a restricted forage (hay/lucerne) allowance. Once ad libitum intake of concentrate was reached, CI was recorded on a fresh weight basis. Diet information was not available on all historic data, so feed intake continued to be expressed on a fresh weight basis. Feeding regimen, diets, and data edits were outlined in detail by Crowley et al. (2010).

Briefly, data were edited for length on test (bulls not on test for at least 96 d were discarded), age, completeness of records, breed, and abnormal growth patterns, resulting in 2,605 bulls (Crowley et al., 2010). Only purebred Aberdeen Angus (**AN**), Charolais (**CH**), Hereford (**HE**), Limousin (**LI**), and Simmental (**SI**) bulls with pedigree records were retained. Concentrate intake and BW records during the last 70 d of the test period were retained; this period is subsequently referred to as the "test period."

Performance Test Animals with Records for Feed Efficiency

Performance traits measured on the bulls in the performance test station were described previously by Crowley et al. (2010). In brief, ADG during the test period for each bull was represented by the slope of the linear regression through all BW observations of each bull. Midtest BW was taken as BW at 35 d before the end of the test, which was estimated from the intercept and slope of the regression line. Similarly, midtest 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. Feed conversion ratio (**FCR**) was calculated as the average CI divided by ADG. Relative growth rate (**RGR**; Webster et al., 1982) and Kleiber ratio (**KR**; Kleiber, 1936) were computed as follows:

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

$$KR = ADG/\text{midtest } BW^{0.75}.$$

Residual feed intake (**RFI**; Koch et al., 1963) was defined as the residual from the multiple regression model of CI on ADG and $BW^{0.75}$, with batch included as a contemporary group effect. Similarly, residual BW gain (**RG**; Koch et al., 1963) was defined as the residual from the multiple regression model of ADG on CI and $BW^{0.75}$, with batch included as a contemporary group effect in the model.

Ultrasonic Measures

Ultrasonic measures of body composition taken on 1,476 animals between 1994 and 2005 were available. Each animal was ultrasonically scanned at close to 500 kg of BW to determine muscle (musculus longissimus dorsi) area, muscle depth, and fat depth, similar to the method described by Conroy et al. (2009).

Commercial Data

Linear Type Traits. In Ireland, cattle registered with a herdbook, those in herds participating in a progeny test scheme, or those in otherwise progressive herds may be linearly scored. These data are collated by the Irish Cattle Breeding Federation (**ICBF**) and used in genetic evaluations. Live animal linear scores were available on 70,699 commercial animals scored between the years 2005 and 2008, inclusively. The subjective measurements taken, based on the French "Pointage" system (Linear Scoring Reference Guide; ICBF, 2002), included a variety of skeletal, muscle, and functionality traits, as well as scores for docility and BCS. Muscle traits (Table 1) were width at withers, width behind withers, hind-quarter development, thigh width, and loin development, and were recorded on a scale of 1 to 15. Skeletal traits (Table 1) were length of back,

Table 1. Number of records (n), contemporary groups (CG), and herds, as well as the scale of measurement, mean, genetic SD (σ_g), coefficient of genetic variation (CV_g), and heritability estimates (h^2) for skeletal, muscle, and functional linear type traits

Item	n	CG	Herds	Scale	Mean	σ_g	CV_g	h^2 (SE)
Height at withers	44,816	3,870	1,676	1 = small; 10 = tall	5.95	0.47	0.08	0.34 (0.02)
Length of back	44,818	3,870	1,676	1 = short; 10 = long	7.15	0.48	0.07	0.31 (0.02)
Length of pelvis	31,597	3,529	1,480	1 = short; 10 = long	7.47	0.35	0.05	0.18 (0.02)
Width of hips	44,811	3,870	1,676	1 = narrow; 10 = wide	6.42	0.34	0.05	0.18 (0.01)
Hind-quarter development	44,816	3,870	1,676	1 = low; 15 = high	10.41	0.68	0.07	0.35 (0.02)
Loin development	44,825	3,870	1,676	1 = low; 15 = high	10.07	0.58	0.06	0.24 (0.02)
Thigh	44,811	3,870	1,676	1 = narrow; 15 = wide	10.10	0.63	0.06	0.29 (0.02)
Width at withers	31,958	3,529	1,480	1 = narrow; 15 = wide	9.89	0.52	0.05	0.25 (0.02)
Width behind withers	44,823	3,870	1,676	1 = narrow; 15 = wide	8.95	0.51	0.06	0.22 (0.02)
Foreleg front view	44,819	3,870	1,676	1 = toes out; 10 = toes in	4.91	0.17	0.03	0.07 (0.01)
Hind-leg rear view	44,802	3,870	1,676	1 = toes out; 10 = toes in	5.71	0.09	0.02	0.06 (0.01)
Hind-leg side view	44,810	3,870	1,676	1 = straight; 10 = sickled	7.05	0.26	0.04	0.11 (0.01)
Locomotion	44,674	3,868	1,676	1 = low; 10 = high	7.39	0.34	0.05	0.14 (0.01)
BCS	29,209	3,310	1,411	1 = lean; 10 = fat	6.12	0.34	0.06	0.13 (0.02)
Docility	44,556	3,852	1,670	1 = aggressive; 10 = docile	8.80	0.45	0.05	0.21 (0.02)

length of pelvis, width at hips, and height at withers. Functionality traits (Table 1) were foreleg (front view), hind leg (side and rear view), and locomotion. Skeletal, docility, and BCS were classified on a scale of 1 to 10 (Table 1). Data for each trait were standardized, within scorer by year, to a common variance within trait. Animals with >25% of their breed composition unknown were discarded. Only animals with at least 75% of their breed fraction containing some proportion of AN, Belgian Blue (**BB**), CH, Friesian (**FR**), HE, Holstein (**HO**), LI, and SI were retained. Furthermore, only animals scored between 180 and 550 d of age and with a known sire were included in the analysis. Contemporary groups, defined as herd-date of scoring, with <5 records were omitted. After all edits, 44,827 animals with linear scores remained.

BW and Price. In Ireland, livestock auctions are held at different venues throughout the country, known as marts. In this study, BW and price data on animals sold singly were available from 71 different marts, representing the majority of marts in Ireland. Body weights of some animals recorded on farm, as part of a progeny test program coordinated by the ICBF, were also available. Data on BW (n = 2,506,110) and sale price (n = 2,001,998) were available from 2000 to 2008; additional BW records were available because of the on-farm recording. Animals were characterized as calves, weanlings, and postweanlings, as outlined in detail by Mc Hugh et al. (2010). Briefly, calves were defined as animals <84 d of age; only price data were available on these animals. Weanlings were defined as males and females aged between 6 and 12 mo at weighing. Post-weanlings were defined as females aged between 12 and 30 mo and males aged between 12 and 36 mo; females that had a calving date before weighing or sale were not included as postweanlings.

As with previous edits, only animals with a known sire and with at least 75% of their breed fraction containing some proportion of AN, BB, CH, HE, LI, or SI were retained. Only calves sold for between €2 and €450 were retained; the range of animal price for weanlings was between €200 and €1,200 and between €200 and €1500 for postweanlings (Mc Hugh et al., 2010). Weanlings had to weigh between 150 and 900 kg and postweanlings had to weigh between 200 and 1,000 kg. Mc Hugh et al. (2011) reported a maternal variance for weaning weight, and weanlings with no known maternal grandsire were therefore omitted; this edit was applied only to weanlings. Only the first record in time within a maturity category was retained.

For both BW and price in commercial animals, 2 contemporary groups were defined to account for 1) the effect of mart and how the effect might change with time, and 2) the effect of farm and how it might change with time. The effect of mart × time was accounted for by the contemporary group of mart × date of sale. The effect of herd × time was accounted for by the contemporary group of herd × year × season of sale. This contemporary group was generated using an algorithm described by Crump et al. (1997). Essentially, this algorithm creates contemporary groups based on animals from the same herd that have weigh dates close together. In this study, weigh dates of animals from the same herd differing by up to 10 d were initially grouped together. If the number of records in this immediately defined contemporary group was <8 (the amount chosen for this study), then this group was merged with an adjacent group, so long as the start date of one group and the end date of the other group were within 182 d of each other. Subsequently, contemporary groups with <5 records were omitted. After all edits, 34,855 calves, 25,129 weanlings (8,755 with BW

and price), and 22,250 postweanlings (16,163 with BW and price) remained.

Carcass Traits. Data on carcass conformation, carcass fat, and carcass weight on 2,566,969 singletons slaughtered between 2005 and 2008 were available from the ICBF database. Cold carcass weight as well as carcass conformation and carcass fat grade, scored using the EUROP classification system (where E = excellent, U = very good, R = good, O = fair, and P = poor), is recorded for each animal slaughtered in Ireland. Carcass weight is measured, on average, 2 h after slaughter after the removal of the head, legs, thoracic and abdominal organs, internal fats, and hide (Hickey et al., 2007). In the present study, the EUROP classification grades were transformed to a 15-point linear scale, as outlined by Hickey et al. (2007).

Only males slaughtered between 300 and 1,200 d of age and females slaughtered between 300 and 875 d of age were retained. Similar to the linear type data, only animals with a known sire and with at least 75% of their breed fraction containing some proportion of AN, BB, CH, HE, LI, or SI were retained; 555,064 records remained. Carcass weight records <150 kg and >550 kg (n = 11,150) were also omitted. Contemporary group was defined as finishing herd (i.e., herd immediately before slaughter) × slaughter date × sex, and only contemporary groups with 5 or more records were retained. A total of 279,349 individuals with information on carcass weight, carcass conformation, and carcass fat from 26,681 contemporary groups remained. Of these, one-third of the contemporary groups were randomly chosen to reduce the size of the data set for variance component estimation. The final data set was composed of 8,893 contemporary groups containing a total of 93,442 animals with carcass data.

Of the original 279,349 animals with information on carcass weight, carcass fat, and carcass conformation, 21,208 animals from 2,415 contemporary groups had information on weights of different carcass cuts predicted from digital images, as outlined in detail by Pabiou et al. (2009); these were also used to predict the proportion of the carcass weight represented by each cut. These cut weights were classified as low-value cuts (**LVC**), medium-value cuts (**MVC**), high-value cuts (**HVC**), and very high value cuts (**VHVC**), as described in detail by Pabiou et al. (2009). The LVC cuts included fore and hind shins, flank, ribs, brisket, neck, and lean trimmings; MVC included the shoulder and the chuck cuts; HVC included the sirloin and the round cut weights; and VHVC included the rib roast, strip loin, and fillet cuts. Total meat was defined as the sum of all the carcass cut weights.

Heterosis and Recombination Coefficients

Heterosis and recombination loss coefficients were calculated for all animals and matings as $1 - \sum_{i=1}^{n} \text{sire}_i \cdot \text{dam}_i$ and $1 - \sum_{i=1}^{n} (\text{sire}_i^2 + \text{dam}_i^2)/2$, respec-

tively, where sire_i and dam_i are the proportions of breed i in the sire and dam, respectively (VanRaden and Sanders, 2003). Within the commercial population, mean heterosis was 0.43 (SD = 0.37), whereas mean recombination loss was 0.08 (SD = 0.09).

Analysis

All phenotypic and genetic (co)variance parameters were estimated using linear mixed animal models in ASREML (Gilmour et al., 2009), with the exception that an animal-dam model was used for the analysis of weaning weight. Variance components were estimated using a series of univariate analyses, whereas covariance components were estimated using bivariate analyses. In all models, animal was fitted as a random effect. Additionally, for the analysis of weaning weight, a random effect of dam was also included along with a covariance between the direct and maternal components. The average genetic relationship among all animals was accounted for by tracing both sides of the pedigree back at least 4 generations.

Fixed effects included in the model for the traits measured in the performance test station were as described previously by Crowley et al. (2010); these fixed effects were also included in the analysis of the ultrasound measures. Fixed effects included batch (n = 84), breed of bull (n = 5), dam parity (1, 2, 3 to 4, ≥5, and "missing"), and age of the bull at the end of test (continuous variable). Nonlinear (e.g., quadratic) 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 included in the model.

The fixed effects included in the models used to estimate (co)variances for BW and price have been described previously by Mc Hugh et al. (2011). Fixed effects in all models, common to all 3 maturity categories, were sex, age at sale (continuous variable), fractions of AN, BB, CH, FR, HE, HO, LI, and SI breed composition fitted as separate continuous variables, calving ease (1 = no assistance or unobserved; 2 = slight assistance; 3 = severe assistance; and 4 = veterinary assistance), whether the animal was born as a singleton or twin, heterosis coefficient (continuous variable), and recombination loss coefficient (continuous variable). Parity of dam (1, 2, 3 to 4, ≥5, and "missing"), and dam age in months relative to the median age within parity were also included as fixed effects. Breed proportion was treated as a continuous variable with a separate effect fitted in the models for each breed.

Until 2002, direct subsidies in the form of the Special Beef Premium were available to farmers under the European Union Common Agricultural Policy. These premiums could be claimed on castrated males twice during their lifetime, at 9 and 21 mo of age. Hence, when the dependent variable was weanling and postweanling price, the number of subsidies left to claim (0, 1, or 2) on the animal was also added as a fixed effect.

Nonlinear associations and interactions included in the models for animal price and BW were those identified by Mc Hugh et al. (2011) to be statistically significant. Interactions between age of dam relative to median parity age and dam parity were included in the model for calf price, weanling price, weanling weight, and postweanling price. In the models used to estimate (co)variances for calf price and postweanling price, sex interacted with each individual breed proportion. For the analysis of postweanling weight, only interactions between CH, FR, HE, HO, LI, and SI breed proportions and sex were included in the model. Only a CH breed proportion × sex interaction was included in the models for weanling price and weanling weight. An age × sex interaction was included in the model used to analyze calf price, postweanling price, and postweanling weight. Finally, a quadratic effect of age was fitted in the model for calf price, and quadratic effects for AN, HE, LI, and SI breed proportions were fitted to the model for postweaning weight.

Fixed effects included in the model for carcass and the linear type traits were contemporary group, proportions of AN, BB, CH, FR, HE, HO, LI, and SI composition as continuous variables, age (age at scoring for the linear type traits and age at slaughter for carcass traits), dam lactation (1, 2, 3 to 4, ≥5, and "missing"), sex, heterosis, and recombination loss coefficients. Additionally, nonlinear associations with age, as well as 2-way interactions between age and sex were included in the models. For the analysis of carcass cut weight at a constant carcass weight, carcass weight itself was included as a covariate in the model.

In the final data set, when estimating covariance parameters between traits measured in performance-tested bulls and traits measured in commercial cattle, data on linear type traits, carcass, commercial BW, or price were discarded if the animal itself had undergone performance testing. The residual covariance between the performance test traits and the traits measured on the commercial animals was therefore set to 0.

Data on 212,422 commercial animals from 16,925 sires (mean progeny per sire = 11; SD = 53) and 171,063 dams were included in this study. The 25,129 animals with records from weaning weight were from 17,315 dams and 2,679 maternal grandsires. Of the 16,925 sires, 2,609 were AN (26,365 progeny), 2,616 were CH (32,516 progeny), 1,775 were HE (15,971 progeny), 2,455 were LI (36,719 progeny), and 945 were SI (11,242 progeny). A total of 449 of the 16,925 sires had progeny in both the commercial and performance test data sets. Of the 2,605 performance-tested bulls, 41 had only progeny (n = 329) in the commercial data set and 176 had both progeny and grand progeny (n = 3,676); there were no performance-tested bulls with only grand progeny in the commercial data set. Additionally, 1,882 performance-tested animals had 38,132 paternal half sibs in the commercial data, 670 had 1,817 maternal half sibs, and 215 performance-tested bulls had 322 full sibs.

RESULTS

Summary statistics for animal performance in the test station have been described in detail by Crowley et al. (2010). Average age and BW at the start of test were 309 d and 476 kg, respectively. On average, the animals ate 10.7 kg of DM/d and grew at 1.65 kg/d, and mean FCR was 6.75.

Linear Type Traits

Summary statistics for the linear type traits scored in the commercial cattle are detailed in Table 1; docility, but not other traits, was positively skewed. Heritability estimates for the skeletal linear type traits ranged from 0.18 (width of hips and length of pelvis) to 0.34 (height at withers), and from 0.22 (width behind withers) to 0.35 (hind-quarter development) for the muscularity type traits. In general, the functionality type traits had the least heritability estimates, ranging from 0.06 (hind-leg rear view) to 0.14 (locomotion); they also had the least genetic variances. Heritabilities of BCS and docility were 0.13 and 0.21, respectively. Standard errors associated with heritability estimates of the linear type traits ranged from 0.01 to 0.02.

Phenotypic correlations between performance test measures and linear type traits in performance-tested beef bulls are presented in Table 2. With the exception of RGR and, to a lesser extent, RFI, all performance measures were phenotypically correlated ($P < 0.05$) with muscularity type traits. In addition, apart from the phenotypic correlation between loin development and RFI, correlations with all muscularity type traits, within each efficiency measure, were in the same direction. Additionally, ADG was positively phenotypically correlated with all skeletal and muscularity type traits.

Genetic correlations between traits measured in the performance-tested animals and linear type traits in the commercial animals are presented in Table 3. Genetic correlations when linear type data measured only on the performance-tested animals were included in the analysis were generally consistent with estimates using commercial data; therefore, only the latter are presented. Genetic correlations between CI, midtest BW, and ADG, and the skeletal linear type traits were all positive and ranged from 0.06 (width of hips and CI) to 0.54 (length of back and midtest BW). Apart from the efficiency traits, midtest BW was the only other trait to be correlated with muscularity in commercial animals; genetic correlations with loin development and width at withers were 0.23 and 0.25, respectively. Neither functionality traits nor docility was correlated with CI, midtest BW, or ADG. Increased CI and greater midtest BW measured in the performance test animals were associated with increased BCS in commercial animals.

Height at withers was the only skeletal trait genetically correlated with any of the efficiency traits (Table 3), with a positive genetic correlation with FCR (0.26 ± 0.12) and a negative genetic correlation with RGR

Table 2. Number of animals (n) and phenotypic correlations between performance traits[1] in performance-tested animals and skeletal, functional, and muscle linear type traits in performance-tested bulls

Item	n	CI	Midtest BW	ADG▲	FCR▼	KR▲	RFI▼	RG▲	RGR▲
Height at withers	1,348	0.25*	0.33*	0.46*	−0.02	0.01	−0.04	0.08*	−0.06
Length of back	1,348	0.10*	0.14*	0.26*	0.01	−0.04	−0.14	0.09	−0.08
Length of pelvis	1,348	0.002	0.11*	0.15*	0.07*	−0.08*	−0.15*	0.07*	−0.10*
Width of hips	1,348	0.01	0.02	0.07*	−0.02	−0.03	−0.19*	0.11*	−0.05
Hind-quarter development	1,348	0.40*	0.09*	0.54*	−0.32*	0.11*	−0.09*	0.09*	0.04
Loin development	1,348	0.44*	0.19*	0.61*	−0.29*	0.13*	0.03	0.07*	0.04
Thigh width	1,348	0.42*	0.13*	0.59*	−0.31*	0.11*	−0.05*	0.07*	0.03
Width at withers	1,348	0.44*	0.17*	0.63*	−0.29*	0.11*	−0.02	0.06*	0.03
Width behind withers	1,348	0.44*	0.17*	0.62*	−0.30*	0.11*	−0.02	0.06*	0.03
Foreleg front view	1,324	−0.21*	−0.07*	−0.41*	0.12*	0.01	−0.08*	0.04	0.06*
Hind-leg rear view	529	0.08	0.03	−0.01	−0.05	0.09	−0.002	0.01	0.11*
Hind-leg side view	1,324	0.15*	0.05	0.09*	−0.13*	0.11*	−0.03	0.08*	0.09*
Locomotion	491	0.06	−0.01	0.12*	−0.06	0.004	−0.17*	0.11*	0.004
BCS	442	0.24*	0.17*	0.37*	−0.13*	0.07	−0.11*	0.10*	0.01
Docility	1,081	0.40*	0.31*	0.53*	−0.21*	0.11*	0.09*	0.06	0.03

[1]CI = concentrate intake; FCR = feed conversion ratio; KR = Kleiber ratio; RFI = residual feed intake; RG = residual BW gain; RGR = relative growth rate. ▲ = Indicates a (more) positive value for this trait is desirable; ▼ = indicates a lesser value for this trait is desirable.
*P ≤ 0.05.

(−0.27 ± 0.12). In general, all muscularity type traits were correlated with FCR, RFI, and RG, indicating that selection for either of these feed efficiency traits will result in improved hind-quarter development, loin development, thigh width, and width at and behind withers. Hind-leg rear view was the only functionality trait correlated with efficiency, with a negative genetic correlation with FCR (−0.35 ± 0.16; P < 0.05). No genetic correlations different from 0 were evident between efficiency and either BCS or docility.

Ultrasonic Measures of Fat and Muscle

Heritability estimates for ultrasonic muscle and fat traits ranged from 0.10 to 0.19 (Table 4). Phenotypic and genetic correlations between the ultrasonic measurements and both the performance and efficiency traits are detailed in Table 5. The genetic correlations were, in general, stronger than the respective phenotypic correlations, although the SE of the genetic correlations were relatively large. Absolute phenotypic correlations between ultrasonic measures and midtest BW, CI, and ADG, and between ultrasonic measures and efficiency traits were weak and ranged from 0.01 to 0.21 and from 0.001 to 0.31, respectively. Genetic correlations between fat depth and FCR, RFI, and RG were all different from 0 (0.49, 0.39, and −0.44, respectively), and suggest that selection for improvement in either of these feed efficiency measures will result in reduced fat depth.

Animal BW and Price

Heritability estimates for calf price, weanling price, and postweanling price ranged from 0.42 to 0.44 (Table 6). Heritability estimates for weanling weight and post-

weanling weight were 0.27 and 0.33, respectively (Table 6).

Excluding the efficiency traits, animal price was not correlated with any of the performance test measures (Table 7). The only moderate correlation evident between the efficiency traits and price was that between postweanling price and RFI (−0.39).

Genetic correlations between BW in commercial animals and CI, midtest BW, and ADG in performance-tested animals ranged from 0.14 (weanling weight and ADG) to 0.57 (postweanling weight and midtest BW). Feed efficiency was not genetically correlated with either weanling or postweanling BW in commercial animals.

Carcass

Summary statistics, including variance components for the carcass traits, are detailed in Table 4. Mean carcass conformation and fat score correspond to a conformation score of "O" on the EUROP scale and a grade 2 for carcass fat on the EUROP scale (Hickey et al., 2007). Heritability estimates for carcass weight, carcass conformation, and carcass fat were 0.76, 0.56, and 0.41, respectively. Heritability estimates for carcass cut weights ranged from 0.43 to 0.62 and from 0.19 to 0.50 for the carcass cut proportions.

Concentrate intake, midtest BW, or ADG were not correlated with carcass weight, carcass conformation, or carcass fat (Table 8). The estimated genetic correlations suggest that selection for improved (i.e., lesser) FCR or improved (i.e., greater) RG is expected to increase both carcass conformation and carcass weight. Selection for improved (i.e., reduced) RFI should lead to leaner carcasses with better conformation.

Crowley et al.

Table 3. Genetic correlations (SE) between performance traits[1] in performance-tested animals and skeletal, functional, and muscle linear type traits in commercial animals

Item	Scale	CI	Midtest BW	ADG▲	FCR▼	KR▲	RFI▼	RG▲	RGR▲
Height at withers	1 = small; 10 = tall	0.38 (0.09)	0.48 (0.08)	0.13 (0.12)	0.26 (0.12)	−0.14 (0.12)	0.06 (0.11)	−0.03 (0.13)	−0.27 (0.12)
Length of back	1 = short; 10 = long	0.39 (0.10)	0.54 (0.08)	0.33 (0.12)	−0.04 (0.13)	0.08 (0.13)	−0.11 (0.11)	0.23 (0.12)	−0.05 (0.13)
Length of pelvis	1 = short; 10 = long	0.34 (0.12)	0.53 (0.09)	0.22 (0.14)	0.07 (0.15)	−0.03 (0.14)	−0.05 (0.12)	0.11 (0.14)	−0.18 (0.14)
Width of hips	1 = narrow; 10 = wide	0.06 (0.12)	0.31 (0.10)	0.10 (0.13)	−0.12 (0.14)	−0.03 (0.13)	−0.22 (0.12)	0.13 (0.14)	−0.13 (0.13)
Hind-quarter development	1 = low; 15 = high	−0.04 (0.10)	0.13 (0.09)	0.16 (0.12)	−0.27 (0.12)	0.10 (0.12)	−0.25 (0.10)	0.24 (0.12)	0.14 (0.12)
Loin development	1 = low; 15 = high	0.01 (0.11)	0.23 (0.10)	0.19 (0.12)	−0.32 (0.13)	0.09 (0.13)	−0.30 (0.11)	0.27 (0.13)	0.08 (0.13)
Thigh width	1 = narrow; 15 = wide	0.03 (0.11)	0.19 (0.10)	0.20 (0.12)	−0.25 (0.13)	0.14 (0.13)	−0.22 (0.11)	0.27 (0.12)	0.14 (0.12)
Width at withers	1 = narrow; 15 = wide	−0.01 (0.11)	0.25 (0.10)	0.16 (0.13)	−0.27 (0.13)	0.07 (0.13)	−0.33 (0.11)	0.25 (0.13)	0.06 (0.13)
Width behind withers	1 = narrow; 15 = wide	−0.06 (0.11)	0.09 (0.10)	0.16 (0.13)	−0.33 (0.13)	0.15 (0.13)	−0.24 (0.11)	0.26 (0.13)	0.15 (0.13)
Foreleg front view	1 = toes out; 10 = toes in	0.11 (0.14)	0.14 (0.13)	0.20 (0.15)	−0.13 (0.17)	0.12 (0.16)	−0.07 (0.14)	0.20 (0.16)	0.05 (0.16)
Hind-leg rear view	1 = toes out; 10 = toes in	0.07 (0.15)	−0.08 (0.14)	0.22 (0.16)	−0.35 (0.16)	0.29 (0.16)	0.05 (0.15)	0.22 (0.16)	0.30 (0.16)
Hind-leg side view	1 = straight; 10 = sickled	0.11 (0.13)	0.07 (0.12)	0.08 (0.14)	−0.004 (0.15)	0.07 (0.15)	0.10 (0.13)	0.03 (0.15)	−0.003 (0.15)
Locomotion	1 = low; 10 = high	0.02 (0.12)	0.05 (0.11)	0.12 (0.13)	−0.16 (0.14)	0.08 (0.14)	−0.08 (0.12)	0.13 (0.14)	0.12 (0.14)
BCS	1 = lean; 10 = fat	0.27 (0.13)	0.29 (0.13)	0.25 (0.15)	−0.05 (0.17)	0.17 (0.16)	0.04 (0.14)	0.18 (0.16)	0.11 (0.16)
Docility	1 = aggressive; 10 = docile	0.10 (0.11)	0.04 (0.10)	0.04 (0.13)	0.02 (0.14)	0.004 (0.13)	0.07 (0.12)	−0.01 (0.13)	0.05 (0.13)

[1]CI = concentrate intake; FCR = feed conversion ratio; KR = Kleiber ratio; RFI = residual feed intake; RG = residual BW gain; RGR = relative growth rate; ▲ indicates a (more) positive value for this trait is desirable; ▼ indicates a lesser value for this trait is desirable.

Genetic correlations between CI and carcass cuts were negative or close to 0 and ranged from −0.61 to 0.04; correlations with FCR and RFI were mostly negative or close to 0, whereas correlations with RG and RGR were generally all positive or close to 0. Proportion of MVC was the carcass cut trait most weakly and not significantly correlated (mean genetic correlation = 0.04), whereas proportion of LVC was the most strongly correlated (mean genetic correlation = 0.31) with the performance test measures. Residual feed intake was the only efficiency measure correlated with any of the carcass cut weights or proportions. Genetic correlations suggest that selection for improved RFI will result in a simultaneous increase in the LVC proportion, LVC weight, and VHVC weight.

Throughout, KR and RGR were not generally correlated with any of the traits measured in the commercial population.

DISCUSSION

The main objective of performance testing is to measure growth rate and feed efficiency with the view to identifying potential sires with superior genetic merit for these traits for use in commercial herds. However, the impact of such practices on performance in commercial herds needs to be quantified. The main revenue source for beef farmers is the sale of animals at weaning (i.e., calf to weanling producers) or sale of animals at slaughter (i.e., finishing or feedlot producers). Therefore, the impact of selection for feed efficiency on these traits, in particular, needed to be evaluated. Results from this study show that selection for improved feed efficiency, as measured in a performance test station, should result in better muscled animals, with superior carcass characteristics and greater postweanling value, with no unfavorable correlated responses on functional type traits. Measures of feed intake in the commercial animals would have been advantageous to quantify the impact of selection in performance test stations on feed intake on commercial farms; however, such data were not available. Nonetheless, the observed positive genetic correlations between CI in the performance-tested animals and body-size traits in the commercial animals suggest that selection for increased CI in performance test stations is associated with a correlated increase in feed intake (capacity) in commercial animals.

Population Statistics and Variance Components

The sample population mean and heritability estimates reported in the present study for the commercial animals are similar to those reported elsewhere (Forabosco et al., 2005; Hoque et al., 2006; Lancaster et al., 2009; Pabiou et al., 2009; Bouquet et al., 2010; Mc Hugh et al., 2010); population means and heritability estimates for the performance-tested animals have been discussed previously (Crowley et al., 2010). Heritability

Table 4. Number of records (n) and contemporary groups (CG), as well as scale of measurement, mean, genetic SD (σ_g), and heritability estimates (h^2) for ultrasound measures in the performance-tested bulls and carcass traits in commercial animals

Item	n	CG	Herds	Scale	Mean	σ_g	h^2 (SE)
Fat depth	1,467	47	Performance	cm	0.27	0.04	0.19 (0.08)
Muscle area	1,467	47	Performance	cm^2	103.10	2.11	0.10 (0.06)
Muscle depth	564	16	Performance	cm	8.52	0.19	0.16 (0.14)
Carcass weight	93,442	8,892	4,872	kg	331	29	0.76 (0.02)
Carcass conformation	93,442	8,892	4,872	1 = poor; 15 = excellent	5.62	0.95	0.56 (0.02)
Carcass fat	93,442	8,892	4,872	1 = lean; 15 = fat	6.47	0.82	0.41 (0.02)
Weight of cuts							
Total meat	21,208	2,415	1,395	kg	214.8	14.52	0.58 (0.04)
Low-value cuts	21,208	2,415	1,395	kg	86.35	7.22	0.62 (0.04)
Medium-value cuts	21,208	2,415	1,395	kg	41.28	2.77	0.55 (0.04)
High-value cuts	21,208	2,415	1,395	kg	55.91	4.19	0.61 (0.04)
Very high value cuts	21,208	2,415	1,395	kg	23.99	1.48	0.43 (0.04)
Cut proportion							
Total meat	21,208	2,415	1,395	%	65.45	1.45	0.41 (0.03)
Low-value cuts	21,208	2,415	1,395	%	26.52	0.93	0.43 (0.04)
Medium-value cuts	21,208	2,415	1,395	%	12.40	0.40	0.50 (0.04)
High-value cuts	21,208	2,415	1,395	%	17.05	0.58	0.37 (0.03)
Very high value cuts	21,208	2,415	1,395	%	7.34	0.19	0.19 (0.03)

estimates varied from 0.30 to 0.71 for the performance traits and from 0.28 to 0.45 for the feed efficiency traits (Crowley et al., 2010).

Few heritability estimates for linear type traits in beef cattle are available in the literature, but estimates from this study are similar to those reported previously (Mukai et al., 1995; Fouilloux et al., 2000; Forabosco et al., 2005; Bouquet et al., 2010). The heritability of muscularity linear type traits in this study (0.22 to 0.35) are within the range of 0.31 to 0.35 reported by Bouquet et al. (2010) in Blonde d'Aquitaine and LI cattle. The heritability estimate of 0.34 for height of withers in the present study is similar to that reported by Mukai et al. (1995) in 662 performance-tested Japanese Black cattle.

Heritability estimates for ultrasound characteristics in the present study (0.10 to 0.19) were less than the 0.27 to 0.35 reported by Arthur et al. (2001a) in Angus cattle. Nkrumah et al. (2007) also reported greater heritability estimates for ultrasonic backfat (0.59) and ultrasound LM area (0.39) traits on 464 crossbred beef steers compared with the present study, but estimates similar to the present study were reported by Miglior et al. (1994) for backfat thickness in LI bulls (0.17). Hoque et al. (2006), in a study of carcass traits on field progeny of performance-tested bulls (Japanese Black cattle), documented heritability estimates for carcass weight, carcass subcutaneous fat, and meat quality grade of 0.70, 0.34, and 0.35, respectively, all of which are in agreement with estimates quoted in the present study. More recently, Bouquet et al. (2010) reported heritability estimates similar to those in the present study for carcass weight of 0.53 in Blonde d'Aquitaine cattle and 0.61 in LI. Variance components estimated using Irish data for animal price and BW have been discussed previously by Mc Hugh et al. (2010), and variance components for carcass cut traits have been discussed previously by Pabiou et al. (2009).

Table 5. Phenotypic and genetic correlations (SE) between performance traits[1] and ultrasound measurements in 1,467 performance-tested bulls

	Phenotypic			Genetic		
Item	Fat depth (n = 1,467)	Muscle area (n = 1,467)	Muscle depth (n = 546)	Fat depth (n = 1,467)	Muscle area (n = 1,467)	Muscle depth (n = 546)
CI	0.21*	−0.08*	−0.17*	0.08 (0.19)	0.07 (0.23)	0.03 (0.33)
Midtest BW	0.06*	0.14*	0.02	−0.13 (0.18)	0.37 (0.21)	0.10 (0.30)
ADG	0.01	0.08*	0.04	−0.29 (0.21)	0.05 (0.27)	0.00 (0.36)
FCR	0.15*	−0.12*	−0.14*	0.49 (0.21)	0.07 (0.28)	0.13 (0.35)
KR	−0.02	−0.001	0.02	−0.29 (0.22)	−0.18 (0.27)	−0.17 (0.18)
RFI	0.26*	−0.27*	−0.31*	0.39 (0.18)	−0.28 (0.23)	0.10 (0.33)
RG	−0.10*	0.07*	0.07	−0.44 (0.20)	0.03 (0.28)	−0.02 (0.35)
RGR	−0.02	−0.04	−0.02	−0.18 (0.22)	−0.23 (0.26)	−0.08 (0.34)

[1]CI = concentrate intake; FCR = feed conversion ratio; KR = Kleiber ratio; RFI = residual feed intake; RG = residual BW gain; RGR = relative growth rate.

*$P \leq 0.05$.

Table 6. Number of animals (n), contemporary groups (CG), and herds, as well as arithmetic mean, genetic SD (σ_g), coefficients of genetic variation (CV_g), and heritability estimates (h^2) for price and BW of the 3 different maturity categories

Item	n	CG[1]	Herds	Mean	σ_g	CV_g	h^2 (SE)
Calf price, €	34,855	3,861 and 1,613	1,860	170.11	31.97	0.19	0.42 (0.03)
Weanling weight,[2] kg	25,129	2,318 and 1,143	1,291	351.01	22.74	0.06	0.27 (0.03)
Weanling price, €	8,755	1,190 and 875	787	621.57	56.29	0.09	0.44 (0.08)
Postweanling weight, kg	22,250	3,877 and 2,739	1,842	448.49	26.50	0.06	0.33 (0.03)
Postweanling price, €	16,163	3,177 and 2,195	1,575	644.92	57.54	0.09	0.44 (0.05)

[1]First number is the herd-year-season contemporary group and second number is the mart-date contemporary group.

[2]Maternal $h^2 = 0.08 \pm 0.02$; maternal $\sigma_g = 12.62$; covariance between direct and maternal components $= -0.12 \pm 0.15$.

Genetic Correlations Between CI, Midtest BW, and ADG in Performance-Tested Animals and Performance in Commercial Animals

The moderate, positive genetic correlation between animal size (represented in this study as height at withers, length of back, length of pelvis, and width of hips) in the commercial animals and both CI and midtest BW in performance-tested animals was not unexpected. A larger framed animal will, on average, weigh more (Fouilloux et al., 2000; Nkrumah et al., 2004) and will therefore also likely have a greater growth and maintenance requirement, which must be met by greater feed intake. In addition, larger framed animals will have a larger physical capacity to ingest above-average quantities of feed. This explanation may also be used to explain the positive genetic correlation between CI in performance-tested animals and BW in commercial weanlings and postweanlings. Using the performance test data set in the present study, Crowley et al. (2010) reported a strong positive genetic correlation between CI and midtest BW in performance-tested bulls. Associations between linear muscularity traits (loin development and width at withers) and midtest BW in this study indicate that an increase in muscle will be accompanied by an increase in BW. This agrees with the report of Fouilloux et al. (2000), who estimated a genetic correlation between muscling score and BW of 0.34 in LI.

The weak genetic correlation between midtest BW and carcass weight (0.08 ± 0.10) may suggest that these

2 weight measurements are not under the same genetic control and that selection for increased BW does not affect carcass weight. This is substantiated by the absence of a genetic correlation between midtest BW and total meat (kg). However, the weak correlation between midtest BW and carcass weight may also be explained by the fact that, in this study, the average age at which midtest BW was measured in performance-tested bulls was 354 d of age, measured during the linear phase of their growth curve, whereas the average age at slaughter of the commercial animals was 778 d of age, when growth rate is typically beginning to decline. Furthermore, the majority of carcasses traits were observed on steers and heifers, both of which would have distinctly different growth rates from the performance-tested bulls. The difference between slaughter weight and cold carcass weight is the weight of the head, legs, internal organs, hide, and excess fats; these may also contribute to the weak genetic correlation. However, the moderate (0.41 to 0.56) genetic correlation between midtest BW and direct weaning weight (average of 267 d of age at weighing) and postweanling weight (average of 589 d of age at weighing) suggests that BW measured in performance-tested bulls is indeed correlated with BW in commercial animals of similar age and that selection for increased midtest BW will, on average, result in heavier weanlings and postweanlings. The moderate genetic correlation between midtest BW and BW in commercial animals in the present study agrees with the result of Bouquet et al. (2010), who reported a genetic correlation of 0.74 between weaning weight in commercial animals and BW in performance-tested animals.

Table 7. Genetic correlations (SE) between performance traits[1] and BW, and price of the 3 maturity categories

Item	Calf price	Weanling weight	Weanling price	Postweanling weight	Postweanling price
CI	−0.22 (0.22)	0.20 (0.13)	−0.05 (0.21)	0.57 (0.11)	−0.12 (0.17)
Midtest BW	0.04 (0.21)	0.41 (0.12)	−0.01 (0.19)	0.56 (0.14)	0.15 (0.15)
ADG	−0.19 (0.25)	0.14 (0.12)	0.07 (0.23)	0.33 (0.15)	0.12 (0.18)
FCR	−0.11 (0.27)	0.20 (0.16)	0.08 (0.24)	0.15 (0.16)	−0.24 (0.20)
KR	−0.27 (0.26)	−0.09 (0.15)	0.02 (0.23)	0.03 (0.15)	0.04 (0.09)
RFI	−0.31 (0.23)	−0.12 (0.14)	−0.11 (0.21)	0.02 (0.14)	−0.39 (0.16)
RG	−0.06 (0.26)	0.08 (0.16)	0.11 (0.23)	0.17 (0.16)	0.26 (0.20)
RGR	−0.37 (0.26)	−0.15 (0.15)	0.03 (0.23)	−0.05 (0.15)	0.02 (0.19)

[1]CI = concentrate intake; FCR = feed conversion ratio; KR = Kleiber ratio; RFI = residual feed intake; RG = residual BW gain; RGR = relative growth rate.

Table 8. Genetic correlations (SE) between performance traits[1] and carcass traits

Item	CI	Midtest BW	ADG▲	FCR▼	KR▲	RFI▼	RG▲	RGR▲
Carcass weight	0.002 (0.11)	0.08 (0.10)	0.22 (0.13)	−0.34 (0.13)	0.20 (0.13)	−0.21 (0.12)	0.32 (0.13)	0.16 (0.13)
Carcass conformation	−0.23 (0.12)	−0.05 (0.11)	0.15 (0.14)	−0.46 (0.14)	0.21 (0.14)	−0.37 (0.12)	0.35 (0.14)	0.15 (0.14)
Carcass fat	0.10 (0.13)	−0.17 (0.12)	−0.01 (0.15)	0.11 (0.16)	0.07 (0.15)	0.33 (0.13)	−0.10 (0.15)	0.07 (0.15)
Weight of cuts								
Total meat	−0.21 (0.19)	0.002 (0.17)	0.05 (0.20)	−0.28 (0.22)	0.08 (0.21)	−0.32 (0.19)	0.22 (0.21)	0.16 (0.21)
Low-value cuts	−0.28 (0.18)	0.02 (0.17)	0.01 (0.21)	−0.29 (0.22)	0.04 (0.21)	−0.42 (0.18)	0.23 (0.22)	0.13 (0.21)
Medium-value cuts	−0.09 (0.20)	0.19 (0.18)	0.11 (0.22)	−0.21 (0.24)	0.03 (0.23)	−0.35 (0.20)	0.24 (0.23)	0.08 (0.22)
High-value cuts	−0.16 (0.18)	0.01 (0.17)	0.04 (0.20)	−0.25 (0.21)	0.06 (0.20)	−0.27 (0.18)	0.20 (0.21)	0.10 (0.20)
Very high value cuts	−0.29 (0.21)	0.09 (0.20)	−0.03 (0.23)	−0.23 (0.26)	−0.03 (0.24)	−0.45 (0.21)	0.19 (0.25)	0.04 (0.24)
Cut proportion								
Total meat	−0.32 (0.20)	−0.36 (0.18)	−0.11 (0.22)	−0.23 (0.24)	0.11 (0.23)	−0.04 (0.20)	0.05 (0.23)	0.20 (0.23)
Low-value cuts	−0.61 (0.20)	−0.31 (0.20)	−0.14 (0.24)	−0.46 (0.26)	0.07 (0.25)	−0.43 (0.21)	0.20 (0.26)	0.25 (0.25)
Medium-value cuts	0.04 (0.22)	0.06 (0.20)	0.04 (0.24)	0.03 (0.26)	−0.03 (0.24)	−0.04 (0.21)	0.03 (0.25)	−0.08 (0.24)
High-value cuts	−0.17 (0.23)	−0.30 (0.21)	−0.05 (0.25)	−0.21 (0.27)	0.10 (0.25)	0.06 (0.22)	0.05 (0.26)	0.12 (0.25)
Very high value cuts	−0.31 (0.30)	−0.25 (0.28)	−0.37 (0.32)	0.22 (0.35)	−0.26 (0.33)	0.03 (0.29)	−0.30 (0.33)	−0.30 (0.33)

[1]CI = concentrate intake; FCR = feed conversion ratio; KR = Kleiber ratio; RFI = residual feed intake; RG = residual BW gain; RGR = relative growth rate; ▲ indicates a (more) positive value for this trait is desirable; ▼ indicates a lesser value for this trait is desirable.

Bouquet et al. (2010), however, reported strong genetic correlations of 0.74 to 0.91 between BW measured on test and carcass weight of their male progeny. In addition, the positive genetic correlations (0.28 to 0.32) reported by Bouquet et al. (2010) between BW measured on test and carcass fat measured on male progeny are in contrast to the estimated genetic correlation in the present study. In the present study and that of Bouquet et al. (2010), all traits were adjusted for age. In previous studies (Fouilloux et al., 2000; Robinson and Oddy, 2004), estimates of genetic correlations between BW and carcass fat, whether it be fat trim, backfat, or intramuscular fat, were all positive. However, Lancaster et al. (2009) reported a negative correlation between BW and intramuscular fat measured by ultrasound, and Fouilloux et al. (2000) estimated a negative correlation between BW and internal carcass fat. In the present study, ultrasonic fat depth was negatively correlated with midtest BW, although not twice the SE from 0.

Genetic Correlations Between Efficiency Traits Measured in Performance-Tested Animals and Performance in Commercial Animals

Residual feed intake and RG are both, by definition, phenotypically independent of midtest BW, which is genetically associated with body size (length of back, height at withers, length of pelvis, and width of hips). Therefore, the lack of a genetic correlation between both RG and RFI with most of the skeletal type traits associated with body size in the present study was not unexpected. However, despite the genetic correlation between muscularity and midtest BW, selection for improved RFI (i.e., reduced) and RG (i.e., greater) will result in increased muscularity; the same conclusion is evident when feed efficiency is defined as FCR. These expected responses to selection are in agreement with those of Bouquet et al. (2010), who reported negative

genetic correlations between RFI and muscle score in both Blonde d'Aquitaine and LI bulls (−0.44 ± 0.19 and −0.27 ± 0.17, respectively), and between FCR and muscle score in the same 2 breeds (−0.14 ± 0.18 and −0.44 ± 0.19, respectively) after bending of the matrix to be positive definite.

Because of the positive genetic correlation between muscularity and animal price (N. Mc Hugh, personal communication), selection for improved feed efficiency through RFI, in addition to improving muscularity, is expected to increase animal value, yet with no effect on animal BW. This favorable association between feed efficiency and muscularity in live animals was also evident at slaughter, with improved carcass conformation in more efficient animals. This was also reflected to some extent in the genetic correlations between feed efficiency and carcass cut weights, although not as obvious in the correlations with the cut proportions. These correlations all suggest that selection for improved FCR, RFI, and RG will result in a more valuable product, be it a live animal or carcass. It is interesting that despite no association between feed efficiency and either weaning or postweaning BW, selection for feed efficiency will increase carcass weight, suggesting an improvement in dressing percentage. However, Richardson et al. (2001), although reporting no difference in carcass weight between high- and low-RFI animals, as well as no difference in the weight of external organs, internal organs, or the gastrointestinal tract, reported heavier external organs per unit of BW in low-RFI animals.

After accounting for the directly inverse relationship between RFI defined by Fouilloux et al. (2000) and RFI defined in the present study, the genetic correlation estimated in the present study between RFI and carcass fat (0.32) is in agreement with that documented by Fouilloux et al. (2000) between their definition of feed efficiency and carcass internal fat score (−0.27). In contrast, Hoque et al. (2009) estimated negative genetic correlations between RFI and subcutaneous backfat (−0.08 ± 0.12) and marbling score (−0.59 ± 0.08)

in Japanese Black cattle. Similarly, Jensen et al. (1992) reported a negative genetic correlation between RFI and carcass fat (-0.13); however, the SE of that correlation was large (0.34) and the traits were measured on Holstein-Friesian bull calves. Lancaster et al. (2009) also reported correlations between measures of body fat and RFI similar to those in the present study: 0.36 ± 0.26 between RFI and ultrasound backfat, and 0.17 ± 0.21 between RFI and intramuscular fat. The positive genetic correlations between RFI and both ultrasound fat and carcass fat in the present study are likely to be primarily due to differences in greater energy requirement for the deposition of fat relative to lean. Achieving the same ADG through the deposition of protein is likely, on average, to be more efficient than the deposition of fat for the same ADG (Castro Bulle et al., 2007). Differences in carcass fat from selection on RFI may have implications for traits not measured here, such as meat degree of marbling or cow reproductive performance; Drennan and Berry (2006) reported an association between lower BCS and reduced reproductive performance in lactating beef cows.

One of the objectives of this study was to investigate the potential of routinely recorded data, such as linear type traits, as predictors of feed efficiency, which is costly to measure. Genetic correlations between feed efficiency and the linear type traits were strongest for muscularity type traits. Nonetheless, the maximum proportion of genetic variation in any of the feed efficiency traits explained by any of the muscularity linear type traits was 11%, indicating little potential in achieving large genetic gain in feed efficiency through indirect selection on these type traits.

In conclusion, there is a perception that the best performing animals in a performance test are not necessarily the best on commercial farms or, in other words, that a notable genotype $\times$ environment interaction exists. The present study shows that BW and ADG measured in a performance test station was correlated with performance in commercial herds, but was nonetheless not significantly correlated with carcass weight. This study, using a large data set, shows that selection for improved feed efficiency based on FCR, RFI, and RG will result in better muscled animals with no antagonistic effects on functionality, as well as animals worth more with heavier, leaner, and better conformed carcasses. Not included in this study, however, were a range of traits, such as animal health traits, that should also be evaluated for associations with selection for performance and efficiency in performance test stations.

LITERATURE CITED

Arthur, P. F., J. A. Archer, D. J. Johnson, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805–2811.

Arthur, P. F., G. Renand, and D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. Livest. Prod. Sci. 68:131–139.

Berry, D. P. 2008. Improving feed efficiency in cattle with residual feed intake. Pages 67–99 in Recent Advances in Animal Nutrition 2008. P. Garnsworthy, ed. University of Nottingham Press, Nottingham, UK.

Bouquet, A., M.-N. Fouilloux, G. Renand, and F. Phocas. 2010. Genetic parameters for growth, muscularity, feed efficiency and carcass traits of young beef bulls. Livest. Sci. 129:38–48.

Castro Bulle, F. C. P., P. V. Paulino, A. C. Sanches, and R. D. Sainz. 2007. Growth, carcass quality, and protein and energy metabolism in beef cattle with different growth potentials and residual feed intakes. J. Anim. Sci. 85:928–936.

Conroy, S. B., M. J. Drennan, D. A. Kenny, and M. McGee. 2009. The relationship of live animal muscular and skeletal scores, ultrasound measurements and carcass classification scores with carcass composition and value in steers. Animal 3:1613–1624.

Crowley, J. J., D. A. Kenny, M. McGee, D. H. Crews Jr., R. D. Evans, and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. J. Anim. Sci. 88:885–894.

Crump, R. E., N. R. Wray, R. Thompson, and G. Simm. 1997. Assigning pedigree beef performance records to contemporary groups taking account of within-herd calving patterns. Anim. Sci. 65:2193–2198.

Drennan, M. J., and D. P. Berry. 2006. Factors affecting body condition score, live weight and reproductive performance in spring-calving suckler cows. Ir. J. Agric. Food Res. 45:25–38.

Forabosco, F., R. Bozzi, P. Boettcher, F. Filippini, P. Bijma, and J. A. M. Van Arendonk. 2005. Relationship between profitability and type traits and derivation of economic values for reproduction and survival traits in Chianina beef cows. J. Anim. Sci. 83:2043–2051.

Fouilloux, M.-N., G. Renand, J. Gaillard, and F. Ménissier. 2000. Genetic correlation estimations between artificial insemination sire performances and their progeny beef traits both measured in test stations. Genet. Sel. Evol. 32:483–499.

Gilmour A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009. ASReml User Guide Release 3.0. VSN Int. Ltd., Hemel Hempstead, UK.

Hickey, J. M., M. G. Keane, D. A. Kenny, A. R. Cromie, and R. F. Veerkamp. 2007. Genetic parameters for EUROP carcass traits within different groups of cattle in Ireland. J. Anim. Sci. 85:314–321.

Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006. Genetic relationship between different measures of feed efficiency and its component traits in Japanese Black (Wagyu) bulls. Livest. Sci. 100:111–118.

Hoque, M. A., M. Hosono, T. Oikawa, and K. Suzuki. 2009. Genetic parameters for measures of energetic efficiency of bulls and their relationships with carcass traits of field progeny in Japanese Black cattle. J. Anim. Sci. 87:99–106.

ICBF (Irish Cattle Breeding Federation). 2002. Linear Scoring Reference Guide. Accessed Jun. 2, 2011. http://www.icbf.com.

Jensen, J., I. L. Mao, B. B. Andersen, and P. Madsen. 1992. Phenotypic and genetic relationships between residual energy intake and growth, feed intake, and carcass traits of young bulls. J. Anim. Sci. 70:386–395.

Keane, M. G. 2005. Comparison of sugar-beet pulp and barley with and without soya bean meal as supplements to silage for growing steers. Ir. J. Agric. Food Res. 44:15–26.

Kleiber, M. 1936. Problems involved in breeding for efficiency of food utilization. J. Anim. Sci. 1:247–258.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. Anim. Sci. 22:486–494.

Lancaster, P. A., G. E. Carstens, D. H. Crews Jr., T. H. Welsh Jr., T. D. A. Forbes, D. W. Forrest, L. O. Tedeschi, R. D. Randel, and F. M. Rouquette. 2009. Phenotypic and genetic relation-

ships of residual feed intake with performance and ultrasound carcass traits in Brangus heifers. J. Anim. Sci. 87:3887–3896.

Liu, M. F., L. A. Goonewardene, D. R. C. Bailey, J. A. Basarab, R. A. Kemp, P. F. Arthur, E. K. Okine, and M. Makarechian. 2000. A study on the variation of feed efficiency in station tested beef bulls. Can. J. Anim. Sci. 80:435–441.

Mc Hugh, N., R. D. Evans, P. R. Amer, A. G. Fahey, and D. P. Berry. 2011. Genetic parameters for cattle price and live-weight from routinely collected data at livestock auctions and commercial farms. J. Anim. Sci. 89:29–39.

Mc Hugh, N., A. G. Fahey, R. D. Evans, and D. P. Berry. 2010. Factors associated with selling price of cattle at livestock marts. Animal 8:1378–1389.

Miglior, F., R. A. Kempl, and E. B. Burnside. 1994. Genetic parameter estimates of conformation and performance traits in station-tested Limousin bulls. Can. J. Anim. Sci. 74:379–381.

Mukai, F., K. Oyama, and S. Kohno. 1995. Genetic relationships between performance test traits and field carcass traits in Japanese Black cattle. Livest. Prod. Sci. 44:199–205.

Nkrumah, J. D., J. A. Basarab, M. A. Price, E. K. Okine, A. Ammoura, S. Guercio, C. Hansen, C. Li, B. Benkel, and S. S. Moore. 2004. Different measures of energetic efficiency and their relationships with growth, feed intake, ultrasound, and carcass measurements in hybrid cattle. J. Anim. Sci. 82:2451–2459.

Nkrumah, J. D., D. H. Keisler, D. H. Crews Jr., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, and S. S. Moore. 2007. Genetic and phenotypic relationships of serum leptin concentration with performance, efficiency of gain, and carcass merit of feedlot cattle. J. Anim. Sci. 85:2147–2155.

Pabiou, T., W. F. Fiske, A. Näsholm, A. R. Cromie, M. J. Drennan, M. G. Keane, and D. P. Berry. 2009. Genetic parameters for carcass cut weight in Irish beef cattle. J. Anim. Sci. 87:3865–3876.

Richardson, E. C., R. M. Herd, V. H. Oddy, J. M. Thompson, J. A. Archer, and P. F. Arthur. 2001. Body composition and implications for heat production of Angus steer progeny of parents selected for and against residual feed intake. Aust. J. Exp. Agric. 41:1065–1072.

Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livest. Prod. Sci. 90:255–270.

VanRaden, P. M., and A. H. Sanders. 2003. Economic merit of cross-bred and purebred US dairy cattle. J. Dairy Sci. 86:1036–1044.

Webster, A. J. F., A. A. M. Ahmed, and J. P. Frappell. 1982. A note on growth rates and maturation rates in beef bulls. Anim. Sci. 35:281–284.

Related Articles	A related article has been published: http://jas.fass.org/content/animalsci/89/11/3372.full.html
References	This article cites 30 articles, 12 of which you can access for free at: http://jas.fass.org/content/89/11/3382#BIBL