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Cooper, A. J.; Ferrell, Calvin; Cundiff, Larry V.; and Van Vleck, L. D., "Prediction of genetic values for feed intake from individual body weight gain and total feed intake of the pen" (2010). *Faculty Papers and Publications in Animal Science.* Paper 752.
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Prediction of genetic values for feed intake from individual body weight gain and total feed intake of the pen

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ABSTRACT: Records of individual feed intake (FI) and BW gain (GN) were obtained from the Germ Plasm Evaluation (GPE) program at US Meat Animal Research Center (USMARC). Animals were randomly assigned to pens. Only pens with 6 to 9 steers (n = 289) were used for this study (data set 1). Variance components and genetic parameters were estimated using data set 1. Estimated genetic values (EGV) for FI were calculated by 5 methods using single and 2-trait analyses: 1) individual FI and individual GN, 2) individual FI alone, 3) 2-trait with individual GN but with FI missing, 4) individual GN and pen total FI, and 5) pen total FI alone. Analyses were repeated but with some of the same records assigned artificially to 36 pens of 5 and 4 paternal half sibs per pen (data sets 2 and 3). Models included year as a fixed factor and birth and weaning weights, age on test, and days fed as covariates. Estimates of heritability were 0.42 ± 0.16 and 0.34 ± 0.17 for FI and GN. The estimate of the genetic correlation was 0.57 ± 0.23. Empirical responses to selection were calculated as the average EGV for the top and bottom 10% based on rank for each method but with EGV from method 1 substituted for the EGV on which ranking was based. With data set 1, rank correlations between EGV from method 1 and EGV from methods 2, 3, 4, and 5 were 0.99, 0.53, 0.32, and 0.15, respectively. Empirical responses relative to method 1 agreed with the rank correlations. Accuracy of EGV for method 4 (0.44) was greater than for method 3 (0.35) and for method 5 (0.29). Accuracies for methods 4 and 5 were greater than indicated by empirical responses and correlations with EGV from method 1. Comparisons of the 5 methods were similar for data sets 2 and 3. With data set 2, rank correlations between EGV from method 1 and EGV from methods 3, 4, and 5 were 0.47, 0.64, and 0.62. Average accuracies of 56, 75, and 75% relative to method 1 (0.67) generally agreed with the empirical responses to selection. As expected, accuracy using pen total FI and GN to obtain EGV for FI was greater than using GN alone. With data set 1, empirical response to selection with method 4 was one-third of that for method 1, although average accuracy was 65% of that for method 1. With assignment of 5 paternal half sibs to artificial pens, using pen total FI and individual GN was about 81% as effective for selection as using individual FI and GN to obtain EGV for FI and was substantially more effective than use of GN alone.

Key words: beef cattle, feed intake, genetic value, selection

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J. Anim. Sci. 2010. 88:1967–1972
doi:10.2527/jas.2009-2391

INTRODUCTION

Selection to improve output traits that are easily measured such as BW is not difficult. Little selection has been possible for traits associated with input costs. Two input traits are feed efficiency (**FE**), defined as BW gain (**GN**) divided by feed intake (**FI**), and feed conversion ratio (**FCR** = FI/GN), the reciprocal of FE. Little direct selection to decrease FI holding GN constant or to increase FE has occurred even though genetic variation for these traits was reported more than 40 yr ago (e. g., Koch et al., 1963). The review by Koots et al. (1994a) reported averages of estimates of heritability of 0.36, 0.42, and 0.41 for FCR, FE, and FI. Both FE and FCR are ratios with arithmetical properties that make them difficult to analyze and interpret economically. An alternative to selection on FE or FCR is to select using an index of estimated genetic values (**EGV**) including GN and FI weighted by net economic values (e.g., Garrick, 2005). Unfortunately, measurement of individual FI needed to estimate genetic values for FI is expensive and difficult. Olson et al. (2006), with simulated records, showed genetic values for FI of individuals can be estimated from total FI of a pen,

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Received August 11, 2009.
Accepted February 11, 2010.

Table 1. Composition of the grower (21-d training period) and finishing (test period) rations

	Percentage of diet DM	
Ingredient	Grower ration	Finishing ration
Alfalfa hay, ground		10.602
Corn silage	68.9	
Corn, dry rolled	23.0	82.668
Supplement C025[1]	8.1	
Soybean meal		5.663
Urea		0.401
Limestone		0.574
Vitamin A, D, and E supplement[2]		0.008
Trace mineral supplement[3]		0.007
Salt		0.062
Rumensin 80[4]		0.015

[1]Supplement contained 4.77% corn; 6.35% salt; 18.05% limestone; 64.71% soybean meal; 5.41% urea; 0.25% Rumensin; 0.27% trace mineral premix; 0.08% vitamin A, D, E supplement; and 0.11% S.

[2]Vitamin supplement contained 8,800,000 IU of vitamin A; 880,000 IU of vitamin D; and 880 IU of vitamin E per kg.

[3]Trace mineral premix contained 13% Ca, 12% Zn, 8% Mn, 10% Fe, 1.5% Cu, 0.2% I, and 0.1% Co.

[4]Rumensin 80 (Elanco Animal Health, Indianapolis, IN).

which is comparatively easier to measure. Olson et al. (2006), however, reported accuracies of EGV that were small, with best results for 2 animals in a pen. The purpose of this study was to extend the method of Olson et al. (2006) to determine whether individual GN and total pen FI could be used to obtain EGV for FI of individuals with greater accuracy than from individual GN or from total pen FI alone using a modification of an open source statistical analysis program (MTDFREML; Boldman et al., 1995). A goal that developed later was to compare empirical response with selection using GN and total pen FI with animals randomly assigned to pens with empirical response when records of some of the same animals were assigned to artificial pens (ignoring actual pen assignment) consisting of paternal half sibs.

MATERIALS AND METHODS

Experimental procedures involving animals were approved by US Meat Animal Research Center (USMARC) Animal Care and Use Committee.

Records were from steers in Cycle VII of the Germplasm Evaluation Program (**GPE**) at USMARC. Paternal grandsires were from 7 breeds with largest numbers of registrations in the United States (Wheeler et al., 2005): Angus, Hereford, Gelbvieh, Charolais, Limousin, Red Angus, and Simmental. Semen from these sires was used to artificially inseminate USMARC Angus, Hereford, and composite MARC III (1/4 Angus, 1/4 Hereford, 1/4 Pinzgauer, and 1/4 Red Poll) cows to produce F_1 progeny. Records of progeny in the F_2 generation were used in this study. The F_1 sires were used in multi-sire pastures across years to produce half-sib families. The progeny were genotyped to determine their sires using the Illumina BovineSNP50 chip and model 2 of option 9 of Mendel version 8.0.1 based on Sobel et al. (2002). The 3-generation families were produced to validate QTL and to combine phenotypic data and QTL into genetic evaluations for the comprehensive series of traits included in the GPE program including individual FI and growth. The crosses created a heterogeneous population to use to search for markers for QTL, which in this study was assumed to represent genetic variation across breeds.

Steer calves were managed according to a standard protocol through the growing phase and were trained to use Calan headgates (American Calan Inc., Northwood, NH) for a 21-d period. During the training period, steers were fed a grower diet (Table 1). The steers were then stepped up to a high concentrate finishing diet (Table 1) via weekly steps (e.g., 25:75, 50:50, 75:25, and 100:00 blends of the finishing and grower diets, respectively). After completion of these steps, steers were fed the finishing diet, and individual intake measurements were taken using the Calan headgates. Steers were weighed on consecutive days when they started the finishing diet and just before slaughter. Days on feed ranged from 131 to 171 d due to different protocols in different years. Body weight gain and intake records were adjusted to 150 d on feed by multiplying ADG and FI by 150.

Steers were randomly assigned to pens before the test period. Data set 1 was limited to records of steers in 39 pens of size 6 to 9 (n = 289). As a consequence of results from data set 1, data sets 2 and 3 were constructed to examine whether accuracy of EGV for FI would be greater with paternal half sibs in a pen. Data set 2 was constructed by assigning groups of 5 paternal sibs from data set 1 to 36 artificial (ignoring actual pen assignment) pens (n = 180). Data set 3 was formed from data set 2 by randomly dropping 1 animal from each pen (n = 144). For data set 1, unadjusted means for FI and GN were 1,492.4 and 223.8 kg with unadjusted SD of

166.5 and 30.7 kg. Statistical models for individual FI and GN included animal genetic and residual random effects with year as a fixed factor and linear covariates of birth and weaning weights, age on test, and days fed. Unadjusted means of the covariates were 42.7 kg, 212.0 kg, 265.1 d, and 152.3 d, respectively. The unadjusted means for birth years of 2003, 2004, and 2005 were 1,489.4, 1,516.4, and 1,439.2 for FI (kg) and were 233.3, 217.8, and 213.1 for GN on test (kg), respectively. Year of birth effects were significantly different ($P < 0.05$) for FI and GN. Coefficients of linear regression of FI on birth weight and weaning weight and of linear regression of GN on birth weight and days fed were significantly different from zero ($P < 0.05$).

The model for total pen FI included individual genetic and environmental effects for each animal in the pen. The residual variance for total pen FI when predicting genetic values was the estimate of residual variance for individual FI multiplied by 8 (approximate average number per pen) for data set 1 and number in a pen (5 and 4) for data sets 2 and 3. The pedigree file included 6,056 animals. Elements of the inverse of the augmented numerator relationship matrix were calculated using the Henderson-Quaas rules (Henderson, 1976; Quaas, 1976). The mixed model equations (Henderson et al., 1959; Henderson, 1963, 1984) were augmented to include animals without records (Henderson, 1977). Estimates of genetic parameters were obtained using data set 1 with single-trait (i.e., FI) and 2-trait (i.e., FI and GN) analyses.

The estimates of genetic parameters from the 2-trait analysis were used for each of the 3 data sets to obtain EGV for FI by 5 methods. Method 1 used a 2-trait analysis with individual FI and GN and was assumed best. Method 2 used a single-trait analysis of individual FI. Both methods 1 and 2 require measurement of individual FI. Method 3 was a 2-trait analysis but with no measurements of FI so that EGV for FI would be predicted from GN (i.e., ranking of EGV for FI would be the same as ranking of EGV for GN because EGV for FI can be obtained from the genetic regression of FI on EGV for GN). Method 4 used a 2-trait analysis of individual GN and total pen FI. Method 5 used a single-trait analysis with total pen FI alone. Methods 3, 4, and 5 do not require individual FI. Estimated genetic values were obtained with the MTDFREML set of programs (Boldman et al., 1995). Analyses with methods 4 and 5 used a modification (Van Vleck and Cassady, 2004) of the MTDFPREP program to accept multiple genetic values in total pen FI as described by Olson et al. (2006). The vector of coefficients of the model equation for total FI of a pen includes coefficients of 1 corresponding to genetic values for FI of each animal in the pen (e.g., Olson et al., 2006).

Pearson and Spearman rank correlation coefficients were computed between EGV from method 1 and EGV from methods 2, 3, 4, and 5. For each data set, animals ranked in the top and bottom 10% based on EGV from each method were identified in an attempt to mimic actual selection. The top and bottom 10% were used to average the effect of selecting a small number of animals. Empirical selection responses relative to method 1 were computed by substituting EGV for FI from method 1 for those from methods 2, 3, 4, and 5. For animals with records, accuracies of EGV were obtained from the inverse of the coefficient matrix of the mixed model equations. The correlations, empirical responses, and accuracies of EGV were used to examine the potential of using total pen FI for prediction of genetic values.

RESULTS AND DISCUSSION

Estimates of Genetic Parameters

Estimates of (co)variances and genetic parameters are reported in Table 2. Estimates of heritability for FI generally agree with the average of 0.41 from the review by Koots et al. (1994a,b) and a later estimate of 0.39 by Arthur et al. (2001). Estimates of heritability of FI and FCR for a 70-d test period after weaning in the range of 0.30 to 0.40 have been reported by Herd et al. (1997), Archer et al. (1998), Archer and Barwick (1999), and Richardson et al. (2001). The estimate of the genetic correlation (0.57) agrees well with the early estimate of 0.64 between GN and FI of (Koch et al., 1963).The review by Koots et al. (1994b) reported average estimates between postweaning GN and FI of 0.53. Estimates have ranged from moderate to large.

Correlation coefficients for EGV and for ranks of EGV between method 1 and those from methods 2, 3, 4, and 5 are in Tables 3, 4, and 5 for data sets 1, 2, and 3. The tables also contain averages of accuracies for animals with records for the 5 methods. Empirical responses are also shown for FI from the top and bottom 10% selected with methods 1, 2, 3, 4, and 5, but with EGV calculated with the usual 2-trait model. As expected, the EGV for FI from the single-trait analysis of individual FI were nearly perfectly correlated with EGV for FI from the 2-trait analysis of individual FI and GN. Further discussion will compare only method 1 with methods 3 to 5.

Data Set 1 (Random Assignment to Pens)

As shown in Table 3, the correlation of EGV from method 1 with EGV from method 3 was 0.56, which shows that some genetic change for reduced FI could be made without measuring FI. In this case, successful selection for decreased FI would also decrease GN. For practical application, however, EGV for GN would have a positive economic value and EGV for FI would have a negative economic value so that selection would be for net economic response when included in an index with other traits. The correlations among ranks are somewhat smaller than among EGV because ranks have a uniform distribution. Ranks do, however, represent how selection would be practiced.

Table 2. Estimates of (co)variance components and genetic parameters (SE) from single-trait and 2-trait analyses of feed intake (FI, kg) and BW gain (GN, kg)

Parameter	Single trait[1]	2 trait[2]
(Co) variance component		
Genetic		
Variance; FI	8,609.3	8,704.6
Covariance; FI, GN	—	854.2
Variance; GN	254.4	253.8
Environmental		
Variance; FI	12,089.0	11,963.5
Covariance; FI, GN	—	1,504.0
Variance; GN	491.3	492.2
Phenotypic		
Variance, FI	20,698.4	21,385.1
Covariance; FI, GN	—	2,358.2
Variance; GN	745.7	745.9
Genetic parameter		
Heritability; FI	0.42 (0.16)	0.42 (0.16)
Heritability; GN	0.34 (0.16)	0.34 (0.17)
Genetic correlation	—	0.57 (0.23)
Environmental correlation	—	0.62 (0.12)

[1]Single-trait analyses of FI and GN.
[2]2-trait analysis of FI and GN.

Table 3 also presents empirical responses from selection based on ranking of the top and bottom 10% by the 5 methods but with the EGV using the most information (method 1) substituted when calculating the average EGV for FI. Method 3, using only GN, resulted in average EGV for FI compared with that for method 1 of 68 and 46% for the greatest and least 10%, and an average of about 57% of empirical response with method 1. This fraction corresponds to EGV and rank correlations of 0.56 and 0.53 between methods 1 and 3, and an average accuracy for method 3 that is 52% of that for method 1. With method 4, empirical response and correlations with EGV and ranks from method 1 are much smaller than those for method 3. Average accuracy, however, is greater for method 4 than for method 3 as expected because more information is available. The empirical responses are small for method 5 relative to method 1, but average accuracy is greater than suggested by the empirical responses. Accuracy of EGV is theoretically proportional to expected genetic response to selection. Accuracy and empirical response using GN and total pen FI or only total pen FI seem too small for methods 4 and 5 to be considered viable alternatives to using GN alone to obtain EGV for FI when animals are randomly assigned to pens.

Data Sets 2 and 3 (Paternal Half Sibs Assigned to Artificial Pens)

For methods 1, 2, and 3 empirical responses, average accuracies, and correlations of EGV and ranks shown in Tables 4 and 5 are similar to those in Table 3. Meth-

Table 3. Average estimates of genetic value (EGV) for feed intake (kg) ranked by 5 methods for greatest and least 10% (29 of 289 animals with records) but with average EGV computed from the most complete model (individual BW gain and feed intake measured), average accuracies (SE) of EGV, and correlations and rank correlations with EGV from method 1

	Average EGV[2]		Accuracy		Correlation with method 1	
Method[1]	Greatest	Least	Average	Fraction[3]	EGV	Rank
1	1.00	1.00	0.67 (0.01)	1.00	1.00	1.00
2	0.99	1.00	0.67 (0.01)	1.00	1.00	0.99
3	0.68	0.46	0.35 (0.01)	0.52	0.56	0.53
4	0.34	0.32	0.44 (0.02)	0.65	0.33	0.32
5	0.05	0.09	0.29 (0.03)	0.43	0.15	0.15

[1]Method 1: 2-trait with individual feed intake and BW gain; method 2: individual feed intake; method 3: 2-trait with individual BW gain but feed intake missing; method 4: 2-trait with individual BW gain and total pen feed intake; method 5: single-trait with total pen feed intake.
[2]Fraction of method 1 (greatest = 120.25, least = −121.09).
[3]Average accuracy as a fraction of average accuracy for method 1.

Table 4. Average estimates of genetic values (EGV) for feed intake (kg) ranked by 5 methods for greatest and least 10% (18 of 180 animals with records of 5 paternal half sibs in each artificially constructed pen) but with average EGV computed from the most complete model (individual gain and feed intake measured), average accuracies (SE) of EGV, and correlations and rank correlations with EGV from method 1

	Average EGV[2]		Accuracy		Correlation with method 1	
Method[1]	Greatest	Least	Average	Fraction[3]	EGV	Rank
1	1.00	1.00	0.67 (0.01)	1.00	1.00	1.00
2	0.99	1.00	0.66 (0.01)	0.99	1.00	0.99
3	0.73	0.48	0.35 (0.01)	0.52	0.51	0.47
4	0.82	0.81	0.49 (0.06)	0.73	0.71	0.64
5	0.74	0.80	0.50 (0.06)	0.75	0.68	0.62

[1]Method 1: 2-trait with individual feed intake and BW gain; method 2: individual feed intake; method 3: 2-trait with individual BW gain but feed intake missing; method 4: 2-trait with individual BW gain and total pen feed intake; method 5: single-trait with total pen feed intake.

[2]Fraction of method 1 (greatest = 125.94, least = −125.62).

[3]Average accuracy as a fraction of average accuracy for method 1.

ods 4 and 5 had much greater empirical responses and average accuracies compared with method 1 than when actual pen assignment was random. Tables 4 and 5 suggest an advantage of method 4 over method 3 based on empirical responses, accuracy, and correlations. Average accuracy for method 3 was substantially less than for method 4 and also less than for method 5. Correlations with EGV and ranks from method 1 also show a definite advantage for method 4 and less of an advantage for method 5 compared with method 3. Although method 4 was generally better than method 5, comparisons with method 1 were surprisingly similar. The comparisons shown in Tables 4 and 5 are similar although the expectation based on the results of Olson et al. (2006) was that smaller pen size might result in increased accuracy and empirical response, but in this case less sib information was available in data set 3 than in data set 2. A shortcoming of comparing methods with empirical responses was the small number of animals in the top or bottom 10% (18 of 180 and 15 of 144 selected).

These exploratory results suggest that assigning related groups to a pen and use of pen total FI and individual GN to obtain EGV for FI is a better alternative than selecting on GN alone or pen total FI alone. This approach would rely on pen effects not being an important source of variation for FI because pens and groups of relatives would be confounded. Most feeding trials are likely to be designed to minimize differences due to pen effects. Analyses with pen effects in the model resulted in estimates of variance due to pen effects of 2.0 and 2.7% of phenotypic variances for FI and GN. Estimates of genetic parameters were not changed. Comparisons of the 5 methods for data sets 1, 2, and 3 were essentially unchanged from those when pen effects were ignored.

Table 5. Average estimates of genetic values (EGV) for feed intake (kg) ranked by 5 methods for the greatest and least 10% (15 of 144 animals with records of 4 paternal half sibs in each artificially constructed pen) but with average EGV computed from the most complete model (individual BW gain and feed intake measured), average accuracies (SE) of EGV, and correlations and rank correlations with EGV from method 1

	Average EGV[2]		Accuracy		Correlation with method 1	
Method[1]	Greatest	Least	Average	Fraction[3]	EGV	Rank
1	1.00	1.00	0.66 (0.01)	1.00	1.00	1.00
2	1.00	1.00	0.66 (0.02)	1.00	1.00	0.99
3	0.64	0.54	0.34 (0.01)	0.52	0.57	0.52
4	0.63	0.78	0.56 (0.04)	0.86	0.76	0.75
5	0.49	0.68	0.50 (0.07)	0.77	0.69	0.67

[1]Method 1: 2-trait with individual feed intake and BW gain; method 2: individual feed intake; method 3: 2-trait with individual BW gain but feed intake missing; method 4: 2-trait with individual BW gain and total pen feed intake; method 5: single-trait with total pen feed intake.

[2]Fraction of method 1 (greatest = 126.67, least = −126.35).

[3]Average accuracy as a fraction of average accuracy for method 1.

Preliminary Simulation Study

A preliminary simulation study with 60 sets of 10 full sibs (60 sires, each mated to one dam; all unrelated) that led to the analyses with actual data will be briefly summarized. Heritability for both traits was 0.40, and the genetic correlation was 0.50 (less than the 0.57 reported in this study). The correlation between true genetic value (**TGV**) and EGV for FI from method 4 when full sibs were in the same pen was 0.59, and between TGV and EGV for FI from method 4 when the same animals were assigned randomly to pens was 0.26. The correlation between TGV for FI and EGV for FI when FI was measured individually was 0.71. The correlation between TGV and EGV for FI from method 3 was only 0.28, which reflects the genetic correlation of 0.50. Accuracies from the sample were 0.75 and 0.37 for methods 2 and 3. For method 4, accuracies were 0.68 with full sibs in the same pen and 0.47 with random assignment to pens (correlations between TGV and EGV were 0.59 and 0.26). With only total pen FI used (method 5), average accuracies were 0.66 with full sibs in the same pen and 0.34 with random assignment (corresponding correlations between TGV and EGV were 0.58 and 0.22). The simulation results are in general agreement with the analysis of actual records and paternal half sibs assigned to artificial pens.

Implications

Feed intake and GN define FE in the feedlot. Individual FI, however, is usually needed to obtain EGV but is costly to measure. In feeding trials, individual GN is relatively easy to obtain and total FI for pens is not difficult to obtain. Two practical alternatives to select for net economic value without the cost of measuring individual FI are to obtain EGV for FI from GN alone (accuracy will depend on the magnitude of the genetic correlation between GN and FI and accuracy of EGV for GN) or to obtain EGV for FI from individual GN combined with total pen FI of sets of paternal half sibs. The latter alternative is similar to sib selection for FI with selection within the sib group based on individual GN. The results of this study are preliminary but show that with a relatively large genetic correlation between GN and FI, genetic values for FI can be predicted using GN alone. If pen total intake is used with GN to predict genetic values for FI, accuracy could be substantially increased by assigning related groups (e.g., paternal half sibs or full sibs) to a pen. However, confounding of a pen effect with the related group may occur. With any of the methods used to obtain EGV for FI, a selection index for net economic merit should include estimates of genetic value for both GN and FI weighted by their positive and negative economic values.

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