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Genetic relationships between feed efficiency in growing males and beef cow performance

J. J. Crowley,*†‡ R. D. Evans,§ N. Mc Hugh,*† 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: Most studies on feed efficiency in beef cattle have focused on performance in young animals despite the contribution of the cow herd to overall profitability of beef production systems. The objective of this study was to quantify, using a large data set, the genetic covariances between feed efficiency in growing animals measured in a performance-test station, and beef cow performance including fertility, survival, calving traits, BW, maternal weaning weight, cow price, and cull cow carcass characteristics in commercial herds. Feed efficiency data were available on 2,605 purebred bulls from 1 test station. Records on cow performance were available on up to 94,936 crossbred beef cows. Genetic covariances were estimated using animal and animal-dam linear mixed models. Results showed that selection for feed efficiency, defined as feed conversion ratio (FCR) or residual BW gain (RG), improved maternal weaning weight as evidenced by the respective genetic correlations of −0.61 and 0.57. Despite residual feed intake (RFI) being phenotypically independent of BW, a negative genetic correlation existed between RFI and cow BW (−0.23; although the SE of 0.31 was large). None of the feed efficiency traits were correlated with fertility, calving difficulty, or perinatal mortality. However, genetic correlations estimated between age at first calving and FCR (−0.55 ± 0.14), Kleiber ratio (0.33 ± 0.15), RFI (−0.29 ± 0.14), residual BW gain (0.36 ± 0.15), and relative growth rate (0.37 ± 0.15) all suggest that selection for improved efficiency may delay the age at first calving, and we speculate, using information from other studies, that this may be due to a delay in the onset of puberty. Results from this study, based on the estimated genetic correlations, suggest that selection for improved feed efficiency will have no deleterious effect on cow performance traits with the exception of delaying the age at first calving.

Key words: beef cattle, cow performance, feed efficiency, fertility

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INTRODUCTION

The profitability of an animal production system is determined by the balance between costs incurred and revenue emanating from the enterprise. Feed remains the single largest variable cost in beef production (Arthur et al., 2005), resulting, therefore, in an ever increasing interest in improving feed efficiency in cattle through improvements in animal management and genetics (Berry, 2008). Improving feed efficiency in younger animals has generally been the focus of most studies to date (Arthur et al., 2001; Basarab et al., 2003; Crowley et al., 2010), including the impact of selection for improved feed efficiency on other performance traits in young animals (Hoque et al., 2006; Bouquet et al., 2010; Crowley et al., 2011). However, in species such as cattle where reproductive rate is relatively low, the impact of selection for improved feed efficiency on cow performance is of particular importance. Despite this, there are few studies that have attempted to estimate the genetic covariance between feed efficiency and cow performance. This is despite the considerable contribution of costs associated with cow maintenance to overall costs of the production system (Montaño-Bermudez et al., 1990). It is therefore imperative to quantify the impact of genetic selection for improved feed efficiency in younger, growing animals on the performance of the beef cow population.

[1]Corresponding author: Donagh.berry@teagasc.ie
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Therefore, the objective of this study was to quantify the genetic covariances between feed efficiency in growing purebred animals measured in a performance-test station and crossbred cow performance in the national beef herd including fertility, survival, calving traits, BW, maternal weaning weight, cow value, and cull cow carcass characteristics. Most of the bulls performance tested are used either through AI or natural mating as sires or grandsires of subsequent generations in commercial herds, and therefore, the impact of selection in these purebred animals on performance in commercial animals is of particular importance.

MATERIALS AND METHODS

All data used in the present study were obtained from a pre-existing 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) pedigree bulls in a performance-test station, and 2) national data from the Irish Cattle Breeding Federation database.

Performance-Tested Animals

The performance-testing procedures used in the current study were 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 between 1995 and 2005 when bulls were weighed at 21-d intervals. The diet offered comprised concentrates and a restricted forage (hay/lucerne) allowance. Once ad libitum intake of concentrates was reached, intake was recorded on a fresh-weight basis. Feeding regimens and diets are outlined in detail in Crowley et al. (2010).

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. This will be subsequently referred to as the test period. Additionally, the most recent BW record before the 70-d cut-off was also retained 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. Data from an additional 50 bulls were omitted due to abnormal growth rates. Only purebred Aberdeen Angus (n = 75), Charolais (n = 521), Hereford (n = 115), Limousin (n = 850), and Simmental (n = 541) bulls with pedigree information were included. A total of 2,605 bulls remained after all edits.

Performance Traits

Performance traits measured on the bulls in the performance-test station were described previously in Crowley et al. (2010). In brief, ADG during the test period for each bull was the slope of 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 mentioned previously, data for 50 bulls were removed due to abnormal growth rates defined as the proportion of variation of the BW of an animal explained by the linear regression being <0.90. Midtest BW was taken as BW 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 was calculated as average CI divided by ADG. Relative growth rate (**RGR**) and Kleiber ratio (**KR**) were computed as follows:

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

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

Residual feed intake (**RFI**) was assumed to represent the residuals from a multiple regression model regressing CI on ADG and $BW^{0.75}$ with batch included as a contemporary group effect. Similarly, residual BW gain (**RG**) was assumed to represent the residuals from a multiple regression model regressing ADG on CI and $BW^{0.75}$ with batch included as a contemporary group effect in the model.

Commercial Data

Weaning Weight. The data editing undertaken to generate records for weaning weight are identical to those reported in detail in Crowley et al. (2011) and are summarized hereafter. Body weights measured at livestock auctions and on farm from 821,940 weanlings between 2000 and 2008 were available; weanlings were defined as animals aged between 6 and 12 mo of age (Crowley et al., 2011). Only the first record in time of animals weighing between 150 and 900 kg, with a known sire and maternal grandsire and with at least

75% of their breed proportion containing some fraction of Aberdeen Angus (**AN**), Belgian Blue (**BB**), Charolais (**CH**), Friesian (**FR**), Hereford (**HE**), Holstein (**HO**), Limousin (**LI**), or Simmental (**SI**), were retained. Two contemporary groups were defined; herd-year-season of weighing and sale date by auction of sale. The herd-year-season contemporary group of weighing was defined using an algorithm described by Crump et al. (1997). Essentially, this algorithm creates contemporary groups based on animals from the same herd that have event dates close together. In this study, weigh date was taken as the event date, so animals from the same herd differing in weigh date by up to 10 d were grouped together. If the number of records in this immediately defined contemporary group was <5, then this group was merged with an adjacent group if the start date of one group and the end date of the other group were within 182 d of each other. Subsequently, all contemporary groups with <5 records were omitted. After all edits, 25,129 BW records remained from 1,143 herd-year-seasons and 2,318 dates (Table 1).

Cow BW and Price. Body weight and price data on 214,708 cows sold at livestock auctions between the years 2000 and 2008 were available. Cows were defined as females older than 22 mo of age with a calving record, or females over 30 mo of age. Only records up to the tenth parity, from cows weighing between 300 kg and 1000 kg and sold in single lots for between €100 and €1,500, were retained. Only cows from a known sire with at least 75% of their breed fraction containing some proportion of AN, BB, CH, FR, HE, HO, LI, or SI were retained. Two contemporary groups were defined: herd-year-season of sale and sale date by auction of sale. The herd-year-season contemporary group was defined using an algorithm suggested by Crump et al. (1997), which has been previously explained. Only contemporary groups with >5 records were retained. After all edits, 7,961 cow records remained from 1,105 herd-year-seasons and 1,312 livestock auction-dates (Table 1).

Fertility and Survival. Service dates of 393,858 artificial and natural matings from 273,287 lactations on 169,105 cows in 16,759 beef herds between 2002 and 2009, inclusive, were available. Only cows with a known sire with at least 75% of their breed proportion containing some fraction of AN, BB, CH, HE, LI, or SI were retained. When a cow had undergone multiple ovulation and embryo transfer, her subsequent fertility records from 1 prior calendar year were discarded.

Fertility traits derived in the present study were age at first calving (**AFC**), calving to first service interval (**CFS**), calving interval (**CIV**), and survival to the next parity. Only data from parities 1 to 5 were retained. Age at first calving records <660 and >1,240 d of age data were omitted. Because of a lack of information on heifers selected to become replacements in the herd, heifers that failed to calve for the first time were not included in the analysis of AFC. The CFS records <10 and >250 d were also discarded. Calving interval

Table 1. Descriptive statistics, genetic SD (σ_g), and heritability estimates (h^2; SE in parentheses) of the beef cow traits

Item	No. of records	No. of animals	No. of CG[1]	Herds	Scale	Mean	σ_g	h^2
Calving difficulty[2]*	94,936	54,538	10,615	3,644	1 = easy; 4 = vet	1.34	0.18; 0.29	0.10 (0.02); 0.24 (0.02)
Perinatal mortality[2]†	82,072	48,486	8,507	2,274	0 = alive; 1 = dead	0.05	0.02; 0.02	0.01 (0.01); 0.01 (0.01)
Age at first calving	28,627	28,627	5,123	2,372	d	937.00	41.64	0.19 (0.02)
Calving interval[3]	88,333	48,706	11,013	1,770	d	396.03	9.64	0.02 (0.004)
Calving to first service[4]	27,525	18,749	4,297	3,614	d	81.92	6.06	0.03 (0.01)
Survival to parity 2	43,786	43,786	7,438	4,005	1 = survived; 0 = culled	0.90	0.05	0.03 (0.01)
Survival to parity 3	29,208	29,208	5,309	2,758	1 = survived; 0 = culled	0.91	0.05	0.04 (0.01)
Survival to parity 4	18,975	18,975	3,568	1,934	1 = survived; 0 = culled	0.90	0.03	0.01 (0.01)
Survival to parity 5	12,127	12,127	2,345	1,323	1 = survived; 0 = culled	0.89	0.03	0.01 (0.02)
Maternal weaning weight[2]‡	25,129	25,129	1,143 and 2,318	1,291	kg	351.01	12.62; 22.74	0.08 (0.02); 0.27 (0.03)
Cow BW	7,961	7,961	1,312 and 1,105	771	kg	596.61	35.07	0.34 (0.05)
Cow price	7,961	7,961	1,312 and 1,105	771	€	555.60	21.05	0.05 (0.03)
Carcass weight	80,119	80,119	11,032	4,588	kg	309.02	17.99	0.32 (0.02)
Carcass conformation	80,119	80,119	11,032	4,588	1 = worst; 15 = best	3.19	0.59	0.29 (0.02)
Carcass fat	80,119	80,119	11,032	4,588	1 = leanest; 15 = fattest	6.49	0.69	0.17 (0.01)

[1]Contemporary groups.

[2]Maternal, followed by direct σ_g and h^2 presented.

[3]Repeatability = 0.04.

[4]Repeatability = 0.08.

*†‡The correlation between maternal and direct components was *−0.75 (0.05), †0.13 (0.46), ‡−0.12 (0.15).

records <300 and >600 d were discarded, with the exception of instances where a cow had a CFS of <150 d, the upper limit for CIV was increased to 800 d; a CFS of <150 d indicated that the farmer had attempted to get the cow to calve again the following calving season. Calving to first service and CIV were both treated as repeated measures across parities, and therefore, all parities for CFS and CIV were grouped together for the definition of contemporary group and subsequent analysis.

Survival, a dichotomous variable, was defined as whether or not a cow survived from parity i to parity $i + 1$ ($i = 1$ to 4). A cow was deemed to have survived parity i if she had a record in parity $i + 1$. Cows recorded as being culled in parity i were recorded as such and were not included in the analysis of survival in the subsequent parities. Where no culling date was recorded but the last known calving date of a cow was within 800 d of the date of data extraction or within 800 d of the last record in that herd, then her survival for that and for subsequent parities was set to missing.

Herd-year-season contemporary groups, defined separately for each trait, were generated using the previously mentioned algorithm described by Crump et al. (1997). For AFC, herd-year-season of birth was the contemporary group. For all other fertility traits, herd-year-season of calving was used. Subsequently, contemporary groups with <5 records were omitted for CIV, whereas contemporary groups with <4 records were omitted for AFC, CFS, survival to parity 2, survival to parity 3, survival to parity 4, and survival to parity 5. The number of records remaining and number of contemporary groups included in the analysis of each of the fertility traits are presented in Table 1.

Calving Performance. Calving difficulty and perinatal mortality records were available on 4,294,044 calvings from 1,606,722 cows in 71,733 beef herds between 2002 and 2009, inclusively. In Ireland, calving difficulty is scored by the farmer on a scale of 1 to 4 as follows: 1 = no assistance; 2 = slight assistance; 3 = considerable assistance; and 4 = veterinary assistance including cesarean section (Mee et al., 2011). Perinatal mortality is a dichotomous variable scored by farmers as calf dead at birth or within 24 h (Mee et al., 2008); recording of this trait is a legal requirement in Ireland. Calvings recorded as abortions were discarded, as were calvings resulting in twin births. Additionally, only calving events from animals in the first 5 parities were retained and only animals calving within 2 yr of the median age within parity were retained; first-parity animals had to be older than 660 d at calving. Records were discarded if either the sire or maternal grandsire of the calf was unknown. Only calves with at least 75% of their breed fraction containing some proportion of AN, BB, CH, HE, LI, or SI were retained. Only herd-years with some incidence of dystocia or perinatal mortality were retained. Contemporary groups were defined, across parities, as herd-year-season of calving and were generated using the previously mentioned algorithm described by Crump et al. (1997). Only contemporary groups with at least 5 animals were retained. After all edits, 94,936 records from 54,538 cows in 3,644 herds had information on calving dystocia and 82,072 records from 48,486 cows in 2,274 herds had information on perinatal mortality (Table 1).

Carcass Traits. Carcass conformation, carcass fat, and carcass weight of 462,549 cows from 45,983 herds slaughtered between 2002 and 2009, inclusive, were available. Cold carcass weight as well as carcass conformation and carcass fat grade, scored using the EUROP classification system, are 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).

Cows in the present study were defined as females that calved at least once or females older than 30 mo of age when slaughtered; only cows slaughtered between 22 and 170 mo of age were retained. Similar to previous edits, only cows with a known sire with at least 75% of their breed fraction containing some proportion of AN, BB, CH, FR, HE, HO, LI, or SI were retained. Carcass weights <150 and >550 kg were omitted, and cows slaughtered more than 800 d since their last calving were discarded. The period between the last calving event and slaughter of a cow was categorized into 13 different classes: <50 d, 50 to 99 d, 100 to 149 d, 150 to 199 d, 200 to 249 d, 250 to 299 d, 300 to 349 d, 350 to 399 d, 400 to 449 d, 450 to 499 d, 500 to 599 d, 600 to 699 d, and 700 to 800 d. Contemporary group was defined as herd by slaughter date, and only contemporary groups with 5 or more records were retained. The final data set consisted of 80,119 cows in 11,032 contemporary groups from 4,588 herds (Table 1).

Coefficients of Heterosis and Recombination Loss

Coefficients of heterosis and recombination loss were calculated for all animals as $1-\sum_{i=1}^{n} sire_i \cdot dam_i$ and $1-\sum_{i=1}^{n}(sire_i^2 + dam_i^2)/2$, respectively, where $sire_i$ and dam_i are the proportion of breed i (across n breeds) in the sire and dam, respectively.

Analysis

Genetic (co)variance parameters were estimated using linear animal mixed models in ASREML (Gilmour et al., 2009) with the exception that an animal-dam model was used for the analysis of weaning weight, calving difficulty, and perinatal mortality. Fixed effects used to adjust traits measured on the performance tested bulls were, as stated in Crowley et al. (2010), batch (n = 84), breed of bull (n = 5), dam lactation (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 included in the model.

In the analysis of cow performance, the models included contemporary group(s) as a class variable and breed proportion, coefficient of heterosis, and coefficient of recombination loss as continuous variables. A separate effect was fitted for each breed proportion. Additionally, CFS, CIV, cow price, cow BW, and cow carcass traits were all adjusted for parity of the cow herself, whereas both calving difficulty and perinatal mortality were adjusted for the parity of the dam. Maternal weaning weight and calving performance were adjusted for sex of the calf, dam heterosis, and dam recombination.

Fixed effects unique to maternal weaning weight were identical to those used in the analysis of weaning weight in the same population described previously in Crowley et al. (2011). Briefly, these fixed effects were age, calving difficulty, whether the animal was born as a singleton or twin, parity of the dam, and dam age group (dam age in months relative to the median age within parity), and the continental breed proportion of the dam. Two interactions were included in the model for maternal weaning weight; age interacted with sex and SI breed proportion interacted with sex.

Fixed effects unique to cow BW and price were cow age group (cow age in months relative to the median age within parity), days since last calving (<50, 51 to 100, 101 to 200, 201 to 300, and >300), fate postsale (slaughter or progression to a subsequent parity), and whether or not the last calving before sale resulted in a twin birth, as well as the calving difficulty of that birth. An interaction between cow age group and lactation group, as well as quadratic effects for BB, CH, and HE breed proportions, were also fitted. Fixed effects unique to the cow carcass traits were a quadratic effect of age at slaughter and days since last calving (continuous).

Animal was included as a random effect in all models. Additionally, for perinatal mortality, calving difficulty, and maternal weaning weight, the additive effects of the dam were also included in the model. Genetic relationships among all animals were accounted for through a relationship matrix created using pedigree traced back at least 4 generations. Furthermore, a permanent environmental effect of dam was fitted as a random effect for perinatal mortality and calving difficulty; a permanent environmental effect of the animal itself was fitted as a random effect for CIV and CFS. A permanent environmental effect of dam was found not to exist ($P > 0.05$) for maternal weaning weight.

In the final data set, when estimating covariance parameters between traits measured in performance tested bulls and traits measured in commercial cattle, data on weanling BW, dystocia, and perinatal mortality 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 312,167 commercial animals from 22,866 sires (with between 1 and 2,858 progeny per sire) and 197,242 dams were included in this study. Of the 22,866 sires, 2,308 were AN (24,771 progeny), 5,558 CH (69,305 progeny), 1,584 HE (15,321 progeny), 4,789 LI (76,894 progeny), and 1,804 SI (23,484 progeny). Of the 2,605 performance-tested bulls, 13 had only grand progeny (n = 162) in the commercial data set and 252 had both progeny and grand progeny (n = 7,715); no bull had only progeny in the commercial data set. Additionally, 2,419 performance tested animals had 65,266 paternal half sibs in the commercial data, 1,078 had 2,637 maternal half sibs, and 344 performance-tested bulls had 435 full sibs.

RESULTS

Summary statistics for all beef cow traits are detailed in Table 1. The maternal and direct heritability estimates for weanling weight were 0.08 and 0.27, respectively. The correlation between the maternal and direct components was −0.12 ± 0.15. Heritability estimates for cow carcass traits ranged from 0.17 to 0.32. Maternal heritability estimates for calving difficulty and perinatal mortality were 0.10 and 0.01, respectively; corresponding correlations between the direct and maternal effects were −0.61 ± 0.05 and 0.13 ± 0.46. Dam repeatability estimates for calving difficulty and perinatal mortality were 0.29 and 0.02, respectively. Heritability estimates for fertility traits were low, ranging from 0.01 (survival to parity 4 and survival to parity 5) to 0.19 (AFC). Repeatability estimates for CIV and CFS were 0.02 and 0.03, respectively.

CI, BW, and ADG

Genetic correlations between CI, midtest BW, and ADG measured in performance-tested bulls and maternal weaning weight, and cow BW, cow price, and carcass traits are summarized in Table 2. In general, SE were large, especially with cow price, which was attributable mainly to the low heritability of that trait (Table 1). Correlations were not >2 SE from 0, with the exception of the positive genetic correlation between ADG and maternal weaning weight; the genetic correlation between ADG and cow BW was almost 2 SE from 0.

Genetic correlations between CI, midtest BW, and ADG measured in the performance-tested bulls and calving performance and fertility traits in beef cows are presented in Table 3. Most genetic correlations with both calving difficulty and perinatal mortality were

Table 2. Genetic correlations (SE) between performance traits and maternal weaning weight, cow BW, cow price, and cow carcass traits[1]

Item	CI	WT	ADG▲	FCR▼	KR▲	RFI▼	RG▲	RGR▲
Maternal weaning weight	0.32 (0.22)	0.20 (0.20)	0.52 (0.17)	−0.61 (0.25)	0.57 (0.26)	0.03 (0.21)	0.57 (0.25)	0.50 (0.26)
Cow BW	0.28 (0.32)	0.35 (0.29)	0.63 (0.33)	−0.62 (0.36)	0.54 (0.34)	−0.23 (0.31)	0.67 (0.34)	0.32 (0.35)
Cow price	−0.29 (0.74)	0.07 (0.70)	0.19 (0.82)	−0.22 (0.88)	0.26 (0.84)	−0.54 (0.72)	0.45 (0.85)	0.23 (0.83)
Carcass conformation	−0.07 (0.16)	−0.09 (0.15)	0.12 (0.19)	−0.29 (0.20)	0.19 (0.19)	−0.06 (0.17)	0.21 (0.19)	0.22 (0.19)
Carcass fat	0.02 (0.21)	−0.27 (0.19)	0.15 (0.23)	−0.10 (0.24)	0.24 (0.23)	0.19 (0.21)	0.11 (0.23)	0.27 (0.22)
Carcass weight	0.16 (0.17)	0.16 (0.16)	0.29 (0.19)	−0.27 (0.20)	0.27 (0.20)	−0.01 (0.17)	0.26 (0.20)	0.28 (0.19)

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

close to 0, varying from 0.01 to 0.35; SE ranged from 0.12 to 0.29. Similarly, most of the genetic correlations between CI, BW, and ADG and cow fertility were close to 0, albeit with large SE ranging from 0.13 to 0.21; absolute genetic correlations ranged from 0.07 to 0.40. Survival to parities 2, 3, and 4 was moderately positively correlated with both CI and midtest BW. This suggests that heavier animals and animals that eat more tend to survive longer in the breeding herd, although correlations with survival to parity 5 were not different from 0. None of the remaining genetic correlations were >2 SE from 0.

Efficiency Traits

Absolute genetic correlations between efficiency traits measured in performance-tested bulls and maternal weaning weight, cow BW, and cow price (Table 2) ranged from 0.03 (RFI and maternal weaning weight) to 0.67 (RG and cow BW). Absolute genetic correlations between efficiency traits and cow carcass traits were ≤0.29 (Table 2). With the exception of the correlation between RFI and carcass fat, correlations between both FCR and RFI and cow BW, cow price, and cow carcass traits were all negative. Conversely, all genetic correlations between RG, KR, and RGR and those traits were positive. Four genetic correlations between efficiency traits and cow performance traits differed from 0; these were the correlations between maternal weaning weight and FCR, KR, RG, and RGR. There was no evident genetic correlation between RFI and maternal weaning weight, cow carcass weight, or carcass conformation.

Genetic correlations between efficiency traits and both calving difficulty and perinatal mortality are detailed in Table 3. All correlations were close to 0, ranging from 0.002 to 0.24.

Age at first calving was moderately correlated with all efficiency traits, and the direction of the correlations suggests that selection for improvement in efficiency will increase the age at first calving. Apart from the genetic correlation between AFC and RFI, the correlations between RFI and the remainder of the fertility traits were all very weak (Table 3), suggesting that selection for RFI will have no impact on fertility in primiparae and pluriparae. Survival was not correlated with feed efficiency (Table 3).

DISCUSSION

Population means and heritability estimates for the performance-tested animals have been discussed in detail by Crowley et al. (2010). Mean survival to subsequent lactation may be artificially inflated in the present study because data from recent years predominate where the incidence of sire recording increased, and because of the editing criteria imposed, animals culled, but not recorded, that have not calved more than 800 d from the last calving or the date of data extraction

Table 3. Genetic correlations (SE) between performance traits[1] and calving performance and fertility traits

Item	CI	WT	ADG▲	FCR▼	KR▲	RFI▼	RG▲	RGR▲
Calving difficulty	0.03 (0.13)	0.24 (0.13)	−0.03 (0.15)	−0.02 (0.16)	−0.12 (0.17)	−0.10 (0.13)	−0.002 (0.16)	−0.13 (0.17)
Calving difficulty$_{\text{maternal}}$	0.18 (0.13)	−0.01 (0.12)	0.09 (0.15)	0.15 (0.16)	0.03 (0.18)	0.20 (0.13)	−0.01 (0.17)	0.05 (0.18)
Perinatal mortality	0.23 (0.26)	0.28 (0.25)	0.16 (0.29)	0.02 (0.32)	0.03 (0.30)	−0.01 (0.26)	0.09 (0.30)	−0.13 (0.31)
Perinatal mortality$_{\text{maternal}}$	−0.35 (0.26)	−0.33 (0.24)	−0.06 (0.28)	−0.12 (0.31)	0.01 (0.29)	−0.24 (0.26)	0.11 (0.29)	0.20 (0.29)
Age at first calving	−0.23 (0.14)	−0.18 (0.13)	0.21 (0.15)	−0.55 (0.14)	0.33 (0.15)	−0.29 (0.14)	0.36 (0.15)	0.37 (0.15)
Calving interval	0.16 (0.15)	0.21 (0.14)	0.08 (0.18)	0.07 (0.19)	−0.05 (0.18)	0.01 (0.16)	−0.01 (0.32)	−0.09 (0.18)
Calving to first service	−0.18 (0.20)	−0.07 (0.19)	−0.22 (0.21)	0.21 (0.22)	−0.22 (0.22)	−0.03 (0.20)	−0.15 (0.22)	−0.19 (0.22)
Survival to parity 2	0.32 (0.19)	0.40 (0.17)	0.31 (0.20)	−0.15 (0.22)	0.18 (0.21)	−0.03 (0.19)	0.21 (0.21)	0.14 (0.21)
Survival to parity 3	0.31 (0.14)	0.34 (0.13)	0.02 (0.16)	0.31 (0.17)	−0.20 (0.16)	0.13 (0.15)	−0.15 (0.17)	−0.26 (0.16)
Survival to parity 4	0.38 (0.16)	0.40 (0.14)	0.28 (0.18)	−0.04 (0.20)	0.06 (0.19)	0.06 (0.17)	0.13 (0.19)	−0.12 (0.19)
Survival to parity 5	0.07 (0.15)	0.18 (0.13)	0.19 (0.17)	−0.12 (0.18)	0.06 (0.17)	−0.17 (0.15)	0.20 (0.18)	−0.05 (0.17)

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

of the herd are censored and therefore not included. The larger decline between parities in the numbers of animals included in the analysis than expected based on mean survival is due to the editing on minimum contemporary group size, with generally more animals in later parities not being included in sufficiently sized contemporary groups. Heritability estimates in the present study for performance in beef cows are within the ranges of most international studies for maternal weaning weight (Garrick et al., 1989; Mwansa et al., 2002), cow BW (Koots et al., 1994a; Meyer, 1995; Arango et al., 2002), cow price (Schierenbeck et al., 2008; Mc Hugh et al., 2011), calving difficulty (MacNeil et al., 1984), perinatal mortality (Eriksson et al., 2004), and fertility (MacNeil et al., 1984). Additionally, heritability estimates presented here for cow carcass traits ranging from 0.17 to 0.32 were less than those estimated in younger Irish animals (Crowley et al., 2011); the authors are unaware of any heritability estimate for carcass traits in mature females.

Corroborating previous studies, a negative covariance was evident between the direct and maternal components of weanling weight (Lee and Pollak, 2002; Speidel et al., 2007), indicating that animals genetically superior for the direct effect are inferior for the maternal effect. This negative covariance is most likely due to the negative correlation between BW of the cow and her milk yield (Meyer et al., 1994).

Genetic Correlations with Maternal Weaning Weight, Cow BW, and Price

Maternal weaning weight is the influence of the genetics of the dam on the weaning weight of her progeny over and above the direct contribution through her genes passed on to the calf. Maternal weaning weight is generally thought to represent the milk yield of the dam (Miller and Wilton, 1999) and possibly some measure of mothering ability. Meyer et al. (1994) stated that milk production of the dam is the main influence on preweaning growth in beef calves, so achieving favorable genetic gain in both direct and maternal weaning weight is desirable. Without detailed physiological measures on animals, however, it is difficult to ascertain the physiological mechanisms underpinning the favorable correlations between FCR, RG, KR, and RGR in growing males and maternal weaning weight in the present study. Residual feed intake measured in the growing performance tested animals in the present study was not correlated with maternal weaning weight, agreeing with a previously published experiment using females divergently selected for RFI (Arthur et al., 2005). In this latter study, where weanling heifers ranked as either high or low on RFI were followed through to lactation, no statistically significant difference in milk yield was observed. In the same study, cows with decreased RFI who had been divergently selected based on their postweaning RFI were lighter and thinner than their high RFI contemporaries, although differences were not statistically significant.

Genetic correlations in the present study between cow BW and both ADG and midtest BW in the performance-tested animals were positive and agree with Herd and Bishop (2000), suggesting that selection for midtest BW or ADG measured on test without subsequent cognizance of cow BW will result in heavier animals that may, in turn, be less efficient. A balanced breeding goal is required to resolve these antagonisms. Even though not different from 0, the negative genetic correlation between FCR and cow BW agrees with many previous international studies (Koots et al., 1994b; Herd and Bishop, 2000), indicating that selection for FCR alone will, over time, lead to a heavier cow with possible unfavorable implications for the cost of maintenance.

The primary reason for development of RFI as a measure of feed efficiency was that its association with mature BW was expected to be negligible given its phenotypic independence of the BW estimate included in the regression model (Koch et al., 1963). Although not different from 0, a negative genetic correlation was found between RFI and cow BW, suggesting that selection for improved RFI may increase cow BW. Arthur et al. (2005) found that low RFI (more efficient) cows were heavier than their high, less efficient counterparts; however, the results were also not significant. These findings need to be investigated further in other large, independent data sets.

Genetic Correlations with Cow Carcass Traits

Cull cow value contributes to the overall profitability of a beef herd (Amer et al., 2001). Although accompanied by large SE, the genetic correlations in the present study suggest a minimal impact on cull cow carcass from selection on any of the performance-test measures. Despite the lack of genetic correlations with cow carcass traits in this study, many studies in younger animals (Fouilloux et al., 2000; Hoque et al., 2006), including those conducted in Ireland (Crowley et al., 2011), reported that selection for RFI would reduce carcass fat and improve carcass conformation, whereas selection for FCR will also improve carcass conformation. In the present study, although not different from 0, the positive genetic correlation between RFI measured in performance-tested bulls and cow carcass fat suggests selection on RFI may indeed reduce carcass fat in the mature cow. Of concern is that because of the phenotypic association between body fat (approximated by BCS in a live animal) and reproductive performance (Drennan and Berry, 2006), selection for RFI may have repercussions for fertility mediated through a reduction in body fat (Berry, 2008). However, apart from AFC, no association between RFI measured in growing animals and fertility performance was observed in this study.

Genetic Correlations with Calving Performance

Although there is no apparent biological rationale as to why feed efficiency should be associated with calving difficulty and perinatal mortality, the authors are nonetheless unaware of any study that has investigated this. Based on the results of the present study, there is no evidence for a deleterious effect on calving performance from long-term selection on feed efficiency. Results do indicate, however, that selection for increased midtest BW may be associated with increased dystocia.

Genetic Correlations with Fertility

It has been well documented in dairy cattle that aggressive selection for milk production resulted in an unfavorable trend in reproductive performance (Royal et al., 2000), and attempts to revert to acceptable levels of reproductive efficiency have proven difficult. This, therefore, shows the necessity to characterize the genetic correlations between traits targeted in breeding goals and traits that in other ways may affect performance. Such potential impacts are particularly important in Ireland where performance-tested bulls are used as sires or grandsires of subsequent generations in the Irish commercial population. Therefore, the effect of selection for increased growth or improved feed efficiency in the performance-tested bulls on reproductive performance in commercial beef cows needs to be quantified. To date, very few studies have attempted to quantify whether such an association exists (Arthur et al., 2005; Basarab et al., 2007), and we are unaware of any study that has attempted to estimate the genetic correlation between feed efficiency and female reproduction, at least using a data set of the magnitude of that used in the present study.

Genetic correlations between survival and both CI and midtest BW suggest that heavier animals that eat more survive longer in the herd. This may be attributable to well-fed, heavier animals having a more positive energy balance, resulting in superior fertility and retention in the breeding herd. Whereas CI, midtest BW, or ADG were not correlated with AFC, selection for increased feed efficiency, irrespective of the definition, was associated with delayed first calving. This suggests that selection for efficiency may influence age at puberty or pregnancy rate in nulliparae. However, genetic correlations in the present study with CIV in primiparae and pluriparae were close to 0, and correlations with CFS were not different from 0, suggesting that pregnancy rate is potentially not the reason, and therefore, the impact of feed efficiency on AFC is likely mediated through a delay in the onset of puberty. Furthermore, in Crowley et al. (2010), early maturing breeds, namely AN and HE, were shown to have a greater RFI ($P < 0.001$) than the later maturing breeds, CH, LI, and SI. In cows stratified into high, medium, and low RFI based on the RFI of their progeny, Basarab et al. (2007) reported no difference in calving interval between groups, but dams of low-RFI progeny calved 5 to 6 d later compared with medium- and high-RFI dams in their subsequent parity; this suggests that the difference in calving date had originated from a later age at first calving for the low RFI group. A delay in the onset of puberty in decreased RFI animals is biologically plausible because the partitioning of energy among animals differing in RFI may be altered with more energy in low RFI partitioned toward growth and away from other bodily functions, such as reproduction during that period. Furthermore, early onset of puberty in females may also be associated with early onset of puberty in males, and if so, greater associated activity in these males while on performance test, which may have influenced their phenotypic (and genetic) RFI.

In conclusion, the large SE associated with the genetic correlations estimated in the current study make it difficult to generate definitive conclusions on the implications of selection on feed efficiency on some measures of beef cow performance. However, it is clear that selection for improved feed efficiency will have an unfavorable effect on the age at which a heifer first calves, although it will not affect subsequent reproductive performance. Selection for improved FCR and RG will result in increased maternal weaning weight, which is likely a reflection of increased milk yield.

LITERATURE CITED

Amer, P. R., G. Simm, M. G. Keane, M. G. Diskin, and B. W. Wickham. 2001. Breeding objectives for beef cattle in Ireland. Lives. Prod. Sci. 67:223–239.

Arango, J. A., L. V. Cundiff, and L. D. Van Vleck. 2002. Breed comparisons of Angus, Charolais, Hereford, Jersey, Limousin, Simmental, and South Devon for weight, weight adjusted for body condition score, height, and body condition score of cows. J. Anim. Sci. 80:3123–3132.

Arthur, P. F., R. M. Herd, J. F. Wilkins, and J. A. Archer. 2005. Maternal productivity for Angus cows divergently selected for post-weaning residual feed intake. Aust. J. Exp. Agric. 45:985–993.

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

Basarab, J. A., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87:489–502.

Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189–204.

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.

Crowley, J. J., R. D. Evans, N. Mc Hugh, T. Pabiou, D. A. Kenny, M. McGee, D. H. Crews Jr., and D. P. Berry. 2011. Genetic associations between feed efficiency measured in a performance test station and performance of growing cattle in commercial beef herds. J. Anim. Sci. 89:3382–3393.

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.

Eriksson, S., A. Näsholm, K. Johansson, and J. Philipsson. 2004. Genetic parameters for calving difficulty, stillbirth, and birth weight for Hereford and Charolais at first and later parities. J. Anim. Sci. 82:375–383.

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.

Garrick, D. J., E. J. Pollak, R. L. Quass, and L. D. Van Vleck. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-Sired calves. J. Anim. Sci. 67:2515–2528.

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.

Herd, R. M., and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Livest. Prod. Sci. 63:111–129.

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.

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.

Koots, K. R., J. P. Gibson, and J. W. Watson. 1994a. Analysis of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62:309–338.

Koots, K. R., J. P. Gibson, and J. W. Watson. 1994b. Analysis of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:309–338.

Lee, C., and E. J. Pollak. 2002. Genetic antagonism between body weight and milk production in beef cattle. J. Anim. Sci. 80:316–321.

MacNeil, M. D., L. V. Cundiff, C. A. Dinkel, and R. M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58:1171–1180.

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.

Mee, J. F., D. P. Berry, and A. R. Cromie. 2008. Prevalence of, and risk factors associated with, perinatal calf mortality in pasture-based Holstein-Friesian cows. Animal 4:613–620.

Mee, J. F., D. P. Berry, and A. R. Cromie. 2011. Risk factors for calving assistance and dystocia in pasture-based Holstein-Friesian heifers and cows in Ireland. Vet. J. 187:189–194. doi:10.1016/j.tvjl.2009.11.018

Meyer, K. 1995. Estimates of genetic parameters for mature cow weight of Australian beef cows and its relationship to early growth and skeletal measures. Livest. Prod. Sci. 44:125–137.

Meyer, K., M. J. Carrick, and B. J. Donnelly. 1994. Genetic parameters for milk production of Australian beef cows and weaning weight of their calves. J. Anim. Sci. 72:1155–1165.

Miller, S. P., and J. W. Wilton. 1999. Genetic relationships among direct and maternal components of milk yield and maternal weaning gain in a multibreed beef herd. J. Anim. Sci. 77:1155–1161.

Montaño-Bermudez, M., M. K. Nielsen, and G. H. Deutscher. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. J. Anim. Sci. 68:2279–2288.

Mwansa, P. B., D. H. Crews Jr., J. W. Wilton, and R. A. Kemp. 2002. Multiple trait selection for maternal productivity in beef cattle. J. Anim. Breed. Genet. 119:391–399.

Royal, M. D., A. O. Darwash, A. P. F. Flint, R. Webb, J. A. Woolliams, and G. E. Lamming. 2000. Declining fertility in dairy cattle: Changes in traditional and endocrine parameters of fertility. J. Anim. Sci. 70:487–501.

Schierenbeck, S., S. Konig, and H. Simianer. 2008. Genetic and environmental impact on auction prices for Holstein cows. Livest. Sci. 121:327–334.

Speidel, S. E., R. M. Enns, and D. J. Garrick. 2007. Weaning weight inheritance in environments classified by maternal body weight change. J. Anim. Sci. 85:610–617.