Genomic Variability and Predictions for Postweaning Ultrasound Traits Using Actual and Imputed Illumina50k SNP Markers in Angus-Brahman Multibreed Cattle

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Synapsis

Higher fractions of additive genomic variation for ultrasound ribeye area, backfat thickness, intramuscular fat, and weight were accounted for by 46,839 actual and imputed Illumina50k SNP compared to 2,899 SNP Illumina3k in a multibreed Angus-Brahman population. However, total genetic variation and heritabilities increased only for ultrasound back fat and ultrasound weight. Rank correlations between estimated breeding value from genomic-polygenic, genomic, and polygenic models were higher with actual-imputed Illumina50k than with the Illumina3k. Low regressions of estimated breeding value on Brahman fraction indicated that animals of comparable estimated breeding value for ultrasound and weight traits existed across all Angus-Brahman fractions.

Summary

The objectives were to estimate additive genetic variance fractions for 4 postweaning ultrasound and weight traits explained by 46,839 actual and imputed SNP genotypes, to compare rankings of calf additive genetic predictions from genomic-polygenic (GP), genomic (G), and polygenic (P) models, and to assess trends for GP, G, and P predicted additive genetic values as functions of calf Brahman fractions in a multibreed Angus-Brahman population. Traits were postweaning ultrasound ribeye area (UREA), backfat thickness (UBF), and percent intramuscular fat (UPIMF), and weight (UW). Phenotypes and Illumina3k genotypes were from 812 bulls, heifers, and steers housed at the Feed Efficiency Facility of the University of Florida from 2006 to 2010. Program findhap2 was used to impute from 2,899 Illumina3k SNP to 46,839 Illumina50k SNP using a reference population of 828 Brangus heifers. Fixed effects for all models 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 (GP and G models), additive polygenic (GP and P models), and residual. Program GS3 was used to compute variance components, heritabilities, and additive genetic predictions. Additive genetic variance fractions explained by the 46,839 actual and imputed SNP were 0.17 for UREA, 0.32 for UBF, 0.25 for UPIMF, and 0.19 for UW. Heritabilities were 0.33 for UREA, 0.22 for UBF, 0.43 for UPIMF, and 0.54 for UW. These additive genetic variance fractions were 1.8, 1.0, 4.4, and 2.1 times greater and heritabilities were 1.0, 1.2, 1.0, and 1.2 times greater than those obtained with the 2,899 SNP from Illumina3k. Rank correlations between estimated breeding value (EBV) from GP and P models were the highest (0.93 to 0.96), followed by those between EBV from GP and G models (0.81 to 0.94), and by those between estimated breeding value from G and P models (0.66 to 0.81). Regression coefficients of EVB on Brahman fraction were small for all traits and models indicating that animals of comparable EBV existed in all breed groups. Imputation from Illumina3k to 50k increased the explained fraction of additive SNP variance resulting in higher rank correlations between additive genetic predictions from G and GP, and from G and P models for all ultrasound traits in this population.

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

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marbling, and lower tenderness than *Bos taurus* cattle, hence the pressing need for accurate genetic predictions for carcass traits in Brahman and Brahman-*Bos taurus* crossbred populations. Although high cost has restricted the availability of carcass data, ultrasound carcass measurements are widely used because they are cheaper, easier to measure, and closely associated with carcass traits (Houghton and Turlington, 1992). Another alternative to increase the accuracy of genetic predictions for carcass traits would be to genotype animals with high-density chips. A combination of low and high-density chips plus imputation (Dassonneville et al., 2011; VanRaden et al., 2013) may be a cost-effective alternative to the use of high-density chips throughout a population. Thus, the objectives of this research were: 1) to estimate fractions of additive genetic variances for postweaning ultrasound ribeye area (UREA), backfat thickness (UBF), percent intramuscular fat (UPIMF), and weight (UW) explained by 46,839 actual and imputed SNP genotypes, 2) to compare rankings of 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, Feeding, and Management

The multibreed Angus-Brahman calves used in this study (n=812; 66 bulls, 413 heifers, and 333 steers) were born at the Beef Research Unit (BRU) of the University of Florida from 2006 to 2010. Calves were the offspring of 64 sires from 6 breed groups mated to 364 dams from these same 6 breed groups according to a diallel mating design (Elzo and Wakeman, 1998). Breed groups were: 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. Numbers of calves per breed group are shown in Table 1. Calves stayed at the BRU from birth to weaning. Postweaning, calves received a preconditioning diet (3.5 lb to 7.9 lb concentrate per day; 14.0 % crude protein; 488 Pellet, Medicated Weaning Ration, Lakeland Animal Nutrition, Lakeland, FL; soy hull pellets, mineral supplement, and bahiagrass hay) for 3 to 4 weeks before moving them to the University of Florida Feed Efficiency Facility (UFFEF) in Marianna, Florida. At UFFEF, calves were randomly assigned to pens within sire group (Angus, ¾ A ¼ B, Brangus, ½ A ½ B, ¼ A ¾ B, and Brahman) by sex (bull, heifer, and steer) subclass and fed an ad libitum ration of corn or corn gluten, cottonseed hulls, molasses, chopped grass hay, and a vitamin-mineral-protein supplement. Average dry matter, crude protein, net energy for maintenance, and net energy for gain were 89.2%, 12.9%, 0.7 mcal/lb DM, and 0.5 mcal/lb DM from 2006 to 2010, respectively.

Traits

Traits were postweaning ultrasound ribeye area (UREA, in^2), ultrasound backfat thickness (UBF, in), ultrasound percent of intramuscular fat (UPIMF, %), and body weight on the day that ultrasound measurements were taken (UW, lb). Ultrasound traits were measured by a certified technician using an Aloka 500 ultrasound system (Hitachi Aloka Medical, Ltd., Wallinford, Connecticut, USA) at the end of the 70-d feed efficiency trial. Phenotypic data for UREA, UBF, and UPIMF were obtained by analyzing the ultrasonic images with UICS Scanning Software by Walter and Associates, LLC (Ames, Iowa, USA).

Tissue sampling, Genotyping, and Imputation

Blood samples were collected at weaning using 10 mL EDTA vacutainer tubes. Samples were processed at New Mexico State University (NMSU) and stored at -80 °C. Genotyping with the Illumina3k was done at GeneSeek (Gene Seek, 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 (Fortes et al., 2012) genotyped with version 1 of the Illumina50k chip. The output file "haplotypes" from findhap2 was matched with a file containing phenotypic data for UREA, UBF, UPIMF, and UW. Only calves with phenotypes for all 4 traits were kept (n=812). Lastly, SNP with minor allele frequencies lower than 0.04 were discarded (n=3,437). This resulted in a genotype file of 812 animals with SNP data on 46,839 loci (2,641 actual Illumina3k SNP plus 44,198 imputed Illumina50k SNP). These phenotype, genotype, and pedigree files were used as input files for the GS3

program (Legarra et al., 2013) used to compute genomic-polygenic variance components and variance ratios, and genomic-polygenic, genomic, and polygenic predictions.

Genomic-Polygenic Variance Components, Variance Ratios, and Predictions

Single-trait genomic-polygenic mixed models (VanRaden, 2008; Legarra et al., 2008; Elzo et al., 2013) were used to obtain variance components for UREA, UBF, UPIMF, and UW. The mixed model contained: 1) contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf as fixed effects; and 2) 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) as random effects. The procedure used to estimate variance components and heritabilities was Markov Chain Monte Carlo (MCMC). Computations were carried out with program GS3, option VCE (Legarra et al., 2013). Additive genomic variances (VAGO), polygenic variances (VAPO), total additive genetic variances (VGTOT), phenotypic variances (PVAR), and heritabilities were computed for each MCMC sample as follows: 1) VAGO = SNP variance × $\sum_{i=1}^{46,839} 2(1-q_i)q_i$, where q_i = frequency of allele "2" in locus i; 2) VGTOT = VAGO + VAPO; 3) PVAR = VAGO + VAPO + residual variance; and 4) heritability = VGTOT/PVAR. Posterior means and standard deviations for VAGO, VAPO, VGTOT, PVAR and heritabilities for UREA, UBF, UPIMF, and UW were computed using 1,000 MCMC samples following the burn-in period. Polygenic variances and heritabilities were also estimated with polygenic models for comparison purposes.

Genomic-Polygenic, Genomic, and Polygenic Predictions

Genomic-polygenic (GPEBV), genomic (GEBV), and polygenic predicted values (PEBV) for each trait were computed with option BLUP of program GS3 (Gauss-Seidel iteration; convergence criterion = 10^{-8}) using genomic-polygenic, genomic, and polygenic models and posterior means of VAGO, VAPO, and VRES. Calf rankings across models were compared using Spearman's rank correlations. Linear regressions of GPEBV, GEBV, and PEBV on calf Brahman fraction were used to assess trends in predicted values as Brahman fraction increased.

Results

Overall means were 9.1 in^2 for UREA, 0.25 in for UBF, 2.78 % for UPIMF, and 761.5 lb for UW (Table 1). The largest means were those of ¼ A ¾ B calves for UREA (9.6 in^2) and UBF (0.28 in), Angus calves for UPIMF (3.16 %), and ¾ A ¼ B for UW (784.2 lb). The smallest means were from Brahman calves for UREA (8.4 in^2), UBF (0.24 in), and UW (691.1 lb), and ¼ A ¾ B calves for UPIMF (2.40 %). The largest SD were in Angus for UREA (2.1 in^2), ¼ A ¾ B and Brahman for UBF (0.17 in), Brahman for UPIMF (1.62 %), and ¾ A ¼ B for UW (131.0 lb), and the smallest SD were those of Brahman calves for UREA (1.7 in^2) and UW (106.9 lb), ¾ A ¼ B, Brangus, and ½ A ½ B calves for UBF (0.15 in) and Brangus calves for UPIMF (1.47 %).

Genomic and Polygenic Variance Components and Variance Ratios

Table 2 contains posterior means and SD 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. Table 3 presents posterior means and SD for variance ratios (VAGO/VGTOT and VAGO/PVAR) and heritabilities from genomic-polygenic and polygenic models for UREA, UBF, UPIMF, and UW. Estimates of VAGO with Illumina50k SNP markers were between 3% (UBF) to 342% (UPIMF) larger than estimates with Illumina3k SNP markers, whereas VAPO estimates with the Illumina50k were lower for UREA and UPIMF and higher for UBF and UW than with the Illumina3k (Table 4). Consequently, estimates of VGTOT with the Illumina50k were similar for UREA and UPIMF but larger for UBF (24%) and UW (16%) than with the Illumina3k. Thus, heritabilities with the Illumina50k were also similar for UREA and UPIMF and larger for UBF (22%) and UW (19%) than with the Illumina3k because PVAR estimates had similar values for all ultrasound traits with both Illumina chips (Table 4). Estimates of VGTOT from genomic-polygenic models were larger

than VGPO from polygenic models for all ultrasound traits (from 21% for UREA to 40% for UBF) indicating that the 46,839 actual-imputed SNP may have accounted for genetic variation beyond that explained by polygenic models. Lastly, because PVAR from genomic-polygenic and polygenic models were similar (Table 5), heritability estimates from genomic-polygenic models for all ultrasound traits were larger than estimates from polygenic models for all traits (from 18% for UREA to 41% for UBF).

Rankings of Animals Evaluated with Genomic-Polygenic, Genomic, and Polygenic Models

The highest rank correlations were between EBV from the GP and P models (from 0.93 for UBF to 0.96 for UW; $P<0.0001$), followed by those between EBV from the GP and G models (from 0.81 for UW to 0.94 for UPIMF; $P<0.0001$), and lastly by those between EBV from the G and P models (from 0.66 for UBF to 0.81 for UPIMF; $P<0.0001$). Rank correlations between EBV from GP and P models here were similar to rank correlations between GP and P models with Illumina3k (Elzo et al., 2013). Conversely, rank correlations between EBV from GP and G and from G and P models here were on the average 26% and 24% higher than corresponding values with Illumina3k SNP markers. These rank correlations suggested that some of the 44,198 imputed SNP from the Illumina50k chip were in linkage disequilibrium with QTL affecting UREA, UBF, UPIMF, and UW that provided additional additive genetic information for these traits, and increased the similarity among calf G, GP and P EBV in this population. Lastly, ultrasound trait EBV rankings from GP, G, and P models with actual-imputed Illumina50k SNP markers here and with Illumina3k SNP markers (Elzo et al., 2013) were compared using a subset of 615 calves present in both datasets. Higher rank correlations existed between EBV from Illumina50k and Illumina3k datasets with GP models (from 0.90 for UBF to 0.95 for UW), than rank correlations between EBV with P models (from 0.88 for UREA to 0.94 for UW) and G models (from 0.62 for UW to 0.78 for UBF). This indicated that the sets of actual-imputed Illumina50k and Illumina3k genotypes captured a substantially lower fraction of the additive genetic variation relative to polygenic effects and that their contribution to the EBV from GP models was small for all ultrasound traits. Thus, rank correlations between EBV from GP, P, and G models within and across Illumina50k and Illumina3k datasets suggested that polygenic models would be enough to rank animals appropriately for ultrasound and feed efficiency traits in this multibreed population.

Trends of genomic-polygenic, genomic, and polygenic EBV from Angus to Brahman

Regression coefficients of calf EVB on Brahman fraction were small for all ultrasound traits and GP, G, and P models. Significant regression values ($P<0.04$ to $P<0.0001$) existed for UREA (G model), UBF (GP and G models), and UW (all models). A similar pattern of significance was obtained with the Illumina3k MAB dataset (Elzo et al., 2013). Although EBV computed with GP, G, and P models tended to decrease as Brahman increased for all ultrasound traits in the actual-imputed Illumina50k and Illumina3k datasets, regression estimates were low for all traits indicating that this population contained animals with analogous EBV for UREA, UBF, UPIMF, and UW across all breed compositions.

Acknowledgements

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Table 1. Numbers of calves, means and standard deviations per breed group and total

		Trait[a]							
		UREA, in^2		UBF, in		UPIMF, %		UW, lb	
Breed group	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angus	121	9.3	2.1	0.26	0.16	3.16	1.57	775.4	126.5
¾ A ¼ B	163	9.2	1.9	0.25	0.15	2.89	1.60	784.2	131.0
Brangus	143	9.0	1.8	0.25	0.15	2.72	1.47	761.7	110.9
½ A ½ B	192	9.0	1.8	0.24	0.15	2.77	1.55	771.2	124.6
¼ A ¾ B	87	9.6	1.9	0.28	0.17	2.40	1.55	763.9	111.6
Brahman	106	8.4	1.7	0.24	0.17	2.57	1.62	691.1	106.9
Total	812	9.1	1.9	0.25	0.16	2.78	1.57	761.5	123.5

[a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.

Table 2. Posterior means and standard deviations for additive genomic, polygenic, total genetic and phenotypic variances

	Trait[a]			
Variance[b]	UREA, in^4	UBF, in^2	UPIMF, %^{2}	UW, lb^2
VAGO	0.09 ± 0.06	0.0003 ± 0.0002	0.08 ± 0.05	712.0 ± 397.6
VAPO	0.44 ± 0.12	0.0008 ± 0.0003	0.24 ± 0.06	3070.3 ± 674.6
VGTOT	0.53 ± 0.13	0.0011 ± 0.0003	0.32 ± 0.07	3782.3 ± 750.9
PVAR	1.34 ± 0.07	0.0036 ± 0.0002	0.59 ± 0.03	5826.6 ± 357.2
VGPO	0.44 ± 0.11	0.0008 ±0.0002	0.25 ± 0.05	3110.1 ± 638.2
PVARPO	1.32 ± 0.07	0.0034 ±0.0002	0.58 ± 0.03	5720.6 ± 347.2

[a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[b]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 3. Posterior means and standard deviations for additive genetic and genomic variance ratios

	Trait[a]			
Variance Ratios[b]	UREA	UBF	UPIMF	UW
VAGO/VGTOT	0.17 ± 0.12	0.32 ± 0.17	0.25 ± 0.13	0.19 ± 0.10
VAGO/PVAR	0.07 ± 0.05	0.10 ± 0.06	0.14 ± 0.08	0.12 ± 0.07
Heritability	0.39 ± 0.08	0.31 ± 0.08	0.55 ± 0.10	0.65 ± 0.10
HeritabilityPO	0.33 ± 0.08	0.22 ± 0.06	0.43 ± 0.08	0.54 ± 0.09

[a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[b]VAGO = additive genomic variance; VGTOT = VAGO + VAPO; PVAR = phenotypic variance; HeritabilityPO = heritability from a polygenic model.

Table 4. Ratios of posterior means of variances and variance ratios from actual-imputed Illumina50k[a] and Illumina3k[b] genomic-polygenic analyses

	Trait[c]			
Ratio 50k/3k[d]	UREA	UBF	UPIMF	UW
VAGO	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

[a]2,641 actual Illumina3k SNP plus 44,198 imputed Illumina50k SNP.
[b]2,899 Illumina3k SNP (Elzo et al., 2013).
[c]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.
[d]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTOT = VAGO + VAPO; PVAR = phenotypic variance.

Table 5. Ratios of posterior means of variances and variance ratios from genomic-polygenic and polygenic models

	Trait[a]			
Ratio[b]	UREA	UBF	UPIMF	UW
VAPO/VGPO	1.00	1.00	0.96	0.99
VGTOT/VGPO	1.21	1.40	1.28	1.22
PVAR/PVARPO	1.01	1.05	1.02	1.02
Heritability/HeritabilityPO	1.18	1.41	1.28	1.20

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