# Genomic-polygenic evaluation of Angus-Brahman multibreed cattle for feed efficiency and postweaning growth using the Illumina 3K chip

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# Genomic-polygenic evaluation of Angus-Brahman multibreed cattle for feed efficiency and postweaning growth using the Illumina 3K chip[1]

**M. A. Elzo,*[2] G. C. Lamb,† D. D. Johnson,* M. G. Thomas,‡ I. Misztal,§ D. O. Rae,# C. A. Martinez,* J. G. Wasdin,* and J. D. Driver***

*Department of Animal Sciences, University of Florida, Gainesville 32611; †North Florida Research and Education Center, University of Florida, Marianna 32446; ‡Department of Animal and Range Sciences, New Mexico State University, Las Cruces 88003; §Department of Animal and Dairy Science, University of Georgia, Athens 30602; and #Department of Large Animal Clinical Sciences, University of Florida, Gainesville 32611

**ABSTRACT:** The objectives of this study were to determine the fraction of additive genetic variance explained by the SNP from the Illumina Bovine3K chip; to compare the ranking of animals evaluated with genomic-polygenic, genomic, and polygenic models; and to assess trends in predicted values from these 3 models for residual feed intake (RFI), daily feed intake (DFI), feed conversion ratio (FCR), and postweaning BW gain (PWG) in a multibreed Angus-Brahman cattle population under subtropical conditions. Data consisted of phenotypes and genotypes from 620 bulls, steers, and heifers ranging from 100% Angus to 100% Brahman. Phenotypes were collected in a GrowSafe automated feeding facility (GrowSafe Systems, Ltd., Airdrie, Alberta, Canada) from 2006 to 2010. Variance components were estimated using single-trait genomic-polygenic mixed models with option VCE (Markov chain Monte Carlo) of the program GS3. Fixed effects were contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf. Random effects were additive SNP, animal polygenic, and residual effects. Genomic predictions were computed using a model without polygenic effects and polygenic predictions with a model that excluded additive SNP effects. Heritabilities were 0.20 for RFI, 0.31 for DFI, 0.21 for FCR, and 0.36 for PWG. The fraction of the additive genetic variance explained by SNP in the Illumina 3K chip was 15% for RFI, 11% for DFI, 25% for FCR, and 15% for PWG. These fractions will likely differ in other multibreed populations. Rank correlations between genomic-polygenic and polygenic predictions were high (0.95 to 0.99; $P < 0.0001$), whereas those between genomic-polygenic and genomic predictions were low (0.65 to 0.74; $P < 0.0001$). Genomic-polygenic, genomic, and polygenic predictions for all traits tended to decrease as Brahman fraction increased, indicating that calves with greater Brahman fraction were more efficient but grew more slowly than calves with greater Angus fraction. Predicted SNP values were small for all traits, and those above and below 0.2 SNP SD were in multiple chromosomes, supporting the contention that quantitative traits are determined by large numbers of alleles with small effects located throughout the genome.

**Key words:** cattle, feed intake, genomic, multibreed, polygenic

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## INTRODUCTION

Beef cattle production in subtropical regions of the United States must rely on cattle that are able to survive, reproduce, and yield meat of excellent quality under hot and humid climatic conditions. Consequently, cattle producers in these regions have made extensive use of crossbreeding *Bos taurus* breeds to Brahman to create a type of animal capable of coping with these harsh environmental conditions. This has created a large multibreed population of *Bos taurus* × *Bos indi-*

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[2] Corresponding author: maelzo@ufl.edu
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*cus* cattle in which Angus has a significant proportion of the represented *Bos taurus* breeds. As in temperate regions, feed costs represent the largest single expenditure of beef cattle operations in subtropical environments. Even small genetic changes in feed efficiency will have a large impact on the profitability of cattle operations. However, the high cost of obtaining phenotypic information for feed efficiency limits the number of animals with phenotypes. Genotyping information from animals tested in feed efficiency facilities obtained using high-density chips could help improve our ability to identify individuals with superior feed efficiency and growth characteristics. The cost of high-density chips has prevented their widespread use. However, a lower-density chip that is reasonably priced is the 2,900 marker Illumina GoldenGate Bovine3K BeadChip (Illumina, Inc., San Diego, CA; Illumina, Inc., 2011a). Thus, the objectives of this research were 1) to determine the fraction of additive genetic variation explained by the markers in the GoldenGate Bovine3K BeadChip (Illumina, Inc., 2011a), 2) to compare the ranking of animals evaluated for 4 postweaning feed efficiency and growth traits using a genomic-polygenic model, a genomic model, and a polygenic model, and 3) to assess trends in calf genomic-polygenic, genomic, and polygenic predictions for these 4 traits as Brahman fraction increased in a multibreed population composed of animals ranging from 100% Angus to 100% Brahman under Florida subtropical conditions. In addition, we have estimated by cross validation the predictive ability of the 3 models.

## MATERIALS AND METHODS

### *Animals and Data*

Standard practices of animal care and use were applied to animals used in this project. Research protocols were approved by the University of Florida Institutional Animal Care and Use Committee (IACUC number D477). Cattle were from the Angus-Brahman multibreed (**MAB**) herd of the University of Florida, located at the Beef Unit in Gainesville, Florida. Breed composition was used to construct 6 breed groups for mating purposes: Angus = (1.0 to 0.80 Angus, 0.0 to 0.20 Brahman), ¾ Angus ¼ Brahman = (¾ **A** ¼ **B**; 0.79 to 0.60 Angus, 0.21 to 0.40 Brahman), Brangus = (0.625 Angus, 0.375 Brahman), ½ Angus ½ Brahman = (½ **A** ½ **B**; 0.59 to 0.40 Angus, 0.41 to 0.60 Brahman), ¼ Angus ¾ Brahman = (¼ **A** ¾ **B;** 0.39 to 0.20 Angus, 0.61 to 0.80 Brahman), and Brahman = (0.19 to 0.0 Angus, 0.81 to 1.00 Brahman). Mating followed a diallel design (Elzo and Wakeman, 1998); that is, sires from the 6 breed groups (Angus, ¾ A ¼ B, Brangus, ½ A ½ B, ¼ A ¾ B, and Brahman) were mated to dams from all 6 breed groups. Between 3 and 5 sires per breed group were used per year, and at least 1 sire from each breed group was used in 2 consecutive yr to create connectedness across years.

Postweaning feed consumption and growth data were collected from 620 calves born between 2006 and 2010 (90 Angus, 122 ¾ A ¼ B, 113 Brangus, 153 ½A ½B, 69 ¼ A ¾ B, and 73 Brahman). Numbers of calves by sex were 56 bulls, 309 heifers, and 255 steers. There was no selection of calves left as bulls. Male calves left as bulls were chosen based on need to produce sires from 3 crossbred groups: ¾ A ¼ B, ½ A ½ B, and ¼ A ¾ B. Calves were the progeny of 64 sires (12 Angus, 11 ¾ A ¼ B, 14 Brangus, 8 ½ A ½ B, 8 ¼ A ¾ B, and 11 Brahman) and 329 dams (53 Angus, 61 ¾ A ¼ B, 52 Brangus, 74 ½ A ½ B, 42 ¼ A ¾ B, and 47 Brahman).

### *Feeding, Management, and Phenotypic Data Collection*

Calves were born between December and March and weaned in August from 2006 to 2010. No selection of calves occurred at weaning. Calves of all sexes were preconditioned postweaning at the Beef Unit in Gainesville, Florida, for 3 to 6 wk before being transported to the Feed Efficiency Facility of the Institute of Food and Agricultural Sciences of the University of Florida (**UFEF**) in Marianna, Florida. Preconditioning of calves consisted of concentrate (1.6 to 3.6 kg per day; 14.0% CP; 488 Pellet, a medicated weaning ration, Lakeland Animal Nutrition, Lakeland, FL; and soy hull pellets), free choice mineral (University of Florida University Special Hi-Cu Mineral, University of Florida, Animal Science Department, Gainesville, FL) and Bahia grass hay.

The UFEF used a GrowSafe system (GrowSafe Systems, Ltd., Airdrie, Alberta, Canada) to measure individual animal feed intake in real time. Upon arrival at the GrowSafe UFEF in Marianna, Florida, calves were assigned to pens (108 $m^2$/pen; 2 GrowSafe nodes per pen) by sire group (Angus, ¾ A ¼ B, Brangus, ½ A ½ B, ¼ A ¾ B, and Brahman) and by sex (bull, heifer, and steer) subclass. Calves were identified with half-duplex passive transponder ear tags (Allflex USA Inc., Dallas-Fort Worth, TX). The mean stocking rate was 15 animals per pen and 7.5 animals per GrowSafe node. Animals were offered a diet composed of various percentages of whole corn or corn gluten, cottonseed hulls, soy hulls, molasses, chopped grass hay, and a vitamin-mineral-protein supplement (FRM, Bainbridge, GA) ad libitum. Dry matter, CP, $NE_m$, and $NE_g$ were 91.2%, 17.3%, 1.7 mcal/kg DM, and 1.2 mcal/kg DM in 2006; 90.0%, 14.1%, 1.5 mcal/kg DM, and 0.9 mcal/kg DM in 2007; 84.5%, 11.1%, 1.6 mcal/kg DM, and 1.0 mcal/kg DM in 2008; 91.1%, 13.2%, 1.1 mcal/kg DM, and 0.6

mcal/kg of DM in 2009; and 93.1%, 14.7%, 1.1 mcal/kg DM, and 0.5 mcal/kg DM in 2010. There was an adjustment period of 21 d before each 70-d trial period. GrowSafe software recorded feed intake information in real time. Full BW (kg) were collected every 2 wk.

### *Blood Sampling and Genotyping*

Blood samples were collected at weaning using 10-mL vacutainer tubes coated with EDTA, refrigerated at 4°C, and then shipped to New Mexico State University for processing. Tubes were then centrifuged for 30 min at 1,875 × *g* at 4°C, and white blood cell supernatant (i.e., buffy coat) was recovered and brought to a volume of 1.0 mL with PBS (Beauchemin et al., 2006). Subsequently, 0.05 mL of each sample was sent to Gene Seek (Lincoln, NE) for DNA extraction and genotyping with the Illumina GoldenGate Bovine3K BeadChip (Illumina, Inc., 2011a).

### *Traits*

Traits were phenotypic daily residual feed intake (**RFI,** kg DM·d$^{-1}$**)**, mean daily feed intake (**DFI,** kg DM·d$^{-1}$), mean daily feed conversion ratio (**FCR,** kg DM·d$^{-1}$/kg weight gain·d$^{-1}$), and postweaning BW gain during the 70-d feeding trial (**PWG,** kg). All 4 traits were measured at the UFEF. Intake traits were expressed on a DM basis. The procedure used to compute RFI, DFI, FCR, and PWG was as described in Elzo et al. (2009). Briefly, RFI was calculated as the difference between actual DFI and expected DFI (Koch et al., 1963; Archer et al., 1997; Arthur et al., 2001a,b) during the 70-d postweaning feeding trial. Expected DFI for each calf was estimated as a linear regression of its individual DFI on ADG and metabolic midweight (Elzo et al., 2009). Individual calf ADG were estimated as a linear regression of the BW of each calf on test day during the 70-d feeding trial. Individual calf metabolic midweights were equal to the midweight of each calf to the power of 0.75, where midweight was equal to the linear regression estimate for initial weight plus ADG times 35 d. Mean DFI was the average of the DFI for each calf over the 70-d trial period measured with the GrowSafe system, and FCR was the ratio of DFI to ADG. Lastly, PWG was the difference between calf weights at the end and at the beginning of the 70-d trial.

### *Statistical Analysis*

***Genomic-Polygenic Variance Components.*** A genomic-polygenic mixed model (Legarra et al., 2008; VanRaden, 2008; Legarra, 2009; Snelling et al., 2011) was used to estimate additive genomic and polygenic variance components for RFI, DFI, FCR, and PWG. The genomic portion of the model was based on the BLUP model of Meuwissen et al. (2001). Fixed effects were contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf. Random effects were animal polygenic (**AP**; mean zero; variance = A × additive polygenic variance; A = additive relationship matrix with 5,864 animals in the pedigree file), additive SNP genomic effects as a function of the number of "2" alleles [**AS**; mean zero; variance = identity matrix (**I**) × additive SNP variance ], and residual effects (mean zero; I × residual variance). Variance components and heritabilities were obtained using Markov chain Monte Carlo (**MCMC**) procedures with option VCE of the program GS3 (Legarra, 2009; number of iterations = 120,000; burn-in = 20,000; thinning = 100; correction = 10,000).

Initial values for additive polygenic and residual variances were REML estimates of variance components obtained using single-trait polygenic mixed model analyses for RFI, DFI, FCR, and PWG. The polygenic mixed model contained the same fixed effects and random effects as the genomic-polygenic model, except for additive SNP genomic effects. The program ASREML was used to perform computations (Gilmour et al., 2006). Initial values for additive SNP variances were computed as $\hat{V}_g / \sum_{i=1}^{2899} 2p_iq_i$ (Habier et al., 2007; VanRaden, 2008; Gianola et al., 2009), where $\hat{V}_g$ = estimate of additive polygenic variance from the polygenic model computed using ASREML, $p_i$ = frequency of allele 1, and $q_i$ = frequency of allele 2 in the *i*th SNP in the Illumina 3K chip. The number of SNP from the Illumina 3K chip used here was 2,899 because one SNP marker (BTB-00291093) provided no information on any of the animals, and it was excluded from the analysis. The GS3 program yielded values of additive SNP (**VSNP**), additive polygenic (**VAPO**), and residual variances for each of the 1,200 MCMC samples. Subsequently, additive genomic variances (**VAGO**) were computed as the product of $\sum_{i=1}^{2899} 2p_iq_i$ times VSNP, total genetic variances (**VGTot**) were computed as VAGO + VAPO, and phenotypic variances were computed as VAGO + VAPO + residual variance. Lastly, these variances were used to compute heritabilities and ratios of VAGO to VGTot. Means and standard deviations of all these variances and variance ratios over the 1,200 MCMC samples were computed to obtain estimates of variance and variance ratios and their dispersion for RFI, DFI, FCR, and PWG in the Angus-Brahman multibreed data set.

***Genomic-Polygenic, Genomic, and Polygenic Predictions.*** Option BLUP (Gauss-Seidel iteration; convergence criterion = 10$^{-4}$) of the program GS3 (Legarra, 2009) was used to compute calf genomic-polygenic and

calf genomic values for RFI, DFI, FCR, and PWG using the variance components for additive SNP, additive polygenic, and residual effects computed with the genomic-polygenic model above. Calf genomic-polygenic predictions were obtained with the same genomic-polygenic model used to compute variance components as the sum of calf breed effect [= calf Brahman fraction × solution (Brahman − Angus) + calf additive genomic value + calf additive polygenic value, where calf additive genomic value = $\sum_{i=1}^{2899} w_i \widehat{SNP}_i$, $w_i$ = number of 2 alleles in the $i$th SNP, and $\widehat{SNP}_i$ = BLUP of $SNP_i$]. Calf genomic predictions were obtained using a genomic model (i.e., the genomic-polygenic model above without polygenic effects). Calf predicted genomic values for each trait were computed as the sum of calf breed effect [= calf Brahman fraction × solution (Brahman − Angus) + calf additive genomic value (= $\sum_{i=1}^{2899} w_i \widehat{SNP}_i$, where $w_i$ = number of 2 alleles in the $i$th SNP and $\widehat{SNP}_i$ = BLUP of $SNP_i$)]. The program GS3 (Legarra et al., 2009) was used to obtain calf polygenic BLUP for RFI, DFI, FCR, and PWG using single-trait polygenic mixed models. Polygenic BLUP were computed as the sum of calf Brahman fraction × solution (Brahman − Angus) + calf polygenic effects.

The rankings of animals evaluated using single-trait, genomic-polygenic, genomic, and polygenic mixed models were compared using Spearman's rank correlations computed using the correlation procedure (SAS Inst. Inc., Cary, NC). Linear regressions of calf genomic-polygenic, genomic, and polygenic BLUP for RFI, DFI, FCR, and PWG on Brahman fraction of calf were used to assess trends as Brahman fraction increased. Computations were carried out with the regression procedure of SAS. Calf predicted values were plotted against Brahman fractions for each trait and model using Microsoft Excel.

To explore the distribution of predicted SNP values for RFI, DFI, FCR, and PWG across the genome, predicted additive SNP values from the genomic-polygenic model were standardized [i.e., additive SNP values for each trait were divided by their additive SNP SD (**SDSNP**) = square root of VSNP] and plotted against chromosome number.

***Validation of Genomic-Polygenic, Genomic, and Polygenic Predictions.*** The Angus-Brahman multibreed data set was divided into training and validation data sets. The training data set included data from years 2006 to 2009 (n = 455; 73% of the data), and the validation data set contained data from year 2010 only (n = 168; 27% of the data). Best linear unbiased predictions were obtained with the training data set for all traits (RFI, DFI, FCR, and PWG) using the same genomic-polygenic, genomic, and polygenic models used with the complete data set. Computation of SE of prediction requires the inverse of the left-hand side of the mixed model equations. However, the program GS3 (Legarra, 2009) computed predictions using Gauss-Seidel iteration; thus, the inverse of the left-hand side was unavailable. Consequently, the predictive abilities of each model for each trait for the validation data set were computed using the correlation between predicted genomic-polygenic, genomic, and polygenic values and phenotypes as suggested by Legarra et al. (2008). In addition, accuracies were computed for each model and trait as predictive abilities divided by the square root of heritabilities, also according to Legarra et al. (2008).

## RESULTS AND DISCUSSION

### *Data*

Table 1 shows numbers of calves, means, and SD per breed group of calf and total. The number of calves per breed group ranged from 69 (¼ A ¾ B) to 154 (½ A ½ B). Trait means per breed group ranged from −0.28 kg DM·d$^{-1}$ for Brahman to 0.08 kg DM·d$^{-1}$ for ¼ A ¾ B for RFI, from 7.68 kg DM·d$^{-1}$ for Brahman to 8.59 kg DM·d$^{-1}$ for ¾ A ¼ B and ½ A ½ B for DFI, from 7.90 kg DM·d$^{-1}$/kg BW gain·d$^{-1}$ for Angus to 9.03 kg DM·d$^{-1}$/kg BW gain·d$^{-1}$ for Brahman, and from 63.13 kg for Brahman to 78.43 kg for ¾ A ¼ B for PWG.

**Table 1.** Numbers of calves, means, and SD per breed group and total

| | | Trait[1] | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | RFI, kg DM·d$^{-1}$ | | DFI, kg DM·d$^{-1}$ | | FCR, kg DM·d$^{-1}$/kg gain·d$^{-1}$ | | PWG, kg | |
| Breed group | No. | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Angus (A) | 90 | −0.21 | 1.32 | 8.29 | 2.18 | 7.90 | 2.27 | 76.92 | 22.00 |
| ¾ A ¼ B | 123 | −0.01 | 1.46 | 8.59 | 2.13 | 8.20 | 2.77 | 78.43 | 23.91 |
| Brangus | 114 | 0.07 | 1.44 | 8.45 | 2.02 | 8.27 | 2.64 | 76.19 | 20.60 |
| ½ A ½ B | 154 | 0.06 | 1.55 | 8.59 | 2.21 | 8.22 | 2.80 | 73.89 | 21.13 |
| ¼ A ¾ B | 69 | 0.08 | 1.02 | 8.63 | 1.70 | 8.55 | 2.52 | 74.65 | 17.58 |
| Brahman (B) | 73 | −0.28 | 1.06 | 7.68 | 1.92 | 9.03 | 2.96 | 63.13 | 17.69 |
| Total | 623 | −0.03 | 1.38 | 8.42 | 2.08 | 8.31 | 2.69 | 74.47 | 21.40 |

[1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

**Table 2.** Posterior means and posterior SD for additive genomic, polygenic, total genetic, and phenotypic variances

| | Trait[2] | | | |
|---|---|---|---|---|
| Variance[1] | RFI, (kg DM·d$^{-1}$)$^2$ | DFI, (kg DM·d$^{-1}$)$^2$ | FCR, (kg DM·d$^{-1}$/ kg BW gain·d$^{-1}$)$^2$ | PWG, kg$^2$ |
| VAGO | 0.05 ± 0.04 | 0.08 ± 0.07 | 0.37 ± 0.30 | 13.9 ± 11.4 |
| VAPO | 0.30 ± 0.13 | 0.65 ± 0.21 | 1.00 ± 0.46 | 73.3 ± 21.9 |
| VGTot | 0.35 ± 0.14 | 0.73 ± 0.22 | 1.37 ± 0.57 | 87.2 ± 25.2 |
| PhenVar | 1.76 ± 0.11 | 2.34 ± 0.15 | 6.51 ± 0.40 | 240.8 ± 15.1 |
| VGPO | 0.31 ± 0.15 | 0.66 ± 0.23 | 1.00 ± 0.49 | 76.7 ± 23.20 |
| PhenVarPO | 1.75 ± 0.11 | 2.33 ± 0.15 | 6.48 ± 0.40 | 238.9 ± 15.13 |

[1]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTot = total genetic variance = VAGO + VAPO; PhenVar = phenotypic variance; VGPO = additive genetic variance from a polygenic model; PhenVarPO = phenotypic variance from a polygenic model.

[2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

### *Genomic and Polygenic Variance Components and Variance Ratios*

Table 2 shows the posterior means for additive genomic, polygenic, total genetic, and phenotypic variances computed with MCMC procedures from the GS3 program (Legarra et al., 2009). Table 3 contains the corresponding means for heritabilities and ratios of additive genomic variances to total additive genetic variances for RFI, DFI, FCR, and PWG. In addition, for comparison purposes, Table 2 includes estimates of posterior means for additive genetic variances, and Table 3 presents estimates of heritabilities for these 4 traits using a polygenic model. The posterior means for VSNP were $4.161 \times 10^{-5}$ (kg DM·d$^{-1}$)$^2$ for RFI, $6.682 \times 10^{-5}$ (kg DM·d$^{-1}$)$^2$ for DFI, $29.854 \times 10^{-5}$ (kg DM·d$^{-1}$ /kg gain·d$^{-1}$)$^2$ for FCR, and $1{,}132.84 \times 10^{-5}$ kg$^2$ for PWG. Products of these VSNP times $\sum_{i=1}^{2899} 2p_iq_i$ (= 1,223.38) yielded the VAGO in Table 2.

***Heritabilities.*** A summary of estimates of heritabilities obtained for RFI, DFI, FCR, and PWG or postweaning ADG from a number of previous studies is presented in Table 4. The MCMC heritability of RFI (0.20) was comparable to and the heritabilities of DFI (0.31), FCR (0.21), and PWG (0.36) were somewhat smaller than the REML estimates of heritability for these 4 traits in a 3-herd Angus-Brahman multibreed population in Florida (Elzo et al., 2009). Similarly, heritability values for RFI, DFI, and FCR were generally less than estimates obtained in Australia (Arthur et al., 2001a; Bolormaa et al., 2011), Canada (Schenkel et al., 2004; Mujibi et al., 2011), France (Arthur et al., 2001b), and the United States (Lancaster et al., 2009; Snelling et al., 2011). On the other hand, the heritability of PWG was within the range of reported values for PWG (Kriese et al., 1991; Davis, 1993; Davis and Simmen, 2006; Snelling et al., 2011) and postweaning ADG in feed efficiency studies (MacNeil et al., 1991; Arthur et al., 2001a,b; Schenkel et al., 2004; Lancaster et al., 2009; Bolormaa et al., 2011; Mujibi et al., 2011). The lower heritabilities of RFI, DFI, and FCR here may be an indication that either that the amount of genetic variability for these traits was less in the Angus-Brahman multibreed herd than in the other cattle populations, perhaps because of the small size of the population, or that environmental conditions in Florida prevented animals from expressing their genetic potential to a greater extent.

***Additive Genomic to Additive Genetic Variance Ratios.*** The trait with the smallest VAGO/VGTot ratio (Table 3) was DFI (0.11). FCR had the largest VAGO/

**Table 3.** Posterior means and posterior standard deviations for additive genetic and genomic variance ratios

| Variance ratios[1] | Trait[2] | | | |
|---|---|---|---|---|
| | RFI | DFI | FCR | PWG |
| VAGO/VGTot | 0.15± 0.12 | 0.11± 0.09 | 0.25± 0.17 | 0.15± 0.11 |
| Heritability | 0.20± 0.07 | 0.31± 0.09 | 0.21± 0.08 | 0.36± 0.10 |
| HeritabilityPO | 0.17± 0.08 | 0.28± 0.09 | 0.15± 0.07 | 0.32± 0.09 |

[1]VAGO = additive genomic variance; VGTot = VAGO + VAPO; VAPO = additive polygenic variance; HeritabilityPO = heritability from a polygenic model.

[2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

**Table 4.** Summary of heritability estimates for RFI, DFI, FCR, and PWG[1]

| | Heritability | | | |
|---|---|---|---|---|
| Source | RFI | DFI | FCR | PWG or PWADG[2] |
| Current study | 0.20 ± 0.07[3] | 0.31 ± 0.09[3] | 0.21 ± 0.08[3] | 0.36 ± 0.10[3] |
| Arthur et al. (2001a) | 0.39 ± 0.03 | 0.39 ± 0.03 | 0.29 ± 0.04 | 0.28 ± 0.04[2] |
| Arthur et al. (2001b) | 0.39 ± 0.04 | 0.48 ± 0.04 | 0.46 ± 0.04 | 0.31 ± 0.05[2] |
| Bolormaa et al. (2011) | 0.18 ± 0.13 | 0.16 ± 0.13 | — | 0.24 ± 0.14[2] |
| Davis (1993) | — | — | — | 0.31 ± 0.08 |
| Davis and Simmen (2006) | — | — | — | 0.45 ± 0.09 |
| Elzo et al. (2009) | 0.19 ± 0.11 | 0.42 ± 0.13 | 0.24 ± 0.11 | 0.40 ± 0.13 |
| Kriese et al. (1991) | | | | 0.15 to 0.56 |
| Lancaster et al. (2009) | 0.47 ± 0.13 | 0.48 ± 0.14 | 0.29 ± 0.12 | 0.21 ± 0.12[2] |
| MacNeil et al. (1991) | — | — | — | 0.38 ± 0.16[2] |
| Mujibi et al. (2011) | 0.29 ± 0.12 | 0.41 ± 0.12 | — | 0.28 ± 0.11[2] |
| Schenkel et al. (2004) | 0.38 ± 0.07 | 0.44 ± 0.06 | 0.37 ± 0.06 | 0.35 ± 0.03[2] |
| Snelling et al. (2011) | 0.40 ± 0.09 | — | — | 0.25 ± 0.08 |

[1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

[2]PWADG = postweaning ADG.

[3]Posterior SD.

VGTot ratio (0.25), and RFI and PWG had intermediate values (0.15). Thus, the 2,900 markers of the Illumina Bovine3K chip accounted for only a small fraction of the total genetic variation for these 4 traits in this multibreed population. Similar studies with the Illumina 3K chip were unavailable in the literature for comparison. However, there were 2 studies (Mujibi et al., 2011; Snelling et al., 2011) involving the 50K Illumina SNP50 (Illumina, Inc., 2011b) with estimates of VAGO and VGTot that permitted the computation of VAGO/VGTot ratios for RFI, DMI, PWG, and ADG during feeding consumption trials. Both studies were conducted in temperate areas (Alberta, Canada: Mujibi et al., 2011; Nebraska: Snelling et al., 2011) and used groups of substantially different breed composition (crossbred animals involving 7 *Bos taurus* breeds) from the Angus-Brahman multibreed population in subtropical Florida.

Estimates of VAGO/VGTot ratios in Mujibi et al. (2011) were 0.32 for RFI, 0.09 for DFI, and 0.85 for ADG when 37,959 SNP were included in their random regression BLUP genomic-polygenic model, which was similar to the one used here. On the other hand, Snelling et al. (2011) used a model that contained animal polygenic and animal SNP effects and computed heritability ratios for the animal polygenic and animal SNP effects for the complete set of SNP from the Illumina SNP50 chip used in the study (44,163 SNP) and various subsets of selected SNP. When all SNP were considered, the VAGO/VGTot ratios for all RFI, DFI, and PWG were all equal to 1 (i.e., they accounted for 100% of the estimated genetic variation for these traits), and when only sets of SNP with significant effects ($P < 0.0001$) were considered, they accounted for 0.22 for RFI, 0.31 for DMI, and 0.27 for PWG. Differences among VAGO/VGTot ratios in these 2 studies may have been due to differences in the number and sets of SNP, different models and assumptions, and differences in breed composition and numbers of animals. These factors may have resulted in different linkage disequilibrium patterns (Snelling et al., 2011) yielding different VAGO/VGTot in the cattle populations used in Mujibi et al. (2011), Snelling et al. (2011), and this study. Except for the VAGO/VGTot ratio for DFI in Mujibi et al. (2011), all VAGO/VGTot ratios with the Illumina Bovine3K chip in this study were less than those obtained with the Illumina SNP50 chip. Both the lower number of SNP and the larger distances between SNP likely contributed to decrease the fraction of the genetic variance explained by the Illumina Bovine3K chip for RFI, DFI, FCR, and PWG. The decreased linkage disequilibrium between SNP markers and QTL due to the sparseness of the Illumina 3K chip likely affected the 4 traits considered here, thus preventing the genomic part of the model from accounting for as large a fraction of the genetic variance of each trait as that accounted for by the Illumina SNP50 chip.

A large number of SNP markers may be unnecessary to account for most of the genetic variance for a trait. Snelling et al. (2011) computed heritability ratios for the genomic and the polygenic components of their model using various sets of SNP associated with 5 traits, including RFI, DFI, and PWG. They reported that a set of 1,536 SNP strongly associated with these traits accounted for 100% of the genetic variance for these traits. In addition, a previous Australian study using a MegAllele Genotyping Bovine 10K SNP Panel (Barendse et al., 2007) reported that 20 SNP with significant effects accounted for 76% of the genetic variance for RFI in a group of 189 animals of 7 *Bos taurus* and *Bos indicus* breeds using regression models with SNP and without SNP effects. Thus, it is conceivable that a low-cost chip with perhaps fewer than 2,000 SNP markers could be constructed that could account for most of the genetic variance for multiple traits. Perhaps initially, SNP that had effects larger than 0.2 SDSNP or sets of SNP that have been found to be strongly associated (Snelling et al., 2011) could be included in this chip. However, to ensure that the set of SNP markers would explain most of the genetic variance, SNP markers in this chip would likely need to be in the QTL or in complete linkage disequilibrium with the QTL (Gianola et al., 2009; Goddard, 2009). This chip would need to be tested for its ability to account for the genetic variance in a variety of purebred and crossbred cattle populations. Also, because of population changes over time, this chip would need to be periodically updated and retested. These chips would be second-tier chips in that they would be constructed on the basis of information obtained with high-density chips such as the Illumina BovineSNP50 chip (Illumina, Inc., 2011b), the Illumina BovineHD chip (Illumina, Inc., 2011c), or an improved chip with functional information using high-throughput RNA sequencing technology (Canovas et al., 2010).

### *Ranking of Animals Evaluated with Genomic-Polygenic, Genomic, and Polygenic Models*

Spearman's rank correlations among predictions of additive genetic values for RFI, DFI, FCR, and PWG using models containing genomic and polygenic effects, genomic effects only, and polygenic effects only are shown in Table 5. The highest rank correlations were between predicted values from genomic-polygenic and polygenic models (from 0.95 for FCR to 0.99 for DFR and PWG; $P < 0.0001$), and the lowest rank correlations were between predicted values from genomic and polygenic models (from 0.42 for FCR to 0.65 for PWG; $P < 0.0001$). Rank correlations between predicted

genomic-polygenic and genomic models were somewhat greater (from 0.65 for RFI to 0.74 for PWG) than those between genomic and polygenic models. The high rank correlations between predictions from the genomic-polygenic and the polygenic models suggest that genotypic information from the Illumina Bovine3K chip had little impact on our ability to identify superior animals for RFI, DFI, FCR, and PWG in the Angus-Brahman multibreed population. The substantially lower rank correlations between predictions from genomic-polygenic and genomic models were a consequence of the low fractions of additive genetic variances for RFI, DFI, FCR, and PWG captured by the 2,899 SNP markers in the Illumina Bovine3K chip. These rank correlations suggest that a genomic-polygenic model would need to be used to account for additive genetic effects and variation not accounted for by low-density chips containing SNP evenly distributed throughout the genome such as the Illumina Bovine3K chip. The low rank correlations between predictions from genomic and polygenic models combined with the low fractions of additive genetic variances accounted for by the set of SNP markers in the Illumina Bovine3K chip indicate that the polygenic model should be preferred. However, considering that rank correlations between genomic-polygenic and genomic models were positive and above 0.6 for all traits, predictions from genomic models might be used for preliminary analyses before computing predictions with a genomic-polygenic (or a polygenic) model for RFI, DFI, FCR, or PWG.

The rank correlations between predictions from a genomic-polygenic and a polygenic model obtained by Snelling et al. (2011) with the Illumina BovineSNP50 chip were 0.99 for RFI, 0.97 for DFI, and 0.95 for PWG. These rank correlations were nearly identical to the ones obtained here with the Illumina Bovine3K chip, suggesting that regardless of the different ranks of accountability of additive genetic variation between the Illumina Bovine3K and BovineSNP50 chip, they had similar overall impact on the ranking of animals evaluated with genomic-polygenic and polygenic models in these 2 studies. Because the goal of genetic evaluations is to select a few animals from a group ranked according to their predicted additive genetic values (Fernando and Gianola, 1986), these high correlations raise the issue of justifying the additional cost of obtaining genotypes to compute genomic-polygenic predicted values instead of using polygenic predicted values when individual postweaning feed consumption and postweaning BW are available. This situation may change in the future as prices of genotyping chips continue to decrease, making the use of chips denser than the Illumina Bovine3K more widespread, increasing the fraction of genetic variation explained by SNP and decreasing the need for including polygenic effects in genetic evaluation models.

**Table 5.** Spearman's rank correlations for animals evaluated using genomic-polygenic, genomic, and polygenic models

| | Trait[2] | | | |
|---|---|---|---|---|
| Correlation[1] | RFI | DFI | FCR | PWG |
| GP Model, G Model | 0.65 | 0.62 | 0.66 | 0.74 |
| GP Model, P Model | 0.98 | 0.99 | 0.95 | 0.99 |
| G Model, P Model | 0.52 | 0.51 | 0.42 | 0.65 |

[1]GP Model = genomic-polygenic model; G Model = genomic model; P Model = polygenic model. All correlations were significant ($P < 0.0001$).

[2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

### *Genomic-Polygenic, Genomic, and Polygenic Prediction Trends from Angus to Brahman*

Calves with high, medium, and low genomic-polygenic, genomic, and polygenic predicted values for RFI, DFI, FCR, and PWG existed throughout the range of breed compositions in the Angus-Brahman multibreed herd. As examples, Figures 1, 2, and 3 show genomic-polygenic, genomic, and polygenic predicted values for RFI for calves ranging in breed composition from 100% Angus to 100% Brahman. Linear regression coefficients of calf genomic-polygenic, genomic, and polygenic predicted values for RFI, DFI, FCR, and PWG on Brahman fraction of calf (Table 6) were negative for all traits and effects (i.e., genomic-polygenic, genomic, and polygenic). However, only 50% of regression coefficients were significant ($P < 0.0311$ to $P < 0.0001$). In particular, FCR regression coefficients were nonsignificant for genomic-polygenic, genomic, and polygenic effects. For the other 3 traits at least 1 regression coefficient was significant. Genomic-polygenic effects showed significant decreas-

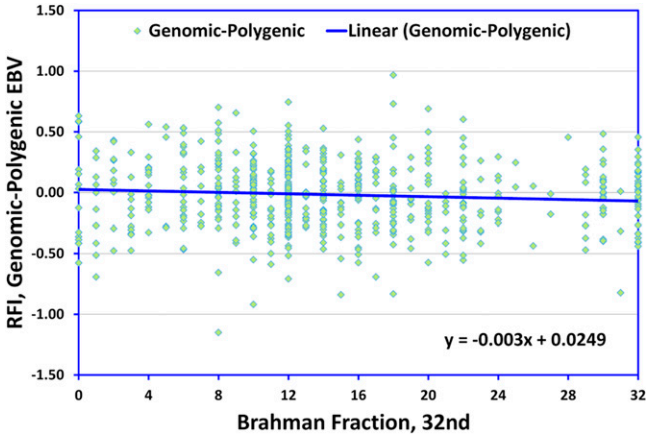


**Figure 1.** Genomic-polygenic predicted genetic values (EBV) for residual feed intake (RFI) as a function of Brahman fraction of calf. See online version for figure in color.

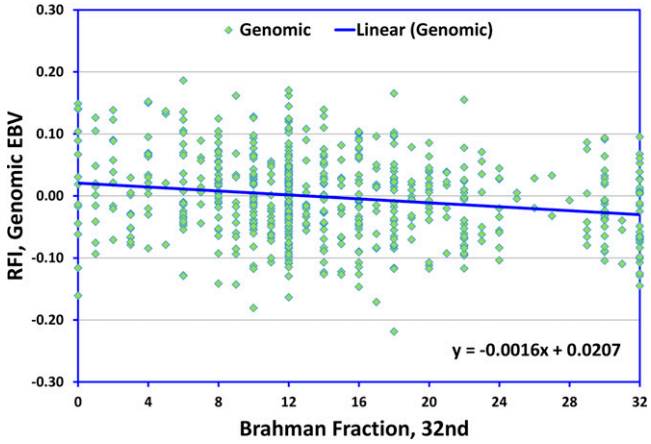


**Figure 2.** Genomic predicted genetic values (EBV) for residual feed intake (RFI) as a function of Brahman fraction of calf. See online version for figure in color.

ing trends for RFI, DFI, and PWG. Trends for genomic effects were significant for RFI and DFI, and polygenic trends were significant only for PWG. Taken together, these trends indicated that calves with larger fractions of Brahman genes tended to be more efficient (less than predicted RFI and FCR values) and eat less feed (less than predicted DFI values), but they also tended to gain less BW (less than predicted PWG values) during the 70-d feeding trial. This suggests that if the selection objective were to produce efficient animals with fast postweaning BW gains under subtropical conditions, then a genetic-economic index combining feed efficiency and postweaning BW gain traits would be an appropriate strategy to achieve this goal.

### *Predicted SNP Values*

Predicted SNP values were small for all SNP and all traits ranging from $-1.791 \times 10^{-3}$ to $1.728 \times 10^{-3}$ kg DM·d$^{-1}$ for RFI, from $-2.188 \times 10^{-3}$ to $2.134 \times 10^{-3}$ kg DM·d$^{-1}$ for DFI, from $-5.609 \times 10^{-3}$ to $6.544 \times 10^{-3}$ kg DM·d$^{-1}$/kg BW gain·d$^{-1}$ for FCR, and from $-46.972 \times 10^{-3}$ to $37.831 \times 10^{-3}$ kg for PWG. To compare predicted SNP values across traits, predicted SNP values for each trait were divided by their SDSNP. The SDSNP were equal to $6.450 \times 10^{-3}$ kg DM·d$^{-1}$ for RFI, $8.174 \times 10^{-3}$ kg DM·d$^{-1}$ for DFI, $17.278 \times 10^{-3}$ kg DM·d$^{-1}$/kg gain·d$^{-1}$ for FCR, and $106.435 \times 10^{-3}$ kg for PWG. The number and percentages of standardized SNP predicted values from the genomic-polygenic model at 0.1 SDSNP intervals are presented in Table 7. Although most SNP values fell within 0.2 SDSNP for all traits, the number and percentage of SNP for RFI (n = 17; 0.59%) and DFI (n = 12; 0.41%) were substantially less than those for FCR (n = 116; 4.01%) and PWG (n = 144; 4.96%), suggesting the Illumina Bovine3K chip contained a larger number of SNP in linkage disequilibrium with QTL that had greater influence on PWG and FCR than RFI or DFI in this Angus-Brahman multibreed population.

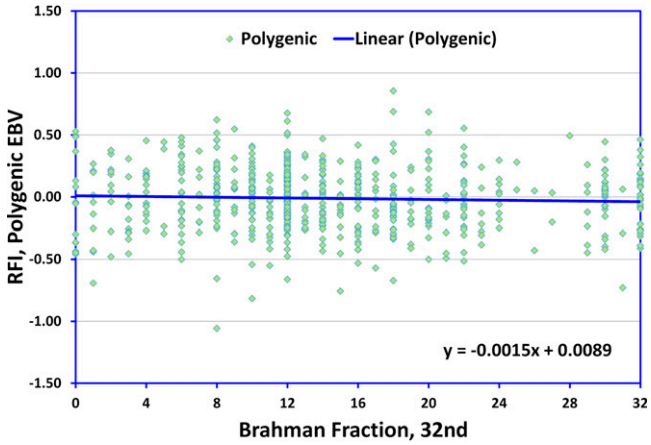


**Figure 3.** Polygenic predicted genetic values (EBV) for residual feed intake (RFI) as a function of Brahman fraction of calf. See online version for figure in color.

**Table 6.** Linear regression coefficients for genomic-polygenic, genomic, and polygenic predictions on Brahman fraction of calf

| | Trait[1] | | | |
|---|---|---|---|---|
| Effect | RFI | DFI | FCR | PWG |
| Genomic-polygenic | −0.0030 | −0.0066 | −0.0020 | −0.0634 |
| | $P < 0.0311$ | $P < 0.0070$ | $P < 0.4812$ | $P < 0.0274$ |
| Genomic | −0.0016 | −0.0030 | −0.0015 | −0.0086 |
| | $P < 0.0001$ | $P < 0.0001$ | $P < 0.1529$ | $P < 0.2825$ |
| Polygenic | −0.0015 | −0.0040 | −0.0007 | −0.0664 |
| | $P < 0.2395$ | $P < 0.1000$ | $P < 0.7772$ | $P < 0.0122$ |

[1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

To explore the location of SNP with predicted values above and below 0.2 SDSNP, standardized SNP values were plotted against chromosome number (Figure 4). There were SNP for RFI with values greater than and less than 0.1 SDSNP in all chromosomes but greater than and less than 0.2 SDSNP only in chromosomes 1, 4, 5, 6, 7, 8, 11, 12, 16, 23, and 24. Conversely, SNP for DFI greater than and less than 0.2 SDSNP were located in chromosomes 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 21, 24, and 28. Similarly, SNP greater than and less than 0.2 SDSNP were located in all chromosomes but 16, 25, 28, and 29 for FCR and in all chromosomes except for chromosome 16 for PWG. These patterns of numbers and locations of SNP lend support to the usual assumption that quantitative traits are predominantly determined by large numbers of alleles of small effect located throughout the genome (Meuwissen et al., 2001; Gianola et al., 2009; Goddard, 2009). An Excel supplemental file with the Illumina Bovine3K SNP name, NCBI SNP identifi-

**Table 7.** Number and percentage of standardized predicted SNP values from the genomic-polygenic model

| | Trait[2] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | RFI | | DFI | | FCR | | PWG | |
| SDSNP Range[1] | No. | % | No. | % | No. | % | No. | % |
| −0.4 to −0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.03 |
| −0.3 to −0.4 | 0 | 0 | 1 | 0.03 | 4 | 0.14 | 1 | 0.03 |
| −0.2 to −0.3 | 8 | 0.28 | 19 | 0.66 | 60 | 2.07 | 66 | 2.28 |
| −0.1 to −0.2 | 187 | 6.45 | 244 | 8.42 | 393 | 13.55 | 371 | 12.80 |
| 0 to −0.1 | 1204 | 41.53 | 1171 | 40.39 | 1007 | 34.74 | 998 | 34.43 |
| 0 to 0.1 | 1289 | 44.46 | 1169 | 40.32 | 1004 | 34.63 | 1010 | 34.84 |
| 0.1 to 0.2 | 202 | 6.97 | 277 | 9.56 | 379 | 13.07 | 376 | 12.97 |
| 0.2 to 0.3 | 9 | 0.31 | 18 | 0.62 | 48 | 1.66 | 72 | 2.48 |
| 0.3 to 0.4 | 0 | 0 | 0 | 0 | 4 | 0.14 | 4 | 0.14 |

[1]SDSNP = additive SNP SD.

[2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

cation, chromosome number, SNP location within chromosome, SNP predicted value, and SNP predicted value/SDSNP is available at http://jas.fass.org/content/volxx/issuexx. Widespread distribution of influential SNP over a large number of chromosomes was also found by Mujibi et al. (2011) for RFI and by Snelling et al. (2011) for RFI, DFI, and PWG. Similar outcomes were also reported by Snelling et al. (2009) for birth weight, weaning weight, and yearling weight and by Bolormaa et al. (2011) for intramuscular fat percentage and meat tenderness.

### *Validation of Genomic-Polygenic, Genomic, and Polygenic Predictions*

Predictive abilities and accuracies (Legarra et al., 2008) of genomic-polygenic, genomic, and polygenic models for all traits (RFI, DFI, FCR, and PWG) in the validation data set are presented in Table 8. Predictive abilities and accuracies were all low, as expected, because of the small size of the data set available for this study. Values of predictive abilities and accuracies tended to be larger for the genomic-polygenic and polygenic models than for the genomic model. Predictive abilities and accuracies for 2 traits (RFI and DFI) were small and negative for the genomic model. For all other traits and models predictive abilities and accuracies were low and positive. There was no clear advantage of the genomic-polygenic model over the polygenic model, but both models were somewhat better than the genomic model. These results support the need to use chips of greater density than the Illumina 3K chip for genomic predictions in multibreed populations.

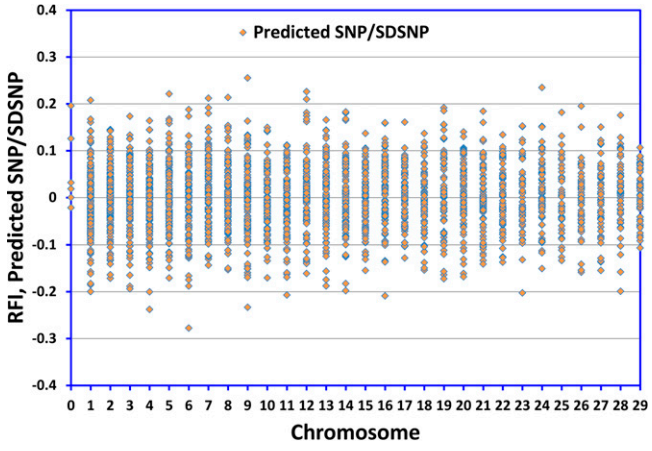


**Figure 4.** Standardized predicted SNP values associated with residual feed intake (RFI) by chromosome number (0 = unassigned). See online version for figure in color.

### *Final Remarks*

Heritabilities of all traits except postweaning BW gain in the Angus-Brahman multibreed herd were somewhat less than those found in other cattle populations. Genomic to genomic plus polygenic variance ratios with the Illumina Bovine3K chip were mostly lower than those obtained with the Illumina BovineSNP50 elsewhere. This suggests that the Illumina 3K chip should perhaps be used

**Table 8.** Predictive abilities and accuracies of genomic-polygenic, genomic, and polygenic models in the validation data set[1]

| | Trait[2] | | | |
|---|---|---|---|---|
| Model | RFI | DFI | FCR | PWG |
| Heritabilities | 0.20 | 0.31 | 0.21 | 0.36 |
| Predictive abilities | | | | |
| Genomic-polygenic | 0.04 | 0.16 | 0.14 | 0.25 |
| Genomic | −0.06 | -0.06 | 0.17 | 0.18 |
| Polygenic | 0.04 | 0.20 | 0.12 | 0.25 |
| Accuracies | | | | |
| Genomic-polygenic | 0.08 | 0.29 | 0.31 | 0.42 |
| Genomic | −0.13 | −0.10 | 0.36 | 0.30 |
| Polygenic | 0.08 | 0.36 | 0.25 | 0.42 |

[1]All correlations were significant ($P < 0.0001$).

[2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio; PWG = postweaning BW gain.

in conjunction with higher-density chips so that genomic-polygenic and genomic analyses could be made on the basis of actual and imputed genotypes. The high correlation animal rankings with the genomic-polygenic and polygenic models and the low rank correlations between the genomic-polygenic and genomic models were likely a consequence of the low fraction of the total genetic variance accounted for by the SNP in the Illumina Bovine 3K chip. Genomic-polygenic, genomic, and polygenic predictions tended to decrease as Brahman fraction increased for all traits, indicating that calves with larger Brahman fractions tended to use feed more efficiently, eat less, and gain less BW postweaning than animals with larger Angus fractions. Predicted SNP values were small for all traits, and those above and below 0.2 additive SDSNP were located in multiple chromosomes, supporting the assumption of quantitative traits being determined by a large number of alleles with small effect located throughout the genome.

## LITERATURE CITED


Archer, J. A., P. F. Arthur, R. M. Herd, P. F. Parnell, and W. S. Pitchford. 1997. Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in British breed cattle. J. Anim. Sci. 75:2024–2032.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805–2811.

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

Barendse, W., A. Reverter, R. J. Bunch, B. E. Harrison, W. Barris, and M. B. Thomas. 2007. A validated whole-genome association study of efficient food conversion in cattle. Genetics 176:1893–1905.

Beauchemin, V. R., M. G. Thomas, D. E. Franke, and G. A. Silver. 2006. Evaluation of DNA polymorphisms involving growth hormone relative to growth and carcass characteristics in Brahman steers. Genet. Mol. Res. 5:438–447.

Bolormaa, S., L. R. Porto Neto, Y. D. Zhang, R. J. Bunch, B. E. Harrison, M. E. Goddard, and W. Barendse. 2011. A genome-wide association study of meat and carcass traits in Australian cattle. J. Anim. Sci. 89:2297–2309.

Canovas, A., G. Rincon, A. Islas-Trejo, S. Wickramasinghe, and J. F. Medrano. 2010. SNP discovery in the bovine milk transcriptome using RNA-Seq technology. Mamm. Genome 21:592–598.

Davis, G. P. 1993. Genetic parameters for tropical beef cattle in northern Australia: A review. Aust. J. Agric. Res. 44:179–198.

Davis, M. E., and R. C. M. Simmen. 2006. Genetic parameter estimates for serum insulin-like growth factor I concentrations, and body weight and weight gains in Angus beef cattle divergently selected for serum insulin-like growth factor I concentration. J. Anim. Sci. 84:2299–2308.

Elzo, M. A., D. G. Riley, G. R. Hansen, D. D. Johnson, R. O. Myer, S. W. Coleman, C. C. Chase, J. G. Wasdin, and J. D. Driver. 2009. Effect of breed composition on phenotypic residual feed intake and growth in Angus, Brahman, and Angus × Brahman crossbred cattle. J. Anim. Sci. 87:3877–3886.

Elzo, M. A., and D. L. Wakeman. 1998. Covariance components and prediction for additive and nonadditive preweaning growth genetic effects in an Angus-Brahman multibreed herd. J. Anim. Sci. 76:1290–1302.

Fernando, R. L., and D. Gianola. 1986. Optimal properties of the conditional mean as a selection criterion. Theor. Appl. Genet. 72:822–825.

Gianola, D., G. de los Campos, W. G. Hill, E. Manfredi, and R. Fernando. 2009. Additive genetic variability and the Bayesian alphabet. Genetics 183:347–363.

Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2006. ASREML user guide, release 2.0. VSN Int. Ltd., Hemel Hempstead, UK.

Goddard, M. 2009. Genomic selection: Prediction of accuracy and maximization of long-term response. Genetica 136:245–257.

Habier, D., R. L. Fernando, and J. C. M. Dekkers. 2007. The impact of genetic relationship information on genome-assisted breeding values. Genetics 177:2389–2397.

Illumina, Inc. 2011a. GoldenGate Bovine3K Genotyping BeadChip. Illumina data sheet. Accessed Sept. 16, 2011. http://www.illumina.com/Documents//products/datasheets/datasheet_bovine3k.pdf.

Illumina, Inc. 2011b. BovineSNP50 Genotyping BeadChip. Illumina data sheet. Accessed Sept. 16, 2011. http://www.illumina.com/Documents/products/datasheets/datasheet_bovine_snp5O.pdf.

Illumina, Inc. 2011c. BovineHD Genotyping BeadChip. Illumina data sheet. Accessed Sept. 16, 2011. http://www.illumina.com/Documents//products/datasheets/datasheet_bovineHD.pdf.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486–494.

Kriese, L. A., J. K. Bertrand, and L. L. Benyshek. 1991. Genetic and environmental growth trait parameter estimates for Brahman and Brahman-derivative cattle. J. Anim. Sci. 69:2362–2370.

Lancaster, P. A., G. E. Carstens, D. H. Crews Jr., T. H. Welsh Jr., T. D. A. Forbes, D. W. Forrest, L. O. Tedeschi, R. D. Randel and F. M. Rouquette. 2009. Phenotypic and genetic relationships of residual feed intake with performance and ultrasound carcass traits in Brangus heifers. J. Anim. Sci. 87:3887–3896.

Legarra, A. 2009. GS3. Inst. Natl. de la Rech. Agron. Accessed March 18, 2010. http://snp.toulouse.inra.fr/~alegarra/manualgs3_2.pdf.

Legarra, A., I. Aguilar, and I. Misztal. 2009. A relationship matrix including full pedigree and genomic information. J. Dairy Sci. 92:4656–4663.

Legarra, A., C. Robert-Granié, E. Manfredi, and J.-M. Elsen. 2008. Performance of genomic selection in mice. Genetics 180:611–618.

MacNeil, M. D., D. R. Bailey, J. J. Urick, R. P. Gilbert, and W. L. Reynolds. 1991. Heritabilities and genetic correlations for postweaning growth and feed intake of beef bulls and steers. J. Anim. Sci. 69:3183–3189.

Meuwissen, T. H. E., B. J. Hayes, and M. E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829.

Mujibi, F. D. N., J. D. Nkrumah, O. N. Durunna, P. Stothard, J. Mah, Z. Wang, J. Basarab, G. Plastow, D. H. Crews Jr., and S. S. Moore. 2011. Accuracy of genomic breeding values for residual feed intake in crossbred beef cattle. J. Anim. Sci. 89:3353–3361.

Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Can. J. Anim. Sci. 84:177–185.

Snelling, W. M., M. F. Allan, J. W. Keele, L. A. Kuehn, T. McDaneld, T. P. L. Smith, T. S. Sonstegard, R. M. Thallman, and G. L. Bennett. 2009. Genome-wide association study of growth in crossbred beef cattle. J. Anim. Sci. 88:837–848.

Snelling, W. M., M. F. Allan, J. W. Keele, L. A. Kuehn, R. M. Thallman, G. L. Bennett, C. L. Ferrell, T. G. Jenkins, H. C. Freetly, M. K. Nielsen, and K. M. Rolfe. 2011. Partial-genome evaluation of postweaning feed intake and efficiency of crossbred beef cattle. J. Anim. Sci. 89:1731–1741.

VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91:4414–4423.