A prototype national cattle evaluation for feed intake and efficiency of Angus cattle\textsuperscript{1,2}

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ABSTRACT: Recent improvement in technologies for measuring individual feed intake has made possible the collection of data suitable for breed-wide genetic evaluation. The goals of this research were to estimate genetic parameters for components of feed efficiency and develop a prototype system for conducting a genetic evaluation of Angus cattle for feed intake. Weaning weight (WWT), postweaning BW gain (PGN), subcutaneous fat depth (SQF), and feed intake data were accumulated by the American Angus Association from a variety of cooperators and augmented with data collected for routine genetic evaluation of Angus cattle. The feed intake data were standardized (SFI, mean 0 and variance 1) within contemporary groups. Numbers of animals with observed phenotypes were 18,169, 7,107, 4,976, and 4,215 for WWT, PGN, SQF, and SFI, respectively. The 4-generation pedigree for animals with records contained 45,120 individuals. (Co) variance components were estimated with ASREML, fitting a 4-trait animal model with fixed contemporary groups for WWT, PGN, SQF, and SFI. Heritability estimates were 0.33 ± 0.03, 0.31 ± 0.04, 0.26 ± 0.04, and 0.42 ± 0.05 for direct genetic effects on WWT, PGN, SQF, and SFI, respectively. Genetic correlations of WWT and PGN with SFI were 0.40 ± 0.07 and 0.55 ± 0.10, respectively, and indicate their value as indicator traits in predicting EPD for feed intake. The genetic correlation of SQF and SFI was not different from 0. For all animals with a recorded feed intake phenotype, accuracy of their EPD for feed intake ranged from 0.16 to 0.64 with a mean of 0.26. However, 9,075 animals had an accuracy that was equal to or exceeded 0.2 for their feed intake EPD. Postanalysis calculation of measures of efficiency EPD was pursued. This work demonstrates the feasibility of conducting a national cattle evaluation for feed intake using indicator traits to reduce opportunity for selection bias, increase accuracy of the evaluation for a substantial number of animals, and ultimately facilitate calculation of selection indexes including feed intake.

Key words: beef cattle, genetic difference, performance index

INTRODUCTION

It has long been recognized that differences among animals in conversion of feed into BW is an important determinant of profit from beef production. The potential importance of considering feed efficiency in genetic improvement programs was identified by Gregory (1965) and further discussed in the context of national cattle evaluation by Crews (2005). Archer et al. (2004) demonstrated increased profitability of commercial beef production when feed intake was measured for a proportion of bulls generated by a nucleus breeding unit...
and used in index selection. However, until recently the extensive collection of feed intake data was not feasible and thus improvement in efficiency relied on increasing productivity. As Koch et al. (1963) pointed out, efficiency of feed use is not a directly measurable trait, but must be calculated from component traits. Combining feed intake and growth to calculate a single measure of feed efficiency does not add additional information to that which can be obtained directly from the component traits (Kennedy et al., 1993). Further, selection response may be reduced relative to that which can be obtained from a linear index of component traits (Smith, 1967; Gunsett, 1984). Therefore, the objective of this study was to develop an approach for national single-breed cattle evaluation of postweaning feed intake with the goals of providing a genetic evaluation of efficiency to breeders and incorporating cost of feed consumed into economic indexes.

**MATERIALS AND METHODS**

Animal Care and Use Committee approval was not obtained for this study because the data were accumulated by the American Angus Association (AAA) as part of their breed improvement program. However, it is assumed that Animal Care and Use Committee approval was obtained for the research conducted at cooperating universities that contributed to the data used here.

Feed intake of bulls, heifers, and steers was measured by cooperating universities and bull test stations consistent with protocol prescribed by the AAA (2008) using both GrowSafe (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) and Calan gate (American Calan Inc., Northwood, NH) technologies. Weaning (WWT) and yearling weights reported by breeders to AAA were adjusted to 205 and 365 d of age, respectively. Postweaning BW gain (PGN) was the difference between age-adjusted BW. Ultrasound images of fat depth were collected from yearling Angus bulls and heifers by certified field technicians, interpreted through centralized processing laboratories, and reported to AAA for use in genetic evaluation. The individual ultrasound measurements were adjusted by AAA to 365 d for bulls and 390 d for heifers. Following Tait et al. (2002), the subcutaneous fat (SQF) measurement used in genetic evaluation and herein was calculated as 0.6(rib fat) + 0.4(rump fat).

The feed intake data were collected in 51 groups as defined by sex of calf, test location, and date of the first reported feed intake observation by each animal (n = 3,931). These test groups ranged in number from 6 to 479 animals with a median of 34.5. For each test group, feed intake was standardized (i.e., mean = 0, variance = 1) using the within-group phenotypic SD. Animals having standardized feed intake (SFI) with absolute value greater than 4.0 were considered outliers, and their SFI observation was not included in any subsequent analyses. There were only 3 such outliers, and all were from contemporary groups of more than 200 calves.

For growth and ultrasound data, contemporary groups were defined by the AAA as used in their national cattle evaluation system. At weaning, contemporary group is initially defined by whether or not a calf has been fed creep, a breeder-defined group code, sex of calf, weaning within 3 d of other calves in the same group, herd code, whether or not the dam is registered, and whether the calf was born to its dam or was the result of embryo transfer. If the calf results from embryo transfer, then the breed of recipient dam is also considered in the definition of contemporary group. For calves to be considered members of the same contemporary group, their WWT records must also be submitted to AAA simultaneously. The WWT contemporary group was concatenated with test group to form contemporary groups for SFI. For PGN, weaning contemporary groups were further divided to account for differences in the ration fed during the postweaning period. For SQF, contemporary groups considered for PGN were further divided by differences in scanning date, scanning technician, and image processing date.

The weaning, yearling, and ultrasound scanning contemporary groups of each animal with a SFI measurement were identified, and WWT, PGN, and SQF observations from the members of each respective group were extracted from the AAA database for use in these analyses. There were 18,169, 7,107, and 4,976 calves with observations for WWT, PGN, and SQF in 509, 758, and 480 contemporary groups, respectively.

A 4-generation pedigree was extracted from the AAA herd-book for all animals with 1 or more traits to be included in the subsequent analyses. It contained 45,120 individuals. The additional phenotypic information from these ancestors and their cohorts was not used herein.

With the data described above, a 4-trait animal model analysis was conducted to estimate genetic variances and covariances to be used as input to the AAA national cattle evaluation (NCE) using ASREML (Gilmour et al., 2009). The linear model used in these analyses can be described as

\[
Y_i = X_i \beta_i + Z_i u_i + W_i u_i + S i + e_i
\]

where \(Y_i\) is the vector of data for the ith trait; \(i = 1\) to 4 for SFI, WWT, PGN, and SQF, respectively. The \(X_i\), \(Z_i\), \(W_i\), and \(S\) are design matrices relating the data to their respective fixed contemporary group effects (\(\beta_i\)), random direct genetic effects (\(u_i\), \(i = 1\) to 4), random maternal genetic effects (\(u_i\)), and random permanent environmental effects due to dams (pe), respectively.
The $e_i$ represent random residual effects. The random genetic effects were assumed to have null means and variances ($VAR$):

$$
\begin{bmatrix}
u_1 \\
u_2 \\
u_3 \\
u_4 \\
u_5 \\
\end{bmatrix} = \begin{bmatrix}
\sigma_{u_1}^2 & \sigma_{u_{12}} & \sigma_{u_{13}} & \sigma_{u_{14}} & 0 \\
\sigma_{u_{12}} & \sigma_{u_2}^2 & \sigma_{u_{23}} & \sigma_{u_{24}} & 0 \\
\sigma_{u_{13}} & \sigma_{u_{23}} & \sigma_{u_3}^2 & \sigma_{u_{34}} & 0 \\
\sigma_{u_{14}} & \sigma_{u_{24}} & \sigma_{u_{34}} & \sigma_{u_4}^2 & 0 \\
0 & 0 & 0 & 0 & \sigma_{u_5}^2 \\
\end{bmatrix},
$$

where $A$ represents the numerator relationship matrix with rank equal to the number of animals in the pedigree. The random residual effects were assumed to have null means and

$$
\begin{bmatrix}
e_1 \\
e_2 \\
e_3 \\
e_4 \\
\end{bmatrix} = \begin{bmatrix}
I_{e_{11}} & I_{e_{12}} & I_{e_{13}} & I_{e_{14}} \\
I_{e_{21}} & I_{e_{22}} & I_{e_{23}} & I_{e_{24}} \\
I_{e_{31}} & I_{e_{32}} & I_{e_{33}} & I_{e_{34}} \\
I_{e_{41}} & I_{e_{42}} & I_{e_{43}} & I_{e_{44}} \\
\end{bmatrix},
$$

where $I$ represents an identity matrix with rank equal to the number of observations for the traits being analyzed.

The (co)variance components estimated as described above were then used as input for a prototype NCE conducted using procedures described by Tsuruta et al. (2001) and Misztal et al. (2002). Accuracy estimates for the resulting EPD were computed following Beef Improvement Federation (BIF, 2010) guidelines. Subsequent to the prototype NCE, estimates of genetic residual gain were calculated from the estimated genetic (co)variances, as defined above.

Let $V = \begin{bmatrix}
\sigma_{u_1}^2 & \sigma_{u_{12}} & \sigma_{u_{13}} & \sigma_{u_{14}} \\
\sigma_{u_{12}} & \sigma_{u_2}^2 & \sigma_{u_{23}} & \sigma_{u_{24}} \\
\sigma_{u_{13}} & \sigma_{u_{23}} & \sigma_{u_3}^2 & \sigma_{u_{34}} \\
\sigma_{u_{14}} & \sigma_{u_{24}} & \sigma_{u_{34}} & \sigma_{u_4}^2 \\
\end{bmatrix}$, and $C = \begin{bmatrix}
\sigma_{u_{11}} \\
\sigma_{u_{12}} \\
\sigma_{u_{13}} \\
\sigma_{u_{14}} \\
\end{bmatrix}$.

$$
V^{-1}C = \begin{bmatrix}
b_2 \\
b_3 \\
b_4 \\
\end{bmatrix};
$$

breeding value for RFI = $u_1 - b_2u_2 - b_3u_3 - b_4u_4$. Similar methodology was described by Crews (2005) and used previously by Hoque et al. (2006) for calculation of genetic RFI.

**RESULTS AND DISCUSSION**

Means (phenotypic SD) for WWT, PGN, and SQF were 278.8 kg (30.0 kg), 213.1 kg (36.0 kg), and 0.68 cm (0.11 cm), respectively. The work of Kelly et al. (2010), Mujibi et al. (2010), and Durunna et al. (2011) supports the need to include test groups in the specification of contemporary groups for feed intake. Only 2 feed intake test groups had fewer than 12 calves. Thus, for the vast majority of the test groups, the within-group phenotypic SD of feed intake is estimated with some precision. Data pertaining to feed intake have been reported in a variety of units (i.e., as-fed, DM, TDN, and ME). As-fed feed intake is the most precise of these measures because additional variance is introduced through ration formulation, sampling diets for laboratory analysis and analytical procedures. Further, the ability of data providers to present data in units that are uniform across all providers may be limited to an as-fed basis. On a within-test-group basis, the various units of measure used in reporting feed intake may differ one to another only by multiplicative constants and thus have identical values when standardized (i.e., transformed to z-scores). Further, use of different technologies for measuring feed intake may affect feeding behavior (Crews, 2005) with resultant consequences affecting the variance between animals. These circumstances led to transformation of all phenotypic feed intake data to standard measure (mean 0.0, variance 1.0) using the respective within-test-group SD.

Estimates of direct genetic and residual variances and covariances and estimates of both genetic and environmental parameters calculated from them are presented in Table 1. Estimated heritability of maternal effects on WWT was 0.12 ± 0.02. Estimates of heritability reported in the literature for feed intake include 0.54 ± 0.15 for mixed breeds of cattle in Canada (Nkrumah et al., 2007), 0.48 ± 0.04 for Charolais cattle in France (Arthur et al., 2001a), 0.48 ± 0.14 for Brangus heifers in Texas (Lancaster et al., 2009), 0.45 ± 0.17 for Hereford and Angus cattle in the Northern Plains of North America (MacNeil et al., 1991), 0.39 ± 0.03 for Angus cattle in Australia (Arthur et al., 2001b), 0.34 ± 0.11 for Japanese Black cattle (Hoque et al., 2006), and 0.27 ± 0.06 for tropically adapted breeds in Australia (Robinson and Oddy, 2004). Estimates of heritability for ADG ranged from 0.59 to 0.20 in these studies. Likewise, heritability of subcutaneous fat depth mea-
measurements in these studies ranged from 0.59 to 0.36. Thus, the estimates of heritability for SFI, PGN, and SQF were consistent with previous estimates across a diverse sample of breeds and locations. The estimated heritability for direct genetic effects on WWT reported here is greater than the average of all corresponding estimates of heritability summarized by Koots et al. (1994), but still well within the range of previously published estimates. Postweaning BW gain was strongly correlated genetically and to a lesser degree environmentally with SFI and WWT. Genetic correlations of SQF with the other traits were not different from 0.0, but the corresponding environmental correlations were stronger. The genetic correlation between SFI and PGN found in this study is consistent with the average of estimates from the studies referenced above. However, the genetic correlation of SQF with SFI appears less than the previous estimates, with the exception of MacNeil et al. (1991).

Weaning weight was included in this analysis of feed intake for 2 reasons. First, because WWT is almost universally reported by Angus breeders, its use as a correlated trait facilitates prediction of feed intake EPD for a larger number of animals. Second, implementing a 2-stage selection strategy, such as that proposed by Arthur and Herd (2005), may introduce the possibility of selection bias affecting the genetic evaluation. It is likely that breeders select calves at weaning or shortly thereafter for evaluation of feed intake and that this selection is based at least in part on weaning weight performance. Therefore, including weaning weight in the proposed multiple-trait analysis may reduce the potential for selection bias to affect the EPD for feed intake (Pollak and Quaas, 1981). It should be recognized that if postweaning growth is assumed to be linear, use of weaning weight rather than mid-test weight provides no net change in the information included in the analysis that is related to body size.

Postweaning BW gain measures, as used here, were the adjusted 160-d BW gain from 205 to 365 d. It has been demonstrated that duration of the test period for collection of postweaning feed intake can be shorter than that used to determine BW gain (Archer et al., 1997; Wang et al., 2006). In addition, genetic correlations among feed intake measures from 1 period to the next are sufficiently large so as to consider these measures the same trait (Archer et al., 1997). Here, some of the measures of feed intake were collected over shorter periods of time during the evaluation of postweaning BW gain. This practice was thought to allow for better use of costly facilities for measuring intake with little compromise in accuracy of the feed intake measurement (Wang et al., 2006). Economies of scale facilitate measurement of more traits, such as feed intake, in a test station than it might be feasible for an individual breeder to record. Beyond the need to consider selection bias arising from sending only a fraction of calves produced to a test station, there is also a need to consider ramifications on contemporary grouping. Subdivision of weaning contemporary groups to facilitate data collection at a test station may compromise accuracy of the genetic evaluation for traits, such as feed intake. In the extreme, a contemporary group of 1 would entirely negate the value of having measured feed intake.

Average BIF accuracy of the EPD for feed intake was 0.08 for those animals (n = 26,224) whose predicted breeding value resulted only from pedigree relationships to other animals with recorded phenotypic data. In contrast, the average accuracy of the EPD for feed intake was 0.27 for those animals with a complete set of phenotypes (n = 2,027). For all animals with a recorded feed intake phenotype, irrespective of information from correlated traits, average accuracy of their EPD for feed intake was 0.26. Animals with a record for WWT only (n = 9,874) had an average accuracy of their EPD for feed intake of 0.11. If the phenotypic measures include both WWT and PGN (n = 1,523) then the average accuracy increased to 0.13, and with the addition of a record of SQF it was 0.15 (n = 2,838). Using only the correlated trait information, without including any measures of feed intake, similar to what is done in genetic evaluation of energy requirements of cows (MacNeil and Mott, 2000; Evans, 2001) increased prediction error variance by 56% in the evaluation of feed intake.

Table 1. Estimates of variance and covariance components and genetic parameters for direct effects on standard-ized feed intake (SFI), weaning weight (WWT), postweaning BW gain (PGN), and subcutaneous fat depth (SQF) of Angus cattle

<table>
<thead>
<tr>
<th>Trait</th>
<th>Additive genetic (co)variance components (above diagonal) and estimates of heritability and genetic correlation (below diagonal)</th>
<th>Residual (co)variance components (above diagonal) and environmental correlation (below diagonal)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SFI</td>
<td>WWT, kg 0.36 ± 0.05 3.66 4.29 −0.0055</td>
<td>SFI 0.48 5.10 6.46 0.05</td>
</tr>
<tr>
<td>WWT, kg 0.40 ± 0.07 310.68 71.47 0.267</td>
<td>WWT 0.35 ± 0.05 442.16 −95.42</td>
<td></td>
</tr>
<tr>
<td>PGN, kg 0.55 ± 0.10 0.27 ± 0.06 0.26 ± 0.04 0.319</td>
<td>PGN 0.37 ± 0.04 −0.18 ± 0.05</td>
<td></td>
</tr>
<tr>
<td>SQF, mm −0.07 ± 0.13 0.10 ± 0.19 0.14 ± 0.11 0.42 ± 0.05</td>
<td>SQF 0.41 ± 0.06 0.25 ± 0.07</td>
<td></td>
</tr>
</tbody>
</table>

1Phenotypic variance of WWT (including maternal effect components) = 959.9 kg.
Overall, 9,075 animals had an accuracy that was equal to or exceeded 0.2 for their feed intake EPD.

There were 604 sires that had an average of 6.5 progeny feed intake records. The BIF accuracy of their genetic evaluations is shown in Figure 1. Variation in accuracy at a fixed number of progeny results from variation in the amount of collateral data and relationships with other animals in the evaluation. This has been illustrated by distinguishing those sires having a record for feed intake themselves from those sires that do not. Average accuracy of the feed intake EPD for all sires with at least 1 progeny having a record for feed intake was 0.23. Average accuracy for the subset of sires (26.8 progeny per sire) that had a record of feed intake themselves was 0.34.

The need to include measures of feed intake in selection indexes has been recognized (e.g., MacNeil et al., 1994; MacNeil and Herring, 2005). Additional profit may be generated by the commercial beef production sector when bull candidates for selection in the nucleus sector are evaluated for postweaning feed intake and results of that evaluation are incorporated into selection indexes (Kahi et al., 2003; Archer et al., 2004; Garrick, 2005). Derivation of an economic value for feed intake is straightforward. However, derivation of economic values for efficiency measures is not as easily accomplished. It is difficult to envision how the economic values for the expected and residual components of an efficiency measure differ. Further combining feed intake and growth to derive a measure of efficiency does not yield information that cannot be obtained from the component traits (Kennedy et al., 1993). In some cases, selection response may also be reduced (Smith, 1967; Gunset, 1984). Relative economic values, from MacNeil and Herring (2005), for Angus cattle may be interpreted to indicate daily BW gain is approximately 4.7 times more important than daily feed intake in an economic index of efficiency.

Here, producing a genetic evaluation for feed intake in units of standard measure requires that the result be transformed back to units of mass or energy upon which feed is valued for selection index calculations. This transformation could be guided by using the mean and SD from 1 (or more) of the large contemporary groups for which the ration is characterized with a high degree of fidelity, or the results could be customized to a particular production situation.

Archer et al. (1999) put forward a coherent argument for presentation of efficiency EPD to breeders. Here, the rank correlation of all animals evaluated for RG and RFI was −0.78. Crowley et al. (2010) estimated a genetic correlation of RG with RFI as −0.46 ± 0.11. Thus, ranking of candidates for selection may depend to some extent on the definition of feed efficiency and there is potential for reranking based on the choice of efficiency measure. It should be noted that use of feed intake as an economically relevant trait in a selection index obviates this potential problem. Koch et al. (1963) recommended use of BW gain adjusted for feed intake as the preferred measure of biological efficiency because it was considered the most accurate mathematical description of cause and effect and noted the potential need to consider composition of BW gain. However, using RFI may have some appeal due to its relative independence from already published evaluations for growth traits (van Arendonk, 1986).
Calculation of phenotypic residual BW gain (or RFI) has merit in nutrition and some production systems studies and may facilitate technology transfer (P. F. Arthur, Department of Primary Industries, Narellan, New South Wales, Australia, personal communication). However, a priori calculation of phenotypic residual BW gain (or RFI) followed by analysis in a single-trait NCE cannot be recommended because it compromises value of indicator traits, increases opportunity for selection bias, reduces accuracy of the evaluation for animals without recorded feed intake, and unnecessarily complicates calculation of selection indexes. If the prediction error from a priori calculation of an efficiency value is not taken into account in the NCE, then accuracy of the associated EPD also may be overestimated. Further, calculation of a genetic residual efficiency measure insures the genetic independence of the efficiency measure and its components. Thus, as in Hoque et al. (2006), the strategy of a postanalysis calculation of EPD for efficiency was pursued here. The intent of the breeding value for residual BW gain is to reflect composition constant genetic potential for postweaning growth when all candidates for selection are provided an equal quantity of feed.

The approach developed here integrates calculation of a genetic evaluation for feed intake into the broader context of an existing national cattle evaluation. It imposes fairly minimal requirements for data collection beyond those for measuring feed intake. Use of correlated traits in the evaluation allows for many more animals to be evaluated than can feasibly have feed intake recorded. However, achieving an evaluation of high accuracy requires measurement of feed intake on candidates for selection and their close relatives. Reliance on indicator traits alone will not fulfill that goal. Of the 90 animals with accuracy of their feed intake EPD greater than 0.4, all had a recorded phenotype for feed intake and all but 4 also had at least 10 progeny with recorded phenotypes for feed intake in these data. Reliance on indicator traits will also not facilitate breaking the genetic antagonism between intake and performance (MacNeil et al., 1991) as is necessary to improve efficiency. To break this antagonism requires identification of individuals with breeding values that deviate from the relationships among traits inferred by the population genetic covariance structure. Going forward, developing standard protocols for the collection of feed intake data has merit as does re-estimation of the genetic parameters using additional data and improved statistical modeling to allow inclusion of genomic relationships (Rolf et al., 2010) and predictions (Meuwissen, 2007; Spangler et al., 2007) and possibly additional indicator traits. Based on precedents established with carcass traits (MacNeil et al., 2010), incorporation of molecular breeding values into the national cattle evaluation system for feed intake is also foreseen. In addition, Cooper et al. (2010) show the potential for using total intake of pens of animals to add accuracy for genetic prediction of breeding value for intake beyond that which can be obtained from correlated traits alone. Use of data from pen-fed animals would increase the feasibility with which data could be recorded by individual seedstock producers, and it is plausible that such data might also be used in a future national cattle evaluation.

**LITERATURE CITED**


