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# Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection<sup>1,2,3</sup>

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**ABSTRACT:** Growth, feed intake, and temperament indicator data, collected over 5 yr on a total of 1,141 to 1,183 mixed-breed steers, were used to estimate genetic and phenotypic parameters. All steers had a portion of Hereford, Angus, or both as well as varying percentages of Simmental, Charolais, Limousin, Gelbvieh, Red Angus, and MARC III composite. Because the steers were slaughtered on various dates each year and the animals thus varied in days on feed, BW and feed data were adjusted to a 140-d feeding period basis. Adjustment of measures of feed efficiency [G:F or residual feed intake (RFI), intake adjusted for metabolic body size, and BW gain] for body fatness recorded at slaughter had little effect on the results of analyses. Average daily gain was less heritable (0.26) than was midtest BW (MBW; 0.35). Measures of feed intake had greater estimates of heritability, with 140-d DMI at 0.40 and RFI at 0.52; the heritability estimate for G:F was 0.27. Flight speed (FS), as an indicator of temperament, had

an estimated heritability of 0.34 and a repeatability of 0.63. As expected, a strong genetic (0.86) correlation was estimated between ADG and MBW; genetic correlations were less strong between DMI and ADG or MBW (0.56 and 0.71). Residual feed intake and DMI had a genetic correlation of 0.66. Indexes for phenotypic RFI and genotypically restricted RFI (no correlation with BW gain) were compared with simple economic indexes incorporating feed intake and growth to elucidate expected selection responses under different criteria. In general, few breed differences were detected across the various measurements. Heterosis contributed to greater DMI, RFI, and MBW, but it did not significantly affect ADG, G:F, or FS. Balancing output (growth) with input costs (feed) is needed in practicing selection, and FS would not be recommended as an indicator trait for selection to change feed efficiency. An index including BW gain and RFI produced the best economic outcome.

**Key words:** cattle, feed intake, flight speed, genetic variation, growth, selection

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## INTRODUCTION

Feed costs represent the largest variable cost in beef production, totaling approximately two-thirds of the cost in US beef cattle (Anderson et al., 2005). In life-cycle beef production, feed energy requirements simply for the maintenance of animals (i.e., not including the

feed costs of productive functions such as growth or lactation above the requirements for maintenance) account for approximately 70% of feed inputs; this results in less than 20% of feed energy converted to beef (Williams and Jenkins, 2006). Research to further characterize genetic variation in feed energy utilization will build the base for effective, profitable selection programs to reduce feed energy requirements for maintenance. This may be especially true as pressure mounts not only to reduce input costs for animal production, but also to reduce waste outputs from livestock production that are deemed detrimental to the environment. Recently, Snelling et al. (2011) reported results of multiple-SNP prediction of breeding value for DMI and residual feed intake (RFI) in crossbred steers; genomic predictors may lessen the need for the amount of phenotypic data collected to incorporate feed intake into a breeding objective. Temperament may be useful in genetic evaluations as an indicator trait for other economic traits

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such as feed intake, or it may have clear economic value in some production settings. Thus, the objectives of this work were to estimate genetic and phenotypic parameters for growth, feed intake, feed efficiency, and a temperament trait in a mixed-breed population of growing beef steers.

## MATERIALS AND METHODS

All animals were reared and handled in accordance with the Guide for the Care and Use of Agricultural Animals in Research and Teaching (<http://www.fass.org>) and as approved by the Animal Care and Use Committee of the US Meat Animal Research Center.

### *Description of Population*

Data were collected on phase 3 steers ( $n = 1165$ ) born in 2003 through 2007 from Cycle VII of the Germ Plasm Evaluation program at the US Meat Animal Research Center (MARC) located near Clay Center, NE. Each cycle of the Germ Plasm Evaluation program is composed of several phases of matings: phase 1 refers to the foundation dams; phase 2 refers to progeny from phase 1 dams; and phase 3 refers to progeny from phase 2 dams.

Phase 1 foundation dams were Angus, Hereford, and MARC III (1/4 Angus, 1/4 Hereford, 1/4 Red Poll, 1/4 Pinzgauer). Identification of breeds of sire to produce phase 2 calves was based on the number of registrations within a breed. The 7 beef breeds in 2003 with the largest number of registrations in the United States were 1) Angus; 2) Hereford; 3) Charolais; 4) Limousin; 5) Simmental; 6) Red Angus; and 7) Gelbvieh (National Pedigreed Livestock Council, 2004), and all these breeds were used as sires. Wheeler et al. (2004) provided a detailed description of the mating system producing phase 2 calves. With collaboration from commercial AI institutions and seedstock producers, representative bulls from each breed were selected on growth EPD.

Phase 2 calves were then either straightbred (Angus or Hereford) or  $F_1$  crosses. The  $F_1$  bulls (phase 2 calves) out of Hereford or Angus dams, but not MARC III dams, were identified and kept for breeding. All heifers (all  $F_1$ , including those from MARC III dams, phase 2 calves) were retained and randomly mated through natural service to  $F_1$  bulls to produce phase 3 calves. Table 1 provides the average breed composition across all phase 3 steers. The  $F_1$  bulls used over the 5 yr produced progeny groups ranging in size from 1 to 8. Additional pedigree information supplemented the phase 3 progeny and, in some cases, went as far back as 12 generations.

### *Animal and Feeding Management*

Steers were born in March through May and were weaned at an average of 165 d in mid to late September. Steers were provided whole oats as a creep feed

**Table 1.** Average breed composition of the population

Breed	% of population
Hereford	22.37
Angus	27.22
Simmental	9.36
Limousin	7.59
Charolais	6.11
Gelbvieh	6.90
Red Angus	6.73
MARC III <sup>1</sup>	13.70

<sup>1</sup>MARC (US Meat Animal Research Center) III = 1/4 Hereford, 1/4 Angus, 1/4 Pinzgauer, 1/4 Red Poll.

from mid-July until weaning. From weaning through December, steers received a series of reduced energy, step-up diets that ranged from 2.55 to 2.73 Mcal of ME/kg.

In early December, steers were randomly assigned to pens of 4 or 8 animals when they entered a facility for measurement of feed intake. At this time, steers were stepped up to the finishing diet. Steers were started on test at approximately 270 d of age in early to mid-January each year and weighed an average of 340 kg. The same finishing diet was offered to steers each year. Table 2 provides the finishing diet composition, which has a calculated energy value of 3.04 Mcal of ME/kg. Diet ME was calculated on a DM basis from tabular values (NRC, 1996). Steers were implanted with Synovex S (200 mg of progesterone and 20 mg of estradiol benzoate, Fort Dodge Animal Health, Overland Park, KS) in December each year.

Individual feed intake for each animal was recorded using the Calan Broadbent Feeding System (American-Calan-Broadbent, Northwood, NH). Feed was delivered to the steers each morning at approximately 0800 h. Feed refusals were collected once per week.

Cattle were weighed on 2 consecutive days at the beginning of the experiment each year. Interim-test BW were collected every 4 wk to monitor BW gain. Two consecutive final BW were obtained approximately 1 wk before slaughter. Each year, steers were serially slaughtered in 4 groups. Steers were slaughtered at a commercial processing facility (JBS-Swift, Grand Island, NE). Hot carcass weight was obtained at slaughter. Trained MARC personnel determined marbling

**Table 2.** Composition of the finishing diet

Ingredient	Dietary DM, %
Alfalfa hay, ground	10.602
Corn, dry rolled	82.668
Soybean meal	5.663
Urea	0.401
Limestone	0.574
Vitamin A, D, and E supplement	0.008
Trace mineral supplement	0.007
Salt	0.062
Monensin <sup>1</sup>	0.015

<sup>1</sup>Rumensin 80 (Elanco Animal Health, Greenfield, IN).

score (**MARB**) and fat thickness (**BF**) at the 12th rib on each carcass after a 36-h chill at 0°C. Numerical scores for marbling ranged from 100 for practically devoid to 900 for abundant.

Flight speed (**FS**) was recorded periodically throughout the finishing phase of production as a measure of temperament. Measurements of FS were coded into 3 periods (December to January, February to March, and April to May) based on season or time of year. Steer BW and hip height were recorded, and then the steer was released from the weigh scale. Each steer traveled around the working chute before crossing the first set of electric eyes, which were placed just outside the barn that held the working facilities. The second set of electric eyes was placed 4.318 m from the first set of electric eyes. Breaking the light beam at each set of electric eyes initiated the start and end of the time measurement. Facility design dictated the structure and length of FS measurement. The wireless electric eyes were manufactured by FarmTek (Wylie, TX). Figure 1 illustrates the method in which FS was measured. Flight speed was calculated as a velocity by the following equation:

$$FS = 4.318 \text{ m}/x \text{ (s)},$$

where  $x$  is the time in seconds it took for a steer to travel 4.318 m.

### Data Editing

Four sets of data were used for analysis: BW data, carcass data, intake data, and FS data. Animals with

an unknown sire or dam were removed from each data set.

Initially, animals without initial and final BW collected on the same days as their pen mates were removed from the BW data set, along with steers missing more than 1 interim BW. Steers that were treated more than once for any illness were also removed; steers treated for bloat received multiple treatments and were thus removed. The traits analyzed from this data set were ADG and midperiod BW. The total number of animals in the BW data set was 1,183.

Animals without any carcass data measurements were removed from the carcass data set. Steers with adjusted BW at 140 d (**BW<sub>140</sub>**) of less than 0.4 cm were removed from the carcass data set. This was assumed to be an incorrect measurement of BF. The total number of animals in the carcass data set was 1,189. Animals without individual feed intake records were removed from the intake data set. Steers fed for fewer than 105 d were removed from the intake data set. In 2006, it was discovered that 2 steers in the same pen had incorrect intake data; therefore, these steers were removed from the data set. Furthermore, the BW and intake data sets were merged, and animals without both BW and feed records were deleted from this data set. Traits analyzed from this data set were DMI, RFI, and G:F. Finally, the aforementioned data set was merged with the carcass data set; animals without BW, feed records, and carcass measurements were deleted from this last data set. Residual feed intake adjusted for fatness was analyzed from this data set. The total number of animals in the intake data set was 1,141.

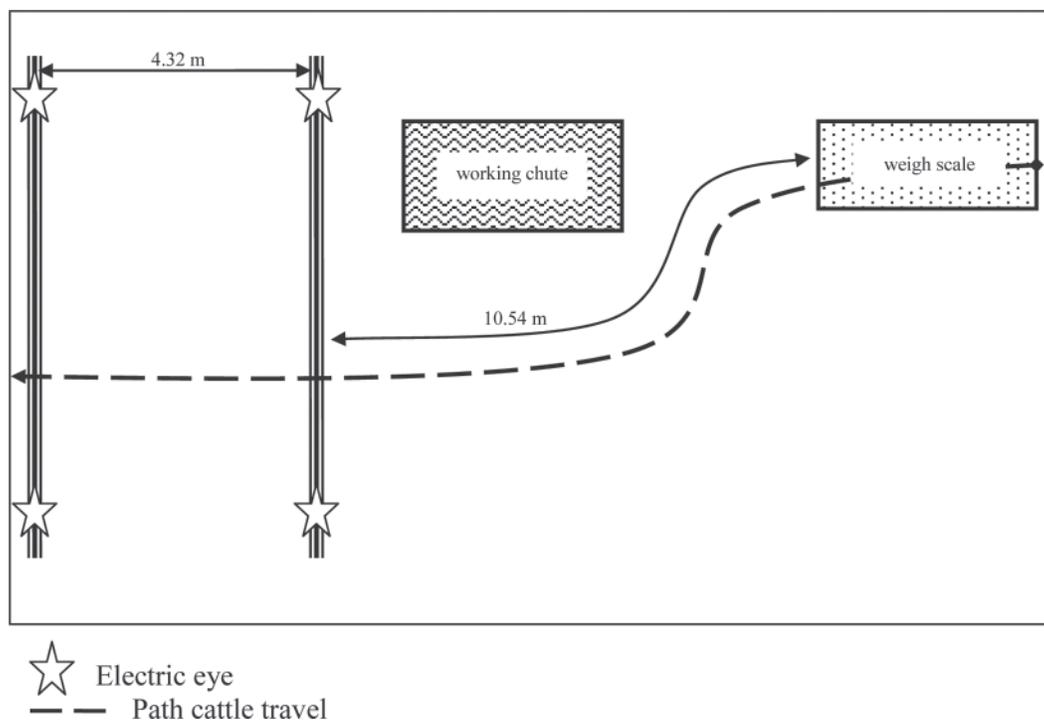


Figure 1. Model of flight speed measurement design.

Animals without any FS measurements were removed from the FS data set, and those without pedigree information were removed. The total number of animals in the FS data set was 1,159. In addition, FS was normalized by truncating flight time at 12 s.

### Statistical Analyses

With the GLM procedure (SAS Inst. Inc., Cary, NC), cumulative DMI and BW were fitted to a quadratic regression on days fed for each animal. Adjusted DMI at 140 d ( $\text{DMI}_{140}$ ) and  $\text{BW}_{140}$  were then predicted for each animal. Adjusted BW gain at 140 d ( $\text{GAIN}_{140}$ ) was determined as follows:

$$\text{GAIN}_{140} = \text{BW}_{140} - \text{BW}_0,$$

where  $\text{BW}_0$  is the actual initial BW for each steer.

Midbody BW ( $\text{MBW}$ ) was predicted at 70 d using the within-animal regression equation, as for predicting  $\text{BW}_{140}$ . Average daily gain was then calculated using the adjusted values as follows:

$$\text{ADG} = \text{GAIN}_{140}/140.$$

In addition, G:F was calculated using the adjusted values as follows:

$$\text{G:F} = \text{GAIN}_{140}/\text{DMI}_{140}.$$

Likewise, BF and MARB were adjusted to a constant age of 140 d for each animal, which was near the mean days on feed ( $\text{DOF}$ ). Linear regression coefficients for adjusting BF and MARB were obtained from Wheeler et al. (2004). The calculations were as follows:

$$\text{BF}_{140} = \text{actual BF} - \text{BF}_{\text{diff}}, \text{ and}$$

$$\text{MARB}_{140} = \text{actual MARB} - \text{MARB}_{\text{diff}},$$

where

$$\text{BF}_{\text{diff}} = 0.0083 \times \text{DOF}_{\text{diff}},$$

$$\text{MARB}_{\text{diff}} = 0.933 \times \text{DOF}_{\text{diff}},$$

$$\text{DOF}_{\text{diff}} = \text{actual DOF} - 140.$$

Residual feed intake was calculated using adjusted values as follows:

$$\text{RFI} = \text{DMI}_{140} - b_g(\text{GAIN}_{140}) - b_w(\text{SUMWT}^{0.75}),$$

where  $b_g$  is the partial regression coefficient associated with adjusted BW gain,  $b_w$  is the partial regression coefficient associated with BW, and

$$\text{SUMWT}^{0.75} = \int_0^{140} \left( \text{individual animal quadratic regression of BW on DOF} \right)^{0.75}.$$

Residual feed intake adjusted for composition of BW gain ( $\text{RFI}_{\text{adj}}$ ) was calculated using adjusted values as follows:

$$\begin{aligned} \text{RFI}_{\text{adj}} = & \text{DMI}_{140} - b_g(\text{GAIN}_{140}) - b_w(\text{SUMWT}^{0.75}) \\ & - b_{\text{bf}}(\text{BF}_{140}) - b_{\text{if}}(\text{MARB}_{140}), \end{aligned}$$

where  $b_g$  is the partial regression coefficient associated with adjusted BW gain,  $b_w$  is the partial regression coefficient associated with BW,  $b_{\text{bf}}$  is the partial regression coefficient associated with deposition of BF, and  $b_{\text{if}}$  is the partial regression coefficient associated with deposition of intramuscular fat. Gain-to-feed ratio ( $\text{G:F}_{\text{adj}}$ ) was also adjusted for BF and marbling, as stated above for  $\text{RFI}_{\text{adj}}$ .

Restricted maximum likelihood procedures were used to obtain estimates of genetic and phenotypic (co)variances and heritabilities by using ASREML (Gilmour et al., 2000) and WOMBAT (Meyer, 2006). In matrix notation, the basic model was

$$\mathbf{Y}_{ij} = \mu + \mathbf{X}\beta_i + \mathbf{Z}\mathbf{u}_j + \mathbf{e}_{ij},$$

where  $\mathbf{Y}$  is a vector of the observations of the  $i$ th trait of the  $j$ th animal,  $\mu$  is the overall mean,  $\beta$  is a vector of the fixed effects of trait  $i$ ,  $\mathbf{u}$  is a vector of the random effects of the  $j$ th animal,  $\mathbf{e}$  is a vector of the random residual errors of the  $i$ th trait of the  $j$ th animal,  $\mathbf{X}$  is an incidence matrix relating observations of fixed effects, and  $\mathbf{Z}$  is an incidence matrix relating observations to random animal effects. Further, the expected value ( $\mathbf{E}$ ) is

$$\mathbf{E}[\mathbf{Y}] = \mathbf{X}\beta.$$

Random animal effects were direct genetic ( $a$ ) and residual ( $e$ ). A preliminary analysis of the first 4 yr of the FS data also included a random permanent environmental effect to facilitate estimation of repeatability. Assumptions for the random effects in the univariate model were

$$\text{Var} \begin{pmatrix} a \\ e \end{pmatrix} = \begin{pmatrix} \mathbf{A}\sigma_a^2 & 0 \\ 0 & \mathbf{I}\sigma_e^2 \end{pmatrix},$$

where matrix  $\mathbf{A}$  is the numerator relationship matrix of all animals in the pedigree, including those without records, and matrix  $\mathbf{I}$  is the identity matrix of appropriate order.

Fixed effects for each trait included year; age at weaning; pen size (either 4 or 8 animals at the start of the test period, with pen size decreasing only if ani-

**Table 3.** Descriptive statistics for ADG, DMI, RFI, G:F, and FS<sup>1</sup>

Variable	Mean	SD	CV, %
ADG, kg	1.59	0.22	14
MBW, kg	465	50	11
DMI <sub>140</sub> , kg	1,202	152	13
RFI, kg	0	86	7 <sup>2</sup>
G:F	0.19	0.03	12
FS, m/s	2.55	1.13	44

<sup>1</sup>MBW = midperiod BW at 70 d on test; DMI<sub>140</sub> = DMI for 140 d; RFI = residual feed intake; FS = flight speed.

<sup>2</sup>Relative to the mean for DMI.

mal losses occurred); fraction of breed heterozygosity to account for different levels of expected heterosis; and fractions of Hereford, Angus, Simmental, Limousin, Charolais, Gelbvieh, Red Angus, and MARC III. For determination of the breed heterozygosity fraction, MARC III (1/4 Angus, 1/4 Hereford, 1/4 Red Poll, 1/4 Pinzgauer) was recognized as a unique breed. Angus and Red Angus were considered the same breed when breed heterozygosity was determined. Breed fraction plus breed heterozygosity were fit as linear regressions, whereas year and pen size were class variables. For FS, season was also included as a class variable. Additional regression effects of SUMWT<sup>0.75</sup> and GAIN<sub>140</sub> were added to the model for DMI to obtain genetic parameters for RFI; further, BF<sub>140</sub> and MARB<sub>140</sub> were added for RFI<sub>adj</sub>. Random effects were animal, pen nested within pen size, and residual error. As mentioned previously, permanent environmental effects were also considered random for FS.

Bivariate analyses were completed to obtain estimates of genetic and phenotypic correlations. Genetic models for specific traits remained the same as in the univariate analyses.

## RESULTS AND DISCUSSION

The mean, SD, and CV for each characteristic are shown in Table 3. Flight speed was by far the most variable characteristic in the data set. Adjusting DMI for MBW<sup>0.75</sup> and for ADG, thus considering average feed costs for maintenance and for production for a

given animal, reduced the variance for RFI to about one-third of the variance in DMI.

Adjusting for carcass fatness (RFI<sub>adj</sub> and G:F<sub>adj</sub>) did reduce residual variance by 11% for RFI and by 9% for G:F. However, adjusting for carcass fatness had little effect on the heritability estimates of RFI and G:F (they agreed within 2%), and adjustment for carcass fatness also had little effect on phenotypic and genetic correlations of RFI and G:F with other traits. In addition, the phenotypic and genetic correlations between RFI and RFI<sub>adj</sub> were  $0.96 \pm 0.003$  and  $0.98 \pm 0.009$ , respectively, and between G:F and G:F<sub>adj</sub>, they were  $0.95 \pm 0.004$  and  $0.95 \pm 0.021$ , respectively. Therefore, only nonadjusted RFI and G:F measures are presented and discussed. Table 4 contains heritability and correlation estimates for the various measures of growth, body size, feed intake, efficiency, and FS.

Average daily gain was less heritable (0.26) than MBW (0.35), the measure of body size. Crowley et al. (2010) reported a heritability of 0.30 for ADG in Irish beef bulls measured at a national test station. Measures of feed intake had greater heritability estimates, with DMI at 0.40 and RFI at 0.52. Heritability estimated by Crowley et al. (2010) in bulls was 0.45 for RFI, similar to our 0.52 heritability estimate for RFI, and was 0.30 for feed conversion ratio, the inverse of G:F, where we found a similar heritability of 0.27. Heritabilities of daily feed intake and RFI in swine have been reported as 0.51 and 0.40, respectively (Cai et al., 2008), which are similar to those reported here, only in reverse order of magnitude. Other estimates of heritability for RFI in swine have been much less (0.14 and 0.24; Gilbert et al., 2007). Methods of calculating RFI differ among various studies and possibly contribute to differences in heritability estimates.

One might expect much greater genetic variability in feed costs for maintenance, adjusted for body size (MBW), as compared with feed costs for production, adjusted for level of production (ADG; Eggert and Nielsen, 2006). Evidence in cows from Ferrell and Jenkins (1985) and Montaño-Bermudez et al. (1990) points to genetic variation in feed costs for maintenance independent of body size. This may be the cause of the greater heritability estimate for RFI than for DMI. The estimated heritability of RFI was greater than the

**Table 4.** Estimates<sup>1</sup> of heritabilities and genetic and phenotypic correlations for ADG, DMI, RFI, G:F, and FS<sup>2</sup>

Item	ADG	MBW	DMI <sub>140</sub>	RFI	G:F	FS
ADG	0.26 (0.10)	0.86 (0.13)	0.56 (0.16)	-0.15 (0.25)	0.31 (0.25)	0.07 (0.27)
MBW	0.51 (0.03)	0.35 (0.12)	0.71 (0.11)	-0.02 (0.24)	-0.02 (0.28)	-0.17 (0.26)
DMI <sub>140</sub>	0.64 (0.02)	0.72 (0.02)	0.40 (0.02)	0.66 (0.12)	-0.60 (0.18)	-0.14 (0.25)
RFI	-0.01 (0.04)	-0.01 (0.04)	0.61 (0.02)	0.52 (0.14)	-0.92 (0.07)	-0.07 (0.24)
G:F	0.51 (0.03)	-0.19 (0.04)	-0.32 (0.03)	-0.67 (0.02)	0.27 (0.10)	0.18 (0.27)
FS	-0.04 (0.04)	-0.28 (0.04)	-0.22 (0.04)	-0.09 (0.04)	0.19 (0.04)	0.34 (0.11)

<sup>1</sup>Heritability estimates are on the diagonal ( $\pm$ SE in parentheses); genetic correlation estimates are above the diagonal ( $\pm$ SE in parentheses); phenotypic correlation estimates are below the diagonal ( $\pm$ SE in parentheses).

<sup>2</sup>MBW = midperiod BW at 70 d on test; DMI<sub>140</sub> = DMI for 140 d; RFI = residual feed intake; FS = flight speed.

heritability (0.39) estimated by Arthur et al. (2001) for RFI in a combined data set of purebred Angus bulls and heifers.

Strong positive genetic ( $r_g$ ) and moderate phenotypic ( $r_p$ ) correlation estimates between ADG and MBW were found ( $r_g = 0.86$ ;  $r_p = 0.51$ ). Further, moderate to strong positive correlation estimates were found between DMI and ADG and between DMI and MBW ( $r_g = 0.56$  and  $0.71$ , respectively;  $r_p = 0.64$  and  $0.72$ , respectively). The genetic and phenotypic correlation estimates between RFI and DMI were strong and positive and were quite similar ( $r_g = 0.66$ ;  $r_p = 0.61$ ). These correlations for RFI with DMI are quite similar to those reported in swine ( $r_g = 0.52$ ;  $r_p = 0.61$ ; Cai et al., 2008). As expected, no phenotypic correlation existed between RFI and ADG or between RFI and MBW, thus demonstrating the desired phenotypic independence. As shown by Kennedy et al. (1993), some genetic correlation still existed between RFI and ADG ( $-0.15$ ), but little correlation existed between RFI and MBW ( $-0.02$ ). Conversely, G:F was correlated with the component trait ADG ( $r_g = 0.31$ ;  $r_p = 0.51$ ). The genetic correlation between RFI and G:F was very strong and negative ( $-0.92$ ), and the phenotypic correlation between these 2 measures was also quite strong ( $-0.67$ ) and was not surprising. Crowley et al. (2010) reported less strong relationships between RFI and feed conversion ratio (the inverse of our G:F); in their Irish bull data, the genetic correlation estimate was 0.48, and the phenotypic correlation was 0.41.

Kennedy et al. (1993) demonstrated that RFI is equivalent to a selection index. The equivalent index for these data are  $I_1 = \text{DMI}_{140} - (0.338)\text{SUMWT}^{0.75} - (1.750)\text{GAIN}_{140}$ . Development of a restricted index, based on genotypic regression such that there is no genetic relationship with component output trait (GAIN; Kennedy et al., 1993), yields  $I_2 = \text{DMI}_{140} - (0.542)\text{SUMWT}^{0.75} + (0.539)\text{GAIN}_{140}$ . Expected responses in DMI and GAIN, given selection on these measures of RFI, were compared with expected responses following selection on single traits of GAIN or DMI along with

indexes constructed based on a simple economic model and definition of overall net merit breeding value. Using relative economic weights (\$/kg; 2005 to 2009 average for US beef production, [http://www.nass.usda.gov/QuickStats/Create\\_Federal\\_All.jsp](http://www.nass.usda.gov/QuickStats/Create_Federal_All.jsp)) of  $-0.134$ , 2.65, and 2.04 for DMI (corn),  $\text{BW}_0$  (feeder calves), and  $\text{BW}_{140}$  (slaughter cattle), respectively, and basing the phenotypic data part of the index on only DMI,  $\text{SUMWT}^{0.75}$ , and  $\text{GAIN}_{140}$  (i.e., the same component traits as RFI), one arrives at an index of  $I_3 = \text{DMI}_{140} - (0.039)\text{SUMWT}^{0.75} - (7.531)\text{GAIN}_{140}$ , with selection in the down direction, as with the 2 RFI indexes, and selection to decrease DMI. The other economic index was constructed to evaluate selection on a phenotypic index of RFI and  $\text{GAIN}_{140}$ , again to predict the overall breeding value definition based on DMI,  $\text{BW}_0$ , and  $\text{BW}_{140}$ , as before. This index was  $I_4 = \text{RFI} - (12.2)\text{GAIN}_{140}$ , again with selection for lower index values.

Predicted responses per generation from selection in kilograms per unit of intensity ( $i$ ) for  $\text{DMI}_{140}$  and  $\text{GAIN}_{140}$  are shown in Table 5. These expected responses could be used to evaluate relative strengths and weaknesses if selection were to be practiced on any of the different criteria within the comparison of the RFI predictors and the single-trait scenarios of selection. Comparison of the 2 economic indexes ( $I_3$  and  $I_4$ ) was evaluated separately because the use of economic weightings changes the definition of breeding values.

As expected, selection solely to reduce  $\text{DMI}_{140}$  produced the greatest reduction in this input cost, but because of a negative genetic correlation estimate with  $\text{GAIN}_{140}$ , BW gain was also reduced, which would be an undesirable economic result. Likewise, selection solely to increase  $\text{GAIN}_{140}$  would be predicted to result in the greatest increase in  $\text{GAIN}_{140}$ , but again because of the correlation,  $\text{DMI}_{140}$  would also increase, and with it the corresponding cost of production. A comparison of the expected selection responses using the phenotypic index ( $I_1$ ) to the genetic index ( $I_2$ ) of RFI showed that these 2 indexes gave similar results because the genetic correlation between RFI and ADG was near zero

**Table 5.** Predicted responses per generation in  $\text{DMI}_{140}$  and total BW gain for 140 d ( $\text{GAIN}_{140}$ ) following various selection criteria

Selection criterion <sup>1</sup>	Direction	Response, kg/units of intensity	
		$\text{DMI}_{140}$	$\text{GAIN}_{140}$
$\text{DMI}_{140}$	Down	-56.7	-5.4
$\text{GAIN}_{140}$	Up	+26.3	+7.5
G:F	Up	-27.5	+2.4
$I_1$	Down	-44.6	+1.9
$I_2$	Down	-38.5	0
$I_3$	Down	-12.4	+5.4
$I_4$	Down	0	+7.7

<sup>1</sup> $I_1 = \text{DMI} - (0.338)\text{SUMWT}^{0.75} - (1.750)\text{GAIN}$ , the phenotypic index of residual feed intake (RFI), where  $\text{SUMWT}^{0.75}$  = sum of BW to the 0.75 power, initial to final (140-d) BW.  $I_2 = \text{DMI} - (0.542)\text{SUMWT}^{0.75} + (0.539)\text{GAIN}$ , the RFI index genetically independent of GAIN.  $I_3 = \text{DMI} - (0.039)\text{SUMWT}^{0.75} - (7.531)\text{GAIN}_{140}$ ; index based on an economic definition of overall breeding value including DMI, initial BW, and final BW.  $I_4 = \text{RFI} - (12.2)\text{GAIN}_{140}$ ; index based on an economic definition of overall breeding value include DMI, initial BW, and final BW.

(−0.15). Perhaps the most balanced predicted selection outcome among the RFI measures and the single traits was that for G:F. Selection on this measure of efficiency had desirable outcomes in DMI and GAIN.

As might be expected, the genotypic index ( $I_2$ ) for RFI appeared to be quite sensitive to the value of the genetic correlation (+0.86) between  $SUMWT^{0.75}$  and  $GAIN_{140}$  that was assumed. Looking at a predicted response with the phenotypic RFI index ( $I_1$ ) of −44.6 kg/i for  $DMI_{140}$  with a +1.9 kg/i for  $GAIN_{140}$  seemed strange when the corresponding predicted response was −38.5 kg/i for  $DMI_{140}$  while holding  $GAIN_{140}$  to no change. The biological implication of reducing feed intake while achieving a little more output with one index compared with the other is a challenge to accept. However, if one changes the genetic correlation between these 2 traits used in the index to +0.73 (increasing the point estimate by the SE), then the genotypic index ( $I_2$ ) becomes  $I = DMI_{140} - (0.418)SUMWT^{0.75} - (0.823)GAIN_{140}$ , thus changing the sign from positive to negative on  $GAIN_{140}$ , and the predicted response in  $DMI_{140}$  becomes −41.1 kg/i, which is closer to that found with the phenotypic index.

Comparison of the 2 economically derived indexes revealed interesting results. The index ( $I_3$  in Table 5) based on the same phenotypic values used in predicting RFI had predicted responses of increased  $GAIN_{140}$  and decreased  $DMI_{140}$ . The index ( $I_4$ ) predicting the same overall net merit breeding value but composed of RFI and  $GAIN_{140}$  had expected results of no change in  $DMI_{140}$  but an even larger increase in  $GAIN_{140}$ . This would be expected. Some decrease in intake could be achieved by decreasing daily costs of maintenance, but increasing BW gain also had a positive energy intake cost. Greater feed costs relative to cattle sale values would, of course, put more emphasis on reducing feed intake relative to increasing cattle growth rate and vice versa.

Flight speed had a moderate estimate of heritability (0.34). Despite this, estimates of both genetic and phenotypic correlations of DMI and RFI with FS were small and negative ( $r_g = -0.14$  and  $-0.07$ ;  $r_p = -0.22$  and  $-0.09$ ), and those of G:F with FS ( $r_g = +0.18$ ;  $r_p = +0.19$ ) were low and positive. In a preliminary analysis of the first 4 yr of the data, permanent environmental variance was found to be almost as great as the additive genetic variance. The estimate of repeatability in this smaller set of data was moderate to high, at 0.63. With this level of repeatability, multiple measures of flight speed did not appear to be necessary to characterize an animal for this trait. Flight speed may be an acceptable measure of temperament in cattle, but in this set of data, it was not an accurate indicator trait for feed intake and efficiency.

Burrow et al. (1988) reported heritability estimates for FS ranging from 0.26 to 0.54, which agreed with the estimate in the present study; the heritability estimate of Nkrumah et al. (2007) of 0.49 was greater. Estimates of repeatability have ranged to a wider degree, from a

high of 0.88 (Burrow et al., 1988) down to 0.18 (Burrow, 2001); differences in age at measurement and in management systems have been possible factors used to explain this wide range. The flight time and flight distance heritability estimates by Halloway and Johnston (2001) and Matsunaga et al. (2002) were less, at 0.08 and 0.13, respectively. Le Neindre et al. (1995) found a docility score and docility criterion to have low heritability, at 0.18 and 0.22, respectively. In their study of temperament, measured during and after a restraint (chute score and exit velocity), and feed measures, Elzo et al. (2009) found no relationship between chute score and daily feed intake, RFI, or feed conversion ratio, whereas exit velocity had an effect only on daily feed intake.

In general, breed differences were small; nevertheless, some breed effects were detected. Relative to Angus, the Limousin breed effect was greater for ADG ( $P < 0.05$ ) and also gave a greater effect for G:F ( $P < 0.01$ ), indicating that this breed contributed toward greater efficiency. The Simmental breed effect contributed to steers that were heavier ( $P < 0.10$ ) midtest. The Charolais breed effect influenced steers to consume less feed throughout the trial ( $P < 0.05$ ), and thus also contributed to a smaller, more favorable RFI ( $P < 0.01$ ). Finally, the Gelbvieh breed effect produced faster FS ( $P < 0.01$ ) and perhaps more excitable steers. Breed heterozygosity, and thus heterosis, contributed to greater DMI ( $P < 0.01$ ), RFI ( $P < 0.05$ ), and MBW ( $P < 0.05$ ), but it was not an important source of variation affecting ADG, G:F, or FS. It was surprising that significant evidence was not found for heterosis affecting growth rate.

In comparisons of bulls of the Angus, Charolais, Hereford, Limousin, and Simmental breeds in the Irish national test, Crowley et al. (2010) found that Limousin had less DMI and that Limousin and Charolais were the most efficient (RFI and feed conversion ratio) breeds, whereas Angus exhibited the poorest measures of feed efficiency. Charolais-, Limousin-, and Hereford-sired calves were more efficient (more negative RFI) than those from Angus sires in an Australian study reported by Moore et al. (2005). Elzo et al. (2009), analyzing data on Angus, Brahman, and Angus-Brahman crossbred bulls, steers, and heifers, noted that RFI decreased as the fraction of Brahman in the animal increased; conversely, feed conversion ratio increased as the fraction of Brahman increased. Heterosis in the cross of Angus and Brahman was positive for daily feed intake and RFI; thus, intake was greater and efficiency was poorer for crossbred animals. Moore et al. (2005) also reported that Brahman-sired calves had better efficiency (more negative RFI) than those sired by Angus.

In conclusion, feed intake, and thus feed costs, can be reduced through selection. Given that BW gain and feed intake are positively correlated, selection that places positive emphasis on growth in addition to negative emphasis on feed intake is the most promising to yield economic results. An index composed of GAIN

and RFI gave the best economic outcome. In growing steers of the age and BW range studied here, no advantage was found for explaining feed intake variation by adjusting for body fatness. Even though heritability was moderate for our measure of temperament (FS), it was not helpful as an indicator of feed intake. Finally, and perhaps most surprising, neither breed differences nor heterosis was a large source of variation in growth and feed intake in this data set.

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