Genomic-Polygenic Evaluation of Multibreed Angus-Brahman Cattle for Postweaning Ultrasound and Weight Traits with Actual and Imputed Illumina50k SNP Genotypes

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ABSTRACT: Additive genomic to total genetic variance fractions (VAGO/VGTOT) for postweaning ultrasound traits explained by 46,909 actual and imputed Illumina50k SNP genotypes were 0.17 for ribeye area (UREA), 0.32 for fat thickness (UFAT), 0.25 for percent intramuscular fat (UPIMF), and 0.19 for weight (UW) in a multibreed Angus-Brahman population. Heritabilities were 0.33 for UREA, 0.22 for UBF, 0.43 for UPIMF, and 0.54 for UW. The VAGO/VGTOT ratios were 1.8, 1.0, 4.4, and 2.1 times whereas heritabilities were 1.0, 1.2, 1.0, and 1.2 times those obtained for these traits with 2,899 Illumina3k SNP. Rank correlations between genomic-polygenic and polygenic EBV were the highest (0.93 to 0.96), followed by those between genomic-polygenic and genomic EBV (0.81 to 0.94), and by those between genomic and polygenic EBV (0.66 to 0.81). Regressions of EVB on Brahman fraction were low for all models and traits suggesting that animals of similar EBV existed in all breed groups.

Keywords:
Beef
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Introduction

Brahman and Brahman-*Bos taurus* crossbred cattle are widely used in Florida and other subtropical regions of the United States because of their superior adaptability to hot and humid climatic conditions. However, Brahman and high-percent crossbred Brahman cattle tend to have smaller ribeye areas, less marbling, and lower tenderness than *Bos taurus* cattle (Johnson et al., 1990; Elzo et al., 2012a). Hence the pressing need for accurate genetic predictions for carcass traits in Brahman and Brahman-*Bos taurus* crossbred populations. Ultrasound carcass traits are widely used because they are easy to measure and are closely associated with carcass traits (Houghton and Turlington, 1992). Genotypic data from could also be used to help increase accuracies of prediction for carcass traits. A combination of genotypes from low and high-density chips plus imputation (VanRaden et al., 2011, 2013) may be a cost-effective alternative to only using high-density chips. Consequently, the objectives of this research were: 1) to estimate fractions of additive genetic variances for postweaning ultrasound ribeye area (UREA), backfat thickness (UFAT), and percent intramuscular fat (UPIMF), and weight (UW) explained by 46,909 actual and imputed SNP genotypes, 2) to compare rankings of calf additive genetic predictions from genomic-polygenic (GP), genomic (G), and polygenic (P) models, and 3) to assess trends for GP, G, and P predicted additive genetic values as functions of Brahman fractions in a multibreed Angus-Brahman population.

Materials and Methods

Animals, management, and traits. Calves (n = 812; 66 bulls, 413 heifers, and 333 steers) were from the multibreed Angus-Brahman (MAB) herd of the University of Florida (UF), Gainesville. Project research protocol was approved by the UF Institutional Animal Care and Use Committee (IACUC #201003744). Calves were the offspring of 64 sires and 364 dams from 6 breed groups. Mating system was diallel (Elzo and Wakeman, 1998). Breed groups were as follows: Angus = (1.0 to 0.80) A (0.0 to 0.20) B, ¾ A ¼ B = (0.79 to 0.60) A (0.21 to 0.40) B, Brangus = (0.625) A (0.375) B, ½ A ½ B = (0.59 to 0.40) A (0.41 to 0.60) B, ¼ A ¾ B = (0.39 to 0.20) A (0.61 to 0.80) B, and Brahman: (0.19 to 0.0) A (0.81 to 1.00) B. Number of calves per breed group were 121 Angus, 163 ¾ A ¼ B, 143 Brangus, 192 ½ A ½ B, 87 ¼ A ¾ B, and 106 Brahman calves. Calves were kept at the UF Beef Unit until weaning. Calves were moved to the UF GrowSafe Feed Efficiency Facility (Marianna, Florida) after weaning to participate in a 70-d feed efficiency trial. Ultrasound measurements were taken at the conclusion of the feed efficiency trial by a trained technician using an Aloka 500 ultrasound system (Hitachi Aloka Medical, Ltd., Wallinford, Connecticut). Traits were ultrasound ribeye area (UREA, cm^2), ultrasound backfat thickness (UBF, cm), ultrasound percent of intramuscular fat (UPIMF, %), and body weight at the time ultrasound measurements were taken (UW, kg). Phenotypic records for UREA, UBF, and UPIMF were obtained by analyzing the ultrasonic images with UICS Scanning Software by Walter and Associates, LLC (Ames, Iowa).

Tissue sampling, genotyping, and imputation. Blood samples were collected at weaning using 10 mL EDTA vacutainer tubes, and stored at -80 °C at New Mexico State University. Genotyping with the Illumina3K chip was done at GeneSeek (GeneSeek, Inc., Lincoln, NE, USA). Imputation from Illumina3k to Illumina50k was done with program findhap2 (VanRaden, 2011) using a reference population of 828 registered Brangus heifers (Peters et al., 2012). A subset of output file "haplotypes" from findhap2 containing SNP marker information for MAB animals was matched with a phenotype file containing data on UREA, UBF, UPIMF, and UW. Only calves with information on all traits were kept (n = 812). Lastly, SNP with minor allele frequencies lower than 0.04 were discarded (n = 3,367). This resulted in a genotype file

of 812 animals with SNP data on 46,909 loci (2,648 actual Illumina3k SNP plus 44,261 imputed Illumina50k SNP).

Genomic-Polygenic Variances, Variance Ratios, and Predictions. Variance components for UREA, UBF, UPIMF, and UW were estimated using single-trait genomic-polygenic models (Legarra et al., 2008; Elzo et al., 2012b). 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 marker locus effect as a function of the number of "2" alleles in each locus (mean zero; variance = additive SNP variance), calf additive polygenic effect (mean zero; variance = A*Vg; A = additive relationship matrix, Vg = additive polygenic variance), and residual (mean zero, common variance). Variances and heritabilities were estimated using Markov Chain Monte Carlo (MCMC) procedures with option VCE of program GS3 (Legarra et al., 2013; Number of iterations = 120,000; Burn-in = 20,000). Starting values for additive polygenic variances (VAPO) and residual variances (VRES) were REML estimates from single-trait polygenic models obtained with program AIREMLF90 (Tsuruta, 2013), and those for additive SNP variances (VSNP) were equal to VAPO divided by the sum of twice the product of the frequencies of the two alleles within a locus over the 46,909 loci (2PQSUM). Posterior means and standard deviations for VAGO (= VSNP × 2PQSUM), VAPO, total additive genetic variances (VGTOT = VAGO + VAPO), phenotypic variances (PVAR), and heritabilities for UREA, UBF, UPIMF, and UW were computed using values from 1,000 MCMC post burn-in samples. Variances and variance ratios were also computed with polygenic models. Genomic-polygenic (GPEBV), genomic (GEBV), and polygenic predicted values (PEBV) for each trait were computed with option BLUP of program GS3 (convergence criterion = 10^{-8}) using the computed posterior means for VAGO, VAPO, and VRES. Calf rankings across models were compared using Spearman's rank correlations. Linear regressions of GPEBV, GEBV, and PEBV on Brahman fraction were used to assess prediction trends as Brahman fraction increased.

Results and Discussion

Genomic and polygenic variance components and variance ratios. Table 1 shows posterior means for VAGO, VAPO, VGTOT and PVAR from genomic-polygenic models, and additive polygenic (VGPO) and phenotypic variances (PVARPO) from polygenic models for UREA, UBF, UPIMF, and UW. Correspondingly, Table 2 presents posterior means for variance ratios from genomic-polygenic and polygenic models these 4 traits. Estimates of VAGO/PVAR ratios here were lower than estimates for UREA (0.22), UBF (0.17), UPIMF (0.28), and 365-d weight (0.19) with 53,692 actual Illumina50k SNP markers in the reference Brangus population perhaps partly due to imputation errors and lower linkage disequilibrium in the MAB population. Estimates of VAGO and VAGO/PVAR ratios were comparable for UBF but larger for the other 3 traits (from 81% for UREA to 343% for UPIMF) than VAGO and VAGO/PVAR estimates with the Illumina3k chip (Table 3; Elzo et al., 2013). However, estimates of PVAR were similar suggesting that the 46,909 actual and imputed SNP from the Illumina50k chip explained a substantially larger fraction of VAGO than the 2,899 SNP from the Illumina3k. However, estimates of VGTOT were only larger for UBF (24%) and UW (16%) and PVAR estimates were alike for all 4 traits here and with the Illumina3k (Elzo et al., 2013). Thus, higher estimates of heritability existed only for UBF (22%) and UW (19%). Lastly, VGTOT from genomic-polygenic models were larger than VGPO from polygenic models for all traits (from 21% for UREA to 41% for UBF) indicating that the 46,909 actual-imputed SNP may have accounted for genetic variation beyond that explained by polygenic models.

Ranking of animals evaluated with genomic-polygenic, genomic, and polygenic models. The highest rank correlations were between EBV from the GP and P models (0.93 to 0.96; $P < 0.0001$), followed by those between EBV from the GP and G models (0.81 to 0.94; $P < 0.0001$), and by those were between EBV from the G and P models (0.66 to 0.81; $P < 0.0001$; Table 4). Rank correlations between GP and P EBV with actual-imputed Illumina50k SNP were similar to rank correlations using Illumina3k SNP (Elzo et al., 2013). Contrarily, rank correlations between GP and G EBV and between G and P EBV here were, on the average, 25% higher (range: 9% to 47%) than corresponding values with Illumina3k SNP. This suggested that, despite imputation errors, the imputed Illumina50k SNP provided sizeable additional information on QTL affecting UREA, UBF, UPIMF, and UW, thus increasing the similarity between G, GP and P EBV. Ultimately, the high rank correlations between P and GP EBV indicated that a polygenic model would be enough to appropriately rank animals for UREA, UBF, UPIMF, and UW in this multibreed Angus-Brahman population.

Trends of genomic-polygenic, genomic, and polygenic EBV from Angus to Brahman. Regressions of EVB on Brahman fraction were low for all traits and models. Significant regression values ($P < 0.0364$ to $P < 0.0001$) existed for UREA (G model), UBF (GP and G models), and UW (all models). Although EBV tended to decrease from Angus to Brahman, these low regression estimates indicated that there were animals of similar EBV for UREA, UBF, UPIMF, and UW across all Angus-Brahman breed compositions.

Conclusion

Higher fractions of additive genomic variation for UREA, UBF, UPIMF, and UW were accounted for by 46,909 actual and imputed Illumina50k SNP than by 2,899 Illumina3k SNP in an Angus-Brahman multibreed population. However, total genetic variation and heritabilities increased only for UBF and UW. Higher rank correlations between genomic and genomic-polygenic and between genomic and polygenic models with the actual-imputed Illumina50k indicated closer agreement among EBV rankings from these models than with the Illumina3k. Low regression values of EBV on Brahman fraction

indicated that similar EBV for ultrasound and weight traits existed in animals of all Angus-Brahman fractions.

Literature Cited

Elzo, M. A., D. D. Johnson, J. G. Wasdin, and J. D. Driver. 2012a. Carcass and meat palatability breed differences and heterosis effects in an Angus-Brahman multibreed population. Meat Sci. 90:87-92.

Elzo, M. A., G. C. Lamb, D. D. Johnson, M. G. Thomas, I. Misztal, D. O. Rae, C. A. Martinez, J. G. Wasdin, J. D. Driver. 2012b. Genomic-polygenic evaluation of Angus-Brahman multibreed cattle for feed efficiency and postweaning growth using the Illumina3k chip. J. Anim. Sci. 90: 2488-2497.

Elzo, M. A., C. A. Martinez, G. C. Lamb, D. D. Johnson, M. G. Thomas, I. Misztal, D. O. Rae, J. G. Wasdin, and J. D. Driver. 2013. Genomic-polygenic evaluation for ultrasound and weight traits in Angus-Brahman multibreed cattle with the Illumina3k chip. Livest. Sci. 153:39-49.

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.

Houghton, P. L., and L. M. Turlington. 1992. Application of ultrasound for feeding and finishing animals: a review. J Anim. Sci. 70:930-941.

Johnson, D. D., R. D. Huffman, S. E. Williams, and D. D. Hargrove, 1990. Breeding, age-season of feeding and slaughter end point on meat palatability and muscle characteristics. J. Anim. Sci., 68:1980-1986.

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

Legarra, A., A. Ricard, and O. Filangi. 2013. GS3. INRA, Auzeville, France. Available at: http://snp.toulouse.inra.fr/~alegarra/manualgs3_last.pdf.

Peters, S. O., K. Kizilkaya, D. J. Garrick, R. L. Fernando, J. M. Reecy, R. L. Weaber, G. A. Silver, and M. G. Thomas. 2012. Bayesian genome wide association analyses of growth and yearling ultrasound measures of carcass traits in Brangus heifers. J. Anim. Sci. 90:3398-3409.

Tsuruta, S. 2013. Average Information REML with several options including EM-REML and heterogeneous residual variances. Available at: http://nce.ads.uga.edu/wiki/doku.php?id=application_programs.

VanRaden, P. M. 2011. Findhap.f90. Available at: http://aipl.arsusda.gov/software/findhap.

VanRaden, P. M., D. J. Null, M. Sargolzaei, G. R. Wiggans, M. E. Tooker, J. B. Cole, T. S. Sonstegard, E. E. Connor, M. Winters, J. B. C. H. M. van Kaam, A. Valentini, B. J. Van Doormaal, M. A. Faust, and G. A. Doak. 2013. Genomic imputation and evaluation using high-density Holstein genotypes. J. Dairy Sci. 96:668-678.

Table 1. Posterior means for additive genomic, polygenic, total genetic and phenotypic variances

Variance[2]	Trait[1] UREA, cm^4	UBF, cm^2	UPIMF, $\%^2$	UW, kg^2
VAGO	3.74	0.002	0.08	146.5
VAPO	18.18	0.005	0.24	631.7
VGTOT	21.92	0.007	0.32	778.2
PVAR	55.79	0.023	0.59	1198.8
VGPO	18.12	0.005	0.25	639.9
PVARPO	55.04	0.022	0.58	1177.0

[1]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[2]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTOT = total genetic variance = VAGO + VAPO; PVAR = phenotypic variance; VGPO = additive genetic variance from a polygenic model; PVARPO = phenotypic variance from a polygenic model.

Table 2. Posterior means for additive genetic and genomic variance ratios

Variance Ratios[2]	Trait[1] UREA	UBF	UPIMF	UW
VAGO/VGTOT	0.17	0.32	0.25	0.19
VAGO/PVAR	0.07	0.10	0.14	0.12
Heritability	0.39	0.31	0.55	0.65
HeritabilityPO	0.33	0.22	0.43	0.54

[1]UREA = ultrasound ribeye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[2]VAGO = additive genomic variance; VGTOT = total genetic variance; PVAR = phenotypic variance; HeritabilityPO = heritability from a polygenic model.

Table 3. Ratios of posterior means of variances and variance ratios from actual-imputed Illumina50k and Illumina3k[1] genomic-polygenic analyses

Ratio 50k/3k	Trait[2] UREA	UBF	UPIMF	UW
VAGO[3]	1.81	1.03	4.42	2.08
VAPO	0.90	1.37	0.82	1.03
VGTOT	0.99	1.24	1.03	1.16
PVAR	0.99	1.02	1.00	0.98
VAGO/VGTOT	1.87	0.83	4.14	2.24
VAGO/PVAR	1.83	1.02	4.43	2.65
Heritability	1.00	1.22	1.04	1.19

[1]Elzo et al. (2013).
[2]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[3]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTOT = VAGO + VAPO; PVAR = phenotypic variance.

Table 4. Spearman rank correlations for animals evaluated using genomic-polygenic, genomic, and polygenic models

Correlation[2]	Trait[1] UREA	UBF	UPIMF	UW
GP Model, G Model	0.86	0.87	0.94	0.81
GP Model, P Model	0.95	0.93	0.95	0.96
G Model, P Model	0.71	0.66	0.81	0.71

[1]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[2]GP Model = genomic-polygenic model; G Model = genomic model; P Model = polygenic model. All correlations were significant ($P < 0.0001$).