Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle

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ABSTRACT: Feed costs are a major economic expense in finishing and developing cattle; however, collection of feed intake data is costly. Examining relationships among measures of growth and intake, including breed differences, could facilitate selection for efficient cattle. Objectives of this study were to estimate genetic parameters for growth and intake traits and compare indices for feed efficiency to accelerate selection response. On-test ADFI and on-test ADG (TESTADG) and postweaning ADG (PWADG) records for 5,606 finishing steers and growing heifers were collected at the U.S. Meat Animal Research Center in Clay Center, NE. On-test ADFI and ADG data were recorded over testing periods that ranged from 62 to 148 d. Individual quadratic regressions were fitted for BW on time, and TESTADG was predicted from the resulting equations. We included PWADG in the model to improve estimates of growth and intake parameters; PWADG was derived by dividing gain from weaning weight to yearling weight by the number of days between the weights. Genetic parameters were estimated using multiple-trait REML animal models with TESTADG, ADFI, and PWADG for both sexes as dependent variables. Fixed contemporary groups were cohorts of calves simultaneously tested, and covariates included age on test, age of dam, direct and maternal heterosis, and breed composition. Genetic correlations (SE) between steer TESTADG and ADFI, PWADG and ADFI, and TESTADG and PWADG were 0.33 (0.10), 0.59 (0.06), and 0.50 (0.09), respectively, and corresponding estimates for heifers were 0.66 (0.073), 0.77 (0.05), and 0.88 (0.05), respectively. Indices combining EBV for ADFI with EBV for ADG were developed and evaluated. Greater improvement in feed efficiency can be expected using an unrestricted index versus a restricted index. Heterosis significantly affected each trait contributing to greater ADFI and TESTADG. Breed additive effects were estimated for ADFI, TESTADG, and the efficiency indices.

Key words: beef cattle, breed differences, selection index

INTRODUCTION

Feed costs represent greater than two-thirds of the cost of production in the U.S. beef industry (Anderson et al., 2005). Weight gain and feed intake (DMI) data combined allow for maximum genetic progress for feed efficiency. Derived phenotypes such as residual feed intake, feed conversion ratio, and residual ADG (Koch et al., 1963; Archer et al., 1997; MacNeil et al., 2011) and, more efficiently, selection indices (Hazel and Lush, 1943; Lin, 1980; Gunsett, 1984) have been proposed as selection criteria. Because collecting individual feed intake data is expensive, estimates of breed differences for intake and gain could provide a tool for producers to increase feed efficiency.

One of the primary objectives of the Germplasm Evaluation Program (**GPE**) at the U.S. Meat Animal Research Center (**USMARC**) is to evaluate breed differences by sampling highly relevant sires from prominent breeds in the United States. Breed differences for a novel phenotypic trait complex such as feed intake and corresponding gain are especially relevant to decision-making in commercial cattle operations.

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The objectives of this study were to estimate the genetic parameters for on-test ADFI and on-test ADG (**TESTADG**) along with postweaning ADG (**PWADG**), determine correlations among these traits, derive indices to select for feed efficiency, and estimate breed additive effects and general heterosis for ADFI, TESTADG, and indices. These parameters will help producers make profitable decisions relative to breed selection.

MATERIALS AND METHODS

Animal Populations and Management

Data on 5,606 growing steers and heifers were collected at the USMARC, Clay Center, NE, on cattle born from 2003 to 2012. Animal procedures were approved by the Institutional Animal Care and Use Committee at the USMARC in accordance with Federation of Animal Science Societies (FASS, 2010) guidelines.

A previous study by Rolfe et al. (2011) used a portion of this population to explore the genetic and phenotypic parameter estimates for steer feed intake and growth and the opportunity to select on these traits. These calves, born from 2003 to 2007, were included as observations in the current study to improve estimation of variance components. Briefly, animals born from 2003 to 2007 were designated as F_1^2 progeny. The $F_1 2$ calves were produced with matings established through the USMARC GPE. In Cycle VII of the GPE, the F_1 animals were produced. Cycle VII comprised Angus, Hereford, and composite MARC III (one-fourth Angus, one-fourth Hereford, one-fourth Pinzgauer, and one-fourth Red Poll) cows mated by AI to purebred Angus, Hereford, Red Angus, Charolais, Gelbvieh, Simmental, and Limousin sires to produce F_1 progeny. The F_1 females born in 1999, 2000, and 2001 along with 2001 F_1 males were kept for breeding. These animals were mated in multiple-sire pastures to produce 2-, 3-, and 4-breed cross descendants, which are referred to as F_1^2 progeny.

More recent GPE generations from fall 2007 through 2012 were produced from continuous sampling from 7 of the breeds involved in Cycle VII and several additional breeds (Beefmaster, Braunvieh, Brahman, Brangus, Chiangus, Maine-Anjou, Salers, Santa Gertrudis, Shorthorn, South Devon, and Tarentaise). Purebred AI sires were mated to purebred or crossbred dams (most from previous GPE cycles) resulting in purebred and crossbred steers and heifers. All sires included in the GPE were introduced through AI. Sampled sires had high accuracy EPD, based on Beef Improvement Federation (2010) guidelines, and represented sires heavily used in the U.S. beef industry, based on breed association registration records. Progeny from AI sires were preferentially assigned to groups for feed intake data collection.

Only records from spring-born steer calves were collected in 2003 and 2004. Records from both spring-born steers and heifers were included for 2005 and 2006. From 2007 on, both spring- and fall-born steers and heifers were evaluated. Male calves were castrated within 24 h of birth. Calves born from 2003 to 2007 were weaned at approximately 165 d of age, whereas calves from subsequent years were weaned at approximately 150 d of age. Age at weaning varied among years due to differing environmental conditions. Once weaned, heifers received a low-concentrate, high-forage diet appropriate for developing breeding heifers. Steers were managed and fed for harvest using a high-concentrate finishing diet.

Data Collection and Editing

Individual feed intake records on F_1^2 calves, born from 2003 to 2007 as described in Rolfe et al. (2011), were acquired using the Calan Broadbent Feeding Systems (American Calan Broadbent, Northwood, NH). Animals were trained on step-up diets and then placed in pens equipped with Calan gates in groups of 4 or 8 animals. Animals were fed at 0800 h and given ad libitum access to feed. Feed refusals were collected once per week. For calves born from 2008 to 2012, feed intake records were collected using an Insentec system (Insentec B.V., Marknesse, The Netherlands). Dry matter intake records were collected for the entire feeding period, ranging from a minimum of 62 d to a maximum of 148 d. On-test ADFI was calculated by dividing total DMI for the period by the number of test days. Individual quadratic regressions were fitted for BW on time using all weights collected from the beginning to the end of the test period to predict final and initial test BW. The TESTADG was then derived as predicted final BW minus predicted initial BW divided by days on trial. Individual weaning and yearling BW were adjusted to a common age and age of dam. The number of weights collected varied by test year, with a minimum of 2 intermediate weights taken each year. The PWADG was calculated by dividing gain from weaning weight to yearling weight by the number of days between the weights; this trait was added to the analysis to increase our ability to accurately estimate genetic relationships between intake and gain measures. No quadratic regression was fitted for PWADG to predict weaning and yearling weight because postweaning gain is derived from only weaning weight and yearling weight in standard genetic evaluations for U.S. cattle breeds.

Data were edited by examining trends of on-test weights and instances of disease to remove any aberrant records. A 4-generation pedigree containing 9,211 animals was used for data analysis. Animals with an unknown sire or dam were removed from the data set. Breed origins of 27 different breed groups were fitted as

covariates (equivalent to genetic groups) in subsequent models. There were 18 different AI breed groups and 9 commercial dam breeds including Angus, Hereford, Simmental, Charolais, Red Angus × Simmental composite, Bonsmarra, Romosinuano, and MARC II and MARC III composite populations. Two separate contemporary groups for on-test data (TESTADG and ADFI) and PWADG were defined based on Beef Improvement Federation (2010) guidelines. The on-test contemporary group was defined by birth location, on-test date, off-test date, and feeding management code. The PWADG contemporary group was defined as birth location, year–season, weaning date, and yearling weight date.

Statistical Analysis

Genetic and phenotypic covariances and heritabilities were estimated using REML procedures of ASReml (version 4.0; VSN International, Ltd., Hemel Hempstead, UK). Data were analyzed using multiple-trait animal models with contemporary groups fitted as fixed effects; age on test, age of dam, percent direct heterosis (fraction of breed heterozygosity to account for expected heterosis), percent maternal heterosis, and percentage of each breed were fitted as covariates in the models. Random effects were additive direct genetic effects and the residual.

Sexes (heifers or steers) were modeled separately to estimate sex-specific covariances. A 6-trait animal model was derived to include all 3 traits (ADFI, TESTADG, and PWADG) from both sexes. Starting values for the multiple trait model were determined from simpler models. Random, fixed, and covariate effects for the multiple trait model were identical to those involved in the simpler animal models. The mixed model equation was

$$
\begin{bmatrix} \mathbf{Y}_1 \\ \mathbf{Y}_2 \\ \mathbf{Y}_3 \\ \mathbf{Y}_4 \\ \mathbf{Y}_5 \\ \mathbf{Y}_6 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1\boldsymbol{\beta}_1 \\ \mathbf{X}_2\boldsymbol{\beta}_2 \\ \mathbf{X}_3\boldsymbol{\beta}_3 \\ \mathbf{X}_4\boldsymbol{\beta}_4 \\ \mathbf{X}_5\boldsymbol{\beta}_5 \\ \mathbf{X}_6\boldsymbol{\beta}_6 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1\mathbf{u}_1 \\ \mathbf{Z}_2\mathbf{u}_2 \\ \mathbf{Z}_3\mathbf{u}_3 \\ \mathbf{Z}_4\mathbf{u}_4 \\ \mathbf{Z}_5\mathbf{u}_5 \\ \mathbf{Z}_6\mathbf{u}_6 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \\ \mathbf{e}_4 \\ \mathbf{e}_5 \\ \mathbf{e}_6 \end{bmatrix},
$$

in which $\mathbf{Y}_i$ was the vector of observations for each trait ($i = 1$ through 6: steer ADFI, steer TESTADG, steer PWADG, heifer ADFI, heifer TESTADG, and heifer PWADG, respectively), $\mathbf{X}i$ was the incidence matrix relating observations to the levels of fixed effects, $\boldsymbol{\beta}i$ was the vector of fixed effects (including breed covariates), $\mathbf{Z}i$ was an incidence matrix relating observations to additive genetic effects, $\mathbf{u}i$ was the vector of random additive genetic effects, and $\mathbf{e}i$ was the vector of random residuals.

Variance assumptions for the random effects of the multiple trait model were

$$
\mathrm{var}\begin{pmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{u}_3 \\ \mathbf{u}_4 \\ \mathbf{u}_5 \\ \mathbf{u}_6 \end{pmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{u1}^2 & \mathbf{A}\sigma_{u12} & \mathbf{A}\sigma_{u13} & \mathbf{A}\sigma_{u14} & \mathbf{A}\sigma_{u15} & \mathbf{A}\sigma_{u16} \\ \mathbf{A}\sigma_{u12} & \mathbf{A}\sigma_{u2}^2 & \mathbf{A}\sigma_{u23} & \mathbf{A}\sigma_{u24} & \mathbf{A}\sigma_{u25} & \mathbf{A}\sigma_{u26} \\ \mathbf{A}\sigma_{u13} & \mathbf{A}\sigma_{u23} & \mathbf{A}\sigma_{u3}^2 & \mathbf{A}\sigma_{u34} & \mathbf{A}\sigma_{u35} & \mathbf{A}\sigma_{u36} \\ \mathbf{A}\sigma_{u14} & \mathbf{A}\sigma_{u24} & \mathbf{A}\sigma_{u34} & \mathbf{A}\sigma_{u4}^2 & \mathbf{A}\sigma_{u45} & \mathbf{A}\sigma_{u46} \\ \mathbf{A}\sigma_{u15} & \mathbf{A}\sigma_{u25} & \mathbf{A}\sigma_{u35} & \mathbf{A}\sigma_{u45} & \mathbf{A}\sigma_{u5}^2 & \mathbf{A}\sigma_{u56} \\ \mathbf{A}\sigma_{u16} & \mathbf{A}\sigma_{u26} & \mathbf{A}\sigma_{u36} & \mathbf{A}\sigma_{u46} & \mathbf{A}\sigma_{u56} & \mathbf{A}\sigma_{u6}^2 \end{bmatrix}
$$

and

$$
\mathrm{var}\begin{pmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \\ \mathbf{e}_4 \\ \mathbf{e}_5 \\ \mathbf{e}_6 \end{pmatrix} = \begin{bmatrix} \mathbf{I}\sigma_{e1}^2 & \mathbf{I}\sigma_{e12} & \mathbf{I}\sigma_{e13} & 0 & 0 & 0 \\ \mathbf{I}\sigma_{e12} & \mathbf{I}\sigma_{e2}^2 & \mathbf{I}\sigma_{e23} & 0 & 0 & 0 \\ \mathbf{I}\sigma_{e13} & \mathbf{I}\sigma_{e23} & \mathbf{I}\sigma_{e3}^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_{e4}^2 & \mathbf{I}\sigma_{e45} & \mathbf{I}\sigma_{e46} \\ 0 & 0 & 0 & \mathbf{I}\sigma_{e45} & \mathbf{I}\sigma_{e5}^2 & \mathbf{I}\sigma_{e56} \\ 0 & 0 & 0 & \mathbf{I}\sigma_{e46} & \mathbf{I}\sigma_{e56} & \mathbf{I}\sigma_{e6}^2 \end{bmatrix},
$$

in which $\mathbf{A}$ was the numerator relationship matrix of all animals in the pedigree, including those without records. Matrix $\mathbf{I}$ was the identity matrix of appropriate dimension. Error covariances between steer and heifer traits were fixed at 0 because no animal had records for those combinations of traits.

Feed Efficiency Indices

Alternative indices combining EBV for ADFI and TESTADG were evaluated. Two separate types of selection indices were compared: 1) an unrestricted selection index where weighting factors were applied to both component traits (TESTADG and ADFI) and 2) a restricted selection index where the change in ADFI was held constant, which mimics a genetic residual gain phenotype in a linear index form. Heritability estimates for both the restricted and unrestricted indices were determined by the following:

$$h^2 = (\mathbf{c}'\mathbf{G}\mathbf{c})/(\mathbf{c}'\mathbf{P}\mathbf{c}),$$

in which $\mathbf{c}$ was the contrast vector for the index, $\mathbf{G}$ was the estimated genetic variance and covariance matrix, and $\mathbf{P}$ was the estimated phenotypic variance and covariance matrix.

For the calculation of the unrestricted index, the weighting of gain was arbitrarily set to 1.0 and the weighting for ADFI was the negative of the average of the intra-contemporary group ratio of mean PWG or ADG divided by mean ADFI, as described by Lin (1980). This index is meant to rank the genetic potential of animals similarly to a G:F; therefore, rankings of animals and breed differences with this index reflect a measure of feed efficiency and where both gain and

intake may increase. Means of ADG and ADFI of the 41 steer and 39 heifer feed efficiency contemporary groups were calculated. For the calculation of the restricted index, the weight of ADG was again set to 1 and the coefficient placed on ADFI was the negative of the genetic covariance of gain and intake divided by the variance of gain (similar to Kennedy et al. [1993] with residual feed intake by genetic regression; MacNeil et al., 2011). Pearson and Spearman rank correlations were used to compare rankings by the alternative indices.

Breed Differences

Breed differences for ADFI and TEST ADG were derived as covariate solutions estimating breed effects for the 18 AI sire breeds as deviations from Angus. Indices of efficiency were similarly expressed.

RESULTS AND DISCUSSION

Descriptive statistics are provided in Table 1. The data set contained a greater number of observations from steers than from heifers. By design, steers were fed a more energy dense ration and had greater mean ADFI and TESTADG than heifers.

Variance components for ADFI, TESTADG, and PWADG are presented in Table 2. All residual covariances between steer and heifer traits were 0. Heritability estimates along with genetic correlations are presented in Table 3. Heritability estimates of both TESTADG and ADFI were moderate, and the genetic correlation between them was less than unity. Therefore, the genetic antagonism between them can be broken and genetic improvement of feed efficiency is feasible with simultaneous selection for increased gain and decreased intake. On-test ADFI, TESTADG, and PWADG for both steers and heifers were moderately to highly heritable, similar to estimates reported in previous literature. Rolfe et al. (2011) found slightly greater heritability estimate (0.26) for TESTADG when the test period was adjusted to 140 d for a subset of the steer data (steers born from 2003 to 2007) in the current analysis. Nkrumah et al. (2007) reported ADG heritability estimates in a population of Angus, Charolais, and Alberta hybrid bulls of 0.59, whereas Arthur et al. (2001) reported heritability estimates of 0.28 for ADG in a population of Angus bulls and heifers on a 70-d test. In a mixed population of Angus, Hereford, and Shorthorn cattle, heritability estimates were maximized with a 70-d test ($h^2 = 0.35$; Archer et al., 1997).

Genetic correlations among traits within sex were positive. Only moderate correlations between TESTADG and PWADG were observed in the steer population. Strong correlations between TESTADG and PWADG in heifers suggested PWADG may be a viable substi-

Table 1. Descriptive statistics for steer and heifer on-test ADFI, on-test ADG (TESTADG) and postweaning ADG (PWADG) in crossbred beef cattle

Trait	Number	Mean, kg	Maximum	Minimum	SD
Steer ADFI	3,212	9.45	17.26	1.63	1.167
Steer TESTADG	3,212	1.64	2.45	−0.35	0.241
Steer PWADG	3,211	1.53	2.34	0.70	0.176
Heifer ADFI	2,394	7.75	12.94	1.72	1.032
Heifer TESTADG	2,394	0.96	1.77	0.07	0.176
Heifer PWADG	2,392	0.97	1.65	0.15	0.145

tute for TESTADG when evaluating feed efficiency for females or could supplement TESTADG data when test periods are shortened. If PWADG was used as an alternative measure for TESTADG to predict feed efficiency, it could allow for a shorter 35-d intake test as supported by previous studies (Archer et al., 1997; Wang et al., 2006). Based on the relationship between PWADG and TESTADG, particularly for heifers on a roughage diet, test lengths could be shortened to optimize intake measurement although further investigation is needed. Shorter testing periods would allow for more animals to be tested with the limited number of feed intake systems currently available in the United States. The increase in animals tested for feed intake will increase the potential selection intensity for greater genetic improvement. An increase in feed efficiency phenotype collection would increase the accuracy of genomic predictions for feed intake by increasing the amount of training data. The lower correlation between PWADG and TESTADG in steers on concentrate diets would indicate that shorter testing periods may result in reranking of animals.

Genetic correlations among traits between steers and heifers were estimable through pedigree relationships. Genetic correlations between steers and heifers were relatively high (0.77 and 0.92) for ADFI and PWADG, respectively. These high correlations suggest that heifer and steer ADFI and especially PWADG may nearly be thought of as the same genetic trait. In National Cattle Evaluation, PWADG is often analyzed as the same trait on heifers and bulls with contemporary group adjustments accounting for the difference in phenotypic means. The correlation between sexes for TESTADG is less. Although the reason for this lower correlation is unknown, it may be related to the amount of time the animals were fed a high-energy diet vs. a forage diet. The diet also likely accounts for the difference in the correlation between TESTADG and PWADG in steers relative to heifers, as the steers had greater TESTADG than the heifers.

Index equations used to combine weighting factors and EBV were as follows for steers and heifers, respectively, under the unrestricted index:

Table 2. Genetic variances (on the diagonal, with SE below), genetic covariances (below the diagonal, with SE below), and residual covariances (above the diagonal, with SE below) for steer and heifer on-test ADFI, on-test ADG (TESTADG), and postweaning ADG (PWADG)[1]

Trait	Steer ADFI	Steer TESTADG	Steer PWADG	Heifer ADFI	Heifer TESTADG	Heifer PWADG
Steer ADFI	0.586 (0.077)	0.135 (0.010)	0.087 (0.008)			
Steer TESTADG	0.029 (0.011)	0.013 (0.003)	0.015 (0.001)			
Steer PWADG	0.048 (0.009)	0.006 (0.002)	0.011 (0.002)			
Heifer ADFI	0.373 (0.048)	0.037 (0.009)	0.048 (0.007)	0.405 (0.058)	0.058 (0.007)	0.045 (0.006)
Heifer TESTADG	0.029 (0.008)	0.006 (0.001)	0.008 (0.001)	0.040 (0.008)	0.009 (0.002)	0.008 (0.001)
Heifer PWADG	0.035 (0.007)	0.005 (0.001)	0.009 (0.001)	0.046 (0.007)	0.008 (0.001)	0.009 (0.001)

[1]Units are g^2 for variances or g × g for covariances.

$$H_{\text{ADG, ADFI}} = \text{EBV}_{\text{TESTADG}} + (-0.17)\text{EBV}_{\text{ADFI}},$$

and

$$H_{\text{ADG, ADFI}} = \text{EBV}_{\text{TESTADG}} + (-0.12)\text{EBV}_{\text{ADFI}},$$

in which **H** the aggregate genotype.

For the restricted indices, the resulting equations for steers and heifers, respectively, were as follows:

$$H_{\text{ADG, ADFI}} = \text{EBV}_{\text{TESTADG}} + (-0.05)\text{EBV}_{\text{ADFI}},$$

and

$$H_{\text{ADG, ADFI}} = \text{EBV}_{\text{TESTADG}} + (-0.10)\text{EBV}_{\text{ADFI}}.$$

Results from the index correlation analysis differed between steers and heifers and between the unrestricted and restricted selection indices. Correlations between EBV used in unrestricted and restricted indices were 0.77 (Pearson) and 0.75 (Spearman) in steers and were 0.89 (Pearson) and 0.88 (Spearman) in heifers. This result implies that selection based on EBV used in the unrestricted index will often select the same cattle as those selected using the intake restricted index, particularly with heifers are fed a roughage diet. The higher heifer correlations are not surprising given that the coefficients on ADFI EBV were similar between the unrestricted and restricted indices. These similar coefficients between the unrestricted and restricted indices suggest that intake will not increase as greatly under a roughage diet relative to the concentrate (steer) diet. As the restricted index is expected to rank animals according to their feed conversion (Lin, 1980), in general, one would expect that the unrestricted index is more optimal, at least from a biological perspective. Economic efficiencies of the indices will depend on relative cost of feed versus increased cattle weight. Further optimization of indices are certainly possible using TESTADG and ADFI as components. As stated by Kennedy et al. (1993), all

Table 3. Heritability estimates (on the diagonal, with SE below), genetic correlations (below the diagonal, with SE below), and residual correlations (above the diagonal, with SE below) for steer and heifer on-test ADFI, on-test ADG (TESTADG), and postweaning ADG (PWADG)

Trait	Steer ADFI	Steer TESTADG	Steer PWADG	Heifer ADFI	Heifer TESTADG	Heifer PWADG
Steer ADFI	0.43 (0.05)	0.72 (0.03)	0.70 (0.03)			
Steer TESTADG	0.34 (0.10)	0.22 (0.05)	0.49 (0.03)			
Steer PWADG	0.59 (0.06)	0.50 (0.09)	0.36 (0.05)			
Heifer ADFI	0.77 (0.08)	0.52 (0.12)	0.70 (0.09)	0.38 (0.05)	0.48 (0.04)	0.50 (0.04)
Heifer TESTADG	0.40 (0.10)	0.54 (0.13)	0.81 (0.10)	0.66 (0.07)	0.29 (0.05)	0.49 (0.04)
Heifer PWADG	0.49 (0.09)	0.42 (0.12)	0.92 (0.07)	0.77 (0.05)	0.88 (0.05)	0.42 (0.05)

Table 4. Across-breed comparisons in grams (SE) of on-test ADFI and on-test ADG (TESTADG) for steers and heifers of 18 AI sire breeds relative to Angus[+]

Breed	Steer ADFI, g	Steer TESTADG, g	Heifer ADFI, g	Heifer TESTADG, g
Angus	0	0	0	0
Hereford	**−788 (286)**	−35 (55)	**−962 (266)**	−21 (44)
Red Angus	−310 (275)	−66 (52)	**−684 (255)**	**−86 (42)**
Shorthorn	**−997 (320)**	−100 (61)	**−1,021 (298)**	**−98 (49)**
South Devon	−1,856 (666)	**−274 (134)**	**−1,576 (641)**	13 (109)
Beefmaster	**−771 (346)**	72 (68)	**−1,556 (334)**	−91 (56)
Brahman	**−1,321 (350)**	−124 (68)	**−1,351 (319)**	**−185 (53)**
Brangus	−173 (335)	−31 (65)	−585 (317)	**−120 (53)**
Santa Gertrudis	−569 (334)	22 (63)	**−1,039 (306)**	**−113 (50)**
Braunvieh	**−1,488 (351)**	**−180 (68)**	**−1,841 (305)**	**−299 (50)**
Charolais	−521 (289)	−18 (55)	**−876 (270)**	−75 (45)
Chiangus	**−1,245 (334)**	−81 (64)	**−1,049 (296)**	**−118 (49)**
Gelbvieh	**−1,051 (278)**	−72 (53)	**−723 (253)**	**−114 (42)**
Limousin	**−1,238 (281)**	−5 (53)	**−1,471 (255)**	**−160 (42)**
Maine Anjou	**−1,646 (334)**	**−150 (64)**	**−1,101 (302)**	**−102 (50)**
Salers	**−1,211 (333)**	**−136 (63)**	**−1,176 (306)**	**−139 (51)**
Simmental	−43 (288)	−19 (55)	−530 (275)	−68 (45)
Tarentaise	−1,178 (678)	−150 (136)	**−1,926 (566)**	**−312 (96)**

[1]Significant breed differences ($P < 0.05$) are bold.

genetic and phenotypic properties of any resulting index (including residual gain or feed intake) are derivable under standard assumptions of linearity of regression.

Breed differences with SE are given in Table 4 with across-breed comparisons and SE represented for 18 AI sired breeds relative to Angus. Breed differences were seen among the 18 AI sired breeds and were statistically significant (17 df test; $P < 0.05$) for both steers and heifers for ADFI and TESTADG. The Angus breed effect for both steers and heifers was greater for ADFI when compared with the other 17 breeds involved, suggesting Angus may have the largest appetite. Similarly, relative to the other breeds for steer TESTADG, Angus, Beefmaster, Santa Gertrudis, Limousin and Simmental breed effects were largest. For TESTADG, the South Devon breed effect was largest in heifers and smallest in steers. It is of note that the South Devon solution (and Tarentaise) had very large SE relative to the other breeds; both of these breeds were added to the GPE fairly late in the feed efficiency program. If this reversal of gain is real, it suggests that the South Devon breed gains less favorably when supplied with a high-concentrate ration than when supplied with a roughage ration. With the exception of South Devon, correlations (and thus rankings) of breed effects were fairly similar between steers and heifers, which is expected given the moderate genetic correlation between steer and heifer TESTADG.

Like the breed effects from this study, Crowley et al. (2010) compared several Irish beef breeds and showed that both Angus and Simmental cattle tended to have greater feed intakes and that Simmental and Charolais cattle had the greatest daily gains. Many populations involved in previous literature consisted of only 1 or 2 purebred breeds and possibly a 2-breed cross (Arthur et al., 2001; Nkrumah et al., 2007; Retallick et al., 2013); the current analysis evaluated 18 different breeds.

Breed differences for the feed efficiency (unrestricted) index for both steers and heifers relative to the Angus breed effects are presented in Table 5. Greater values for the unrestricted index indicate greater efficiency or G:F. For the steer unrestricted index including TESTADG with ADFI, Beefmaster and Limousin had the greatest feed efficiency among all breeds. This is similar to a previous study, involving a population of Angus, Charolais, Hereford, Limousin, and Simmental cattle, where Limousin and Charolais cattle were more efficient based on residual feed intake and feed conversion ratio (Crowley et al., 2010). For the unrestricted index in heifers, South Devon was the most feed efficient heifer breed for the unrestricted heifer index. These breed differences can be used by commercial producers to select more feed-efficient breeds for their production systems.

Both individual direct and maternal heterosis had significant impacts on growth and feed intake. In steers, individual heterosis (SE) was 426.2 (100.3) and 75.8 (21.1) g/d for ADFI and TESTADG, respectively ($P < 0.001$ for all), whereas for heifers for the same traits, heterosis was estimated at 127.5 (89.8) and 6.5 (15.5) g/d and was not significant. Maternal heterosis effects (SE) were reversed in that they were significant ($P < 0.05$) only for heifers, with effects of 359.3 (82.6) and 43.0 (14.2) for ADFI and TESTADG, respectively. These heterosis effects on ADFI echo reports in previous literature (Elzo et al., 2009; Rolfe et al., 2011), showing crossbred cattle have greater feed intake.

Conclusions

Using a combination of intake and gain data, both found to be moderately heritable, should allow for the genetic selection of feed efficiency. The correlations between steer PWADG and TESTADG were moderate and correlations between heifer PWADG and TESTADG were strong. Further research including TESTADG on shortened intervals used in conjunction with PWADG data could lead to shortened feed intake data collection standards. This study is the first of its kind to dissect breed differences in feed efficiency in such a diverse population. Breed differences for feed efficiency were observed and significant in this population, confirming variation among breeds. These observations will enable producers to select breeds or breed mating systems for their operations.

Table 5. Across-breed comparisons of efficiency (SE) evaluated using an unrestricted index of on-test ADFI and on-test ADG (TESTADG) or a restricted index where feed intake is not expected to increase with selection for TESTADG of 18 sire breeds relative to Angus with a more positive number indicating a more efficient breed[1]

Breed	Steers		Heifers	
	Unrestricted	Restricted	Unrestricted	Restricted
Angus	0.000	0.000	0.000	0.000
Hereford	0.099 (0.051)	0.004 (0.049)	**0.094 (0.037)**	**0.075 (0.036)**
Red Angus	−0.014 (0.050)	−0.051 (0.047)	−0.004 (0.035)	−0.018 (0.035)
Shorthorn	0.070 (0.057)	−0.050 (0.055)	0.025 (0.041)	0.005 (0.040)
South Devon	−0.041 (0.118)	−0.182 (0.119)	**0.203 (0.094)**	0.171 (0.092)
Beefmaster	**0.203 (0.062)**	0.110 (0.060)	**0.096 (0.047)**	0.065 (0.047)
Brahman	0.100 (0.063)	−0.058 (0.060)	−0.023 (0.045)	−0.050 (0.044)
Brangus	−0.002 (0.060)	−0.023 (0.058)	−0.049 (0.045)	−0.061 (0.044)
Santa Gertrudis	**0.119 (0.060)**	0.051 (0.057)	0.012 (0.042)	−0.009 (0.042)
Braunvieh	0.073 (0.063)	−0.105 (0.060)	−0.078 (0.042)	**−0.115 (0.042)**
Charolais	0.070 (0.052)	0.008 (0.049)	0.030 (0.037)	0.013 (0.037)
Chiangus	**0.130 (0.060)**	−0.019 (0.057)	0.008 (0.041)	−0.013 (0.040)
Gelbvieh	**0.107 (0.050)**	−0.019 (0.047)	−0.027 (0.035)	−0.042 (0.034)
Limousin	**0.206 (0.051)**	0.057 (0.048)	0.017 (0.035)	−0.013 (0.035)
Maine-Anjou	**0.130 (0.060)**	−0.067 (0.057)	0.031 (0.042)	0.009 (0.041)
Salers	0.070 (0.060)	−0.075 (0.057)	0.002 (0.042	−0.021 (0.042)
Simmental	0.027 (0.052)	0.022 (0.049)	−0.004 (0.038)	−0.015 (0.038)
Tarentaise	0.050 (0.120)	−0.091 (0.121)	−0.081 (0.081)	−0.119 (0.080)

[1]Significant breed differences ($P < 0.05$) are bold.

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