1 Genomic-polygenic evaluation of multibreed Angus-Brahman cattle for postweaning
2 ultrasound and weight traits with actual and imputed Illumina50k SNP genotypes

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Abstract

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 bull, heifer, and steer calves 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. Software GS3 was used to compute variance components and 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 for these 4 traits using only the 2,899 Illumina3k SNP. Rank correlations between 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 EBV 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 Angus-Brahman multibreed population.

Key words: Beef; Imputation; Multibreed; Ultrasound

1. 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 (Elzo et al., 2012a; Johnson et al., 1990; Pringle et al., 1997; Wheeler et al., 2010), 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). Genotypic data from low and high density SNP chips could also be used to help increase accuracies of prediction for carcass traits. However, the cost of high-density chips likely remains an issue for most beef production systems. Thus, a combination of low and high-density chips plus imputation (Dassonneville et al., 2011; Khatkar et al., 2012; Sargolzaei et al., 2011a, b, c; VanRaden et al., 2011, 2013; Weigel et al., 2010) may be a cost-effective alternative to the use of high-density chips throughout a

population. Consequently, 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 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.

2. Materials and methods

2.1. Animals, feeding, and management

The research protocol for this project was approved by the University of Florida Institutional Animal Care and Use Committee (IACUC protocol number 201003744). Calves were from the multibreed Angus-Brahman (MAB) herd of the University of Florida, Gainesville. A total of 812 calves (66 bulls, 413 heifers, and 333 steers) born from 2006 to 2010 were used in this study. 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 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. Numbers 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 reared at the Beef Research Unit (BRU) of the University of Florida from birth to weaning. Calves received a preconditioning diet for 3 to 4 wk postweaning before moving to the University of Florida Feed Efficiency Facility (UFFEF) in Marianna, Florida.

The preconditioning diet consisted of concentrate (1.6 kg to 3.6 kg per day; 14.0 % CP; 488 Pellet, Medicated Weaning Ration, Lakeland Animal Nutrition, Lakeland, Florida; and soy hull pellets), ad libitum mineral supplement, and bahiagrass (*Paspalum notatum*) hay. Upon arrival to UFFEF, calves were identified with half-duplex passive transponder ear tags (Allflex USA Inc., Dallas-Fort Worth, TX). The feed efficiency trial at UFFEF consisted of an adjustment period of 21 d and a trial period of 70 d. Calves from each sire group (Angus, ¾ A ¼ B, Brangus, ½ A ½ B, ¼ A ¾ B, and Brahman) by sex (bull, heifer, and steer) category were randomly allocated to pens (108 m^2/pen; 2 GrowSafe nodes per pen; mean stocking rate = 15 calves/pen; 7.5 calves/GrowSafe node). The components of the ad libitum ration at UFFEF were whole corn or corn gluten, cottonseed hulls, molasses, chopped grass hay, and a vitamin-mineral-protein supplement. Average values of dry matter, crude protein, net energy for maintenance, and net energy for gain were 89.2%, 12.9%, 1.6 mcal/kg DM, and 1.0 mcal/kg DM from 2006 to 2010, respectively.

2.2. Traits

Traits were postweaning ultrasound ribeye area (UREA, cm^2), ultrasound backfat thickness (UBF, cm), ultrasound percent of intramuscular fat (UPIMF, %), and body weight on the day that ultrasound measurements were taken (UW, kg). Ultrasound traits were measured by a certified technician using an Aloka 500 ultrasound system (Hitachi Aloka Medical, Ltd., Wallinford, Connecticut, USA) at the conclusion 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).

2.3. 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. Processing consisted of centrifugation for 30 min at 1,875 g at 4°C, recovery of white blood cell supernatant, and addition of sterile phosphate-buffered saline up to a volume of 1.0 mL (Beauchemin et al., 2006). Subsequently, genotyping with the Illumina3k (Illumina, 2011a) was done at GeneSeek (Gene Seek, Inc., Lincoln, NE, USA). Imputation from the Illumina3k to the Illumina50k (Illumina, 2011b) was done with program Findhap2 (VanRaden, 2011) using a reference population (RP) of 828 registered Brangus heifers (Fortes et al., 2012; Peters et al., 2012, 2013) genotyped with version 1 of the Illumina50k chip. Relationships among animals within MAB and RP were accounted for. However, pedigree data relating animals from the MAB and RP populations were unavailable. Consequently, MAB animals were assumed to be unrelated to RP animals. The combined MAB-RP pedigree file had 8,720 animals (6,674 from MAB and 2,046 from RP).

The SNP markers from the Illumina3k (n = 2900) were matched to a subset of SNP markers in common in versions 1 and 2 of the Illumina50k chip (n = 50,276) using SNP locations from Illumina50k version 2. This intermediate step was required because RP animals were genotyped with version 1 of the Illumina50k chip which specified a different location for an SNP present in the Illumina3k and version 2 of the Illumina50k. A total of 2,816 SNP from the Illumina3k chip were present in the set of 50,276 Illumina50k SNP. Accordingly, the input files for program Findhap2 were: 1) a genotype file with gene content information (i.e., number of "second alleles" = 0, 1, 2, and 5 for unknown) for 2,816 Illumina3k loci from 1,300 MAB animals and from 50,276 Illumina50k loci from 828 RP heifers; 2) a chromosome data file with the SNP name, chromosome number, SNP

number within and across chromosomes, SNP location in base pairs, and SNP number in the Illumina50k and 3k chips; and 3) a pedigree file containing animals, sires and dams from the MAB and RP populations. The subset of output file "haplotypes" from Findhap2 containing SNP marker information for MAB animals was matched with a file containing phenotypic data for UREA, UBF, UPIMF, and UW. Only calves with information on all 4 traits in the phenotype file 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 MAB 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.

2.4. Genomic-Polygenic Variance Components, Variance Ratios, and Predictions

Single-trait genomic-polygenic mixed models (VanRaden, 2008; Legarra et al., 2008; Snelling et al., 2011; Elzo et al., 2012b, 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.

155 The procedure used to estimate variance components and heritabilities was Markov
156 Chain Monte Carlo (MCMC). Computations were done with program GS3, option VCE
157 (Legarra et al., 2013; Number of iterations = 120,000; Burn-in = 20,000; Thinning = 100;
158 Correction = 10,000). Starting values for additive polygenic variances (VAPO) and
159 residual variances (VRES) were REML estimates from single-trait polygenic mixed models
160 obtained with program AIREMLF90 (Tsuruta, 2013). Starting values for additive SNP
161 variances (VSNP) were equal to $\widehat{Vg}$ /2PQSUM, where $\widehat{Vg}$ = AIREML estimate of the
162 additive polygenic variance from a single-trait polygenic model computed using
163 AIREMLF90, and 2PQSUM = $\sum_{i=1}^{46,839} 2p_i q_i$, where p_i = frequency of allele "1" and q_i =
164 frequency of allele "2" in SNP marker locus i. Additive genomic variances (VAGO), total
165 additive genetic variances (VGTOT), phenotypic variances (PVAR), and heritabilities were
166 computed for each MCMC sample as follows: 1) VAGO = VSNP × 2PQSUM; 2) VGTOT
167 = VAGO + VAPO; 3) PVAR = VAGO + VAPO + VRES; and 4) heritability =
168 VGTOT/PVAR. Posterior means and standard deviations for VAGO, VAPO, VGTOT,
169 PVAR and heritabilities for UREA, UBF, UPIMF, and UW were computed using values
170 from the set of 1,000 MCMC samples following the burn-in period. Polygenic variances
171 (VAPO, VRES, and PVAR) and heritability ratios were estimated with polygenic models
172 for the 4 ultrasound traits for comparison purposes. These polygenic models included the
173 same set of fixed and random effects as genomic-polygenic models, except for additive
174 SNP marker locus effects. Computations were also carried out with option VCE of
175 program GS3 using the same number of iterations, burn-in, thinning and correction values
176 as indicated above.

177 Genomic-polygenic (GPEBV), genomic (GEBV), and polygenic predicted values
178 (PEBV) for each trait were computed with option BLUP of program GS3 (Gauss-Seidel
179 iteration; convergence criterion = 10^{-8}) using genomic-polygenic, genomic (no polygenic
180 effects), and polygenic models (no genomic effects) and posterior means of VAGO, VAPO,
181 and VRES. Calf rankings across models were compared using Spearman's rank
182 correlations. Linear regressions of GPEBV, GEBV, and PEBV on calf Brahman fraction
183 were used to assess trends in predicted values as Brahman fraction increased.
184 Predictive abilities of the GP, G, and P models for UREA, UBF, UPIMF, and UW
185 were computed using correlations between predicted genomic-polygenic, genomic, and
186 polygenic values and phenotypes from calves in a validation dataset (Legarra et al., 2008)
187 that produced records in 2010 (n = 186; 22.9% of the dataset). The training dataset was
188 composed of records produced by calves between 2006 and 2009 (n = 626; 77.1% of the
189 dataset). The models used to obtain GPEBV, GEBV, and PEBV in the training population
190 were the same as those used in the complete dataset. Ratios of predictive abilities to square
191 roots of heritabilities yielded accuracies of prediction for the three models in the validation
192 dataset (Legarra et al., 2008).
193

194 **3. Results and discussion**

195 Numbers of calves, means, and SD per breed group and the complete dataset for
196 UREA, UBF, UPIMF, and UW are shown in Table 1. Numbers of calves per breed group
197 ranged from 87 for ¼ A ¾ B to 192 for ½ A ½ B. Complete dataset means were 58.6 cm^2
198 for UREA, 0.64 cm for UBF, 2.78 % for UPIMF, and 345.4 kg for UW. The largest breed
199 group means were those of ¼ A ¾ B calves for UREA (62.0 cm^2) and UBF (0.71 cm),
200 Angus calves for UPIMF (3.16 %), and ¾ A ¼ B for UW (355.7 kg), whereas the smallest

breed group means were from Brahman calves for UREA (54.4 cm^2), UBF (0.60 cm), and UW (313.5 kg), and ¼ A ¾ B calves for UPIMF (2.40 %). The largest SD were observed in Angus for UREA (13.4 cm^2), Brahman for UBF (0.43 cm) and UPIMF (1.62 %), and ¾ A ¼ B for UW (59.4 kg), and the smallest SD corresponded to Brahman calves for UREA (10.8 cm^2) and UW (48.5 kg), and Brangus calves for UBF (0.38 cm) and UPIMF (1.47 %).

3.1. 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. The VAGO/PVAR ratio estimates here were lower than those computed in the Brangus RP (n = 802 heifers) for UREA (0.22), UBF (0.17), UPIMF (0.28), and 365-d weight (0.19) using a Bayes-C procedure (Habier et al., 2011) with 53,692 actual Illumina50k SNP markers (Peters et al., 2012). Reports of imputation accuracy from the Illumina3k to the Illumina50k have ranged from 88% to 100% in dairy cattle (Sargolzaei et al., 2011a, b; Wiggans et al., 2011, 2012). Further, Wiggans et al. (2012) indicated that imputation accuracy increased with the number of genotyped parents. Considering that MAB and Brangus RP calves were assumed to be unrelated, imputation accuracy here may have been closer to the range of values (91% to 97%) found for zero genotyped parents in Wiggans et al. (2012). Thus, imputation errors and lower linkage disequilibrium between SNP markers and QTL in the MAB population than in the Brangus RP may have contributed to dissimilar VAGO/PVAR ratios in these two populations.

225 Estimates of VAGO, VAPO, VGTOT, and PVAR with 46,839 actual and imputed
226 Illumina50k SNP markers tended to be either similar or larger (Table 4) than estimates
227 computed with genomic-polygenic models using 2,899 Illumina3k SNP markers in this
228 MAB population (Elzo et al., 2013). In particular, VAGO estimates with Illumina50k SNP
229 markers were between 3% (UBF) to 342% (UPIMF) larger than estimates with Illumina3k
230 SNP markers, whereas VAPO estimates with the Illumina50k were lower for UREA and
231 UPIMF and higher for UBF and UW than with the Illumina3k (Table 4). Consequently,
232 estimates of VGTOT with the Illumina50k were similar for UREA and UPIMF but larger
233 for UBF (24%) and UW (16%) than with the Illumina3k. Thus, heritabilities with the
234 Illumina50k were also similar for UREA and UPIMF and larger for UBF (22%) and UW
235 (19%) than with the Illumina3k because PVAR estimates had similar values for all
236 ultrasound traits with both Illumina chips (Table 4). Ratios of VAGO/VGTOT and
237 VAGO/PVAR with the Illumina50k to corresponding values with the Illumina3k followed
238 a pattern similar to VAGO across traits (i.e., larger values with the Illumina50k for UREA,
239 UPIMF, and UW than with the Illumina3k, and similar values for UBF with both chips;
240 Table 4). This pattern of Illumina50k/Illumina3k ratios for estimates of variances and
241 variance ratios for ultrasound traits was similar to Illumina50k/Illumina3k ratios obtained
242 for postweaning feed efficiency and weight gain traits in this MAB population (Elzo et al.,
243 2014).

244 Estimates of VGTOT from genomic-polygenic models were larger than VGPO from
245 polygenic models for all ultrasound traits (from 21% for UREA to 40% for UBF) indicating
246 that the 46,839 actual-imputed SNP may have accounted for genetic variation beyond that
247 explained by polygenic models. Conversely, phenotypic variances from genomic-
248 polygenic models had similar values to phenotypic variances from polygenic models (Table

249 5). Consequently, heritability estimates from genomic-polygenic models for all ultrasound
250 traits were larger than estimates from polygenic models for all traits (from 18% for UREA
251 to 41% for UBF). The average increase in heritability for these four ultrasound traits (27%)
252 was approximately 50% lower than the average increase in heritability for four feed
253 efficiency traits (56%) in this MAB population (Elzo et al., 2014). Except for UBF,
254 increments in VAGO estimates due to the utilization of actual and imputed Illumina50k
255 SNP markers were mostly responsible for increases in VGTOT and heritabilities for both
256 ultrasound traits here and feed efficiency traits (Elzo et al., 2014) relative to Illumina3k
257 SNP markers in this MAB population. Percent increments varied widely across ultrasound
258 (3% for UBF to 342% for UPIMF) and feed efficiency traits (68% for postweaning gain to
259 447% for residual feed intake) suggesting a large range of increments in QTL variation
260 explained by these additional SNP markers across traits. In addition to traits, the samples
261 of animals used in the Illumina3k and actual-imputed Illumina50k analyses may also have
262 affected these ranges (only calves with records for all traits and with genotypic information
263 were included in each analysis). Samples of animals used in the Illumina3k analyses were
264 smaller (n = 620 for feed efficiency traits and n = 623 for ultrasound traits) than samples of
265 animals used in the actual-imputed Illumina50k analyses (n = 807 for feed efficiency traits
266 and n = 812 for ultrasound traits). Although the contention that VAGO increments in
267 genomic-polygenic models actually represent additional explained genetic variation is
268 beyond the scope of this research, the fact that increases in VAGO occurred in all traits
269 may be an indication that some genetic variation beyond that accounted for by polygenic
270 models may have been explained by genomic-polygenic models.
271
272 *3.2. Ranking 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; $P < 0.0001$; Table 6). Rank correlations between calf EBV from GP with actual-imputed Illumina50k SNP markers and P models here were similar to rank correlations between GP and P models with Illumina3k SNP markers (Elzo et al., 2013). Conversely, rank correlations between EBV from GP and G models here were on the average 26% higher (from 10% for UBF to 47% for UPIMF) than corresponding values with Illumina3k SNP markers. Similarly, rank correlations between G and P models here were on the average 24% higher (from 9% for UW to 35% for UPIMF) than rank correlations computed with the set of 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 to provide additional information on additive genetic values for these traits, thus increasing the similarity among G, GP and P EBV of calves in this MAB population.

To assess the agreement between ultrasound trait EBV from GP, G, and P models with actual-imputed Illumina50k SNP markers and Illumina3k SNP markers (Elzo et al., 2013), rank correlations were computed between EBV from as 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; Table 7). This pattern of rank correlations between EBV from Illumina50k and Illumina3k analyses (highest for GP models, lower for

297 P models, and lowest for G models) was the same found for feed efficiency traits with 620
298 calves in common in this MAB population (Elzo et al., 2014). This indicated that the sets
299 of actual-imputed Illumina50k and Illumina3k genotypes captured a substantially lower
300 fraction of the additive genetic variation relative to polygenic effects and that their
301 contribution to the EBV from GP models was small for all ultrasound and feed efficiency
302 traits. Thus, rank correlations between EBV from GP, P, and G models within and across
303 Illumina50k and Illumina3k datasets suggested that polygenic models would be enough to
304 rank animals appropriately for ultrasound and feed efficiency traits in this MAB population.
305 Predictive abilities and accuracies (Legarra et al., 2008) were poorly estimated for
306 all models and ultrasound traits (Table 8). Most predictive abilities were close to zero (8
307 out of 12) and 4 of them were negative. The small size of the training (n = 626) and
308 validation datasets (n = 186) was likely the primary factor preventing the estimation of
309 dependable estimates of predictive abilities and accuracies for all models. In addition, the
310 small number of phenotypes (n = 626) relative to the large number of SNP marker effects
311 (n = 46,839) to be predicted (0.017 records per SNP) provided insufficient amount of
312 information to obtain reasonable predictive abilities and accuracies for the GP and G
313 models. Low predictive abilities and accuracies were also obtained with actual-imputed
314 Illumina50k SNP markers (n = 46,909) for feed efficiency traits (Elzo et al., 2014).
315
316 *3.3. Predicted SNP values*
317 Predicted SNP values for ultrasound traits ranged from $-2.83 * 10^{-3}$ cm^2 to $3.18 * 10^{-3}$ cm^2 for UREA, from $-7.60 * 10^{-5}$ cm to $6.91 * 10^{-5}$ cm for UBF, from $-6.47 * 10^{-4}$ % to
319 $6.04 * 10^{-4}$ % for UPIMF, and from $-3.05 * 10^{-2}$ kg to $2,89 * 10^{-2}$ kg for UW. These ranges
320 were all smaller than the ranges obtained with the Illumina3k (Elzo et al., 2013) for UREA

(23%), UBF (11%), UPIMF (60%), and UW (37%) because of smaller additive SNP to residual variance ratios used in the mixed model equations with the set of 46,839 actual-imputed Illumina50k SNP markers that with the 2,899 Illumina3k SNP markers. Values of additive SNP to residual variance ratios with the set of Illumina50k SNP markers were equal to 13% (UREA), 8% (UBF), 33% (UPIMF), and 25% (UW) of the values with the set of Illumina3k SNP markers.

Predicted SNP values for each ultrasound trait were divided by their additive SNP standard deviations to obtain standardized predictions that could be used for comparison across traits. The estimates of additive SNP standard deviations (SDSNP) were 0.0148 cm^2 for UREA, 0.0004 cm for UBF, 0.0022 % for UPIMF, and 0.0928 kg for UW. Table 9 presents the distribution of standardized predicted SNP values in increments of 0.1 SDSNP for UREA, UBF, UPIMF, and UW. The range of standardized predicted SNP values was narrower with actual-imputed Illumina50k than for Illumina3k SNP markers (Elzo et al., 2013) for UREA (-0.2 to 0.3 vs. -0.4 to 0.4), UBF (-0.3 to 0.2 vs. -0.4 to 0.5), and equal for UPIMF (-0.3 to 0.3) and UW (-0.4 to 0.4). The number of SNP in the top 30% according to their standardized predicted SNP value was 47 for UREA (located in 18 chromosomes), 61 for UBF (located in 20 chromosomes), 105 for UPIMF (located in 24 chromosomes), and 106 for UW (located in 25 chromosomes). Markedly smaller numbers of SNP and chromosomes per ultrasound trait were in the top 5% by standardized predicted SNP values (1 SNP in 1 chromosome for UREA, UPIMF, and UW, and 2 SNP in 1 chromosome for UBF). These numbers of SNP and chromosomes in the top 30% and 5% for ultrasound trait were comparable to those obtained with actual-imputed Illumina50k SNP markers for feed efficiency traits (Elzo et al., 2014) suggesting that all these traits would be determined by sizeable numbers of QTL located in numerous chromosomes as expected for

quantitative traits, but that variation in the number of influential SNP and the number of chromosomes involved would likely exist.

3.4. 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 (Table 10). Significant regression values ($P < 0.0364$ 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 MAB population contained animals with analogous EBV for UREA, UBF, UPIMF, and UW across all breed compositions.

4. Conclusions

Higher fractions of additive genomic variation for UREA, UBF, UPIMF, and UW were accounted for by imputation from the Illumina3k to 50k compared to the Illumina3k in a multibreed Angus-Brahman 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 indicated closer agreement in EBV rankings among the GP, G, and P models with the actual-imputed Illumina50k than with the Illumina3k. Low regressions of EBV on Brahman fraction indicated that animals of comparable EBV for ultrasound and weight traits existed across all Angus-Brahman fractions.

369

370 **Conflict of interest**

371 No conflicts of interest influenced this research.

372

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379

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482

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

		Trait[a]							
		UREA, cm^2		UBF, cm		UPIMF, %		UW, kg	
Breed group	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angus	121	59.7	13.4	0.66	0.40	3.16	1.57	351.7	57.4
¾ A ¼ B	163	59.2	12.4	0.64	0.39	2.89	1.60	355.7	59.4
Brangus	143	58.2	11.4	0.63	0.38	2.72	1.47	345.5	50.3
½ A ½ B	192	58.2	11.6	0.62	0.39	2.77	1.55	349.8	56.5
¼ A ¾ B	87	62.0	12.1	0.71	0.42	2.40	1.55	346.5	50.6
Brahman	106	54.5	10.8	0.60	0.43	2.57	1.62	313.5	48.5
Total	812	58.6	12.1	0.64	0.40	2.78	1.57	345.4	56.0

484 [a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent
485 intramuscular fat; UW = ultrasound weight.
486

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

	Trait[a]			
Variance[b]	UREA, cm^4	UBF, cm^2	UPIMF, $\%^2$	UW, kg^2
VAGO	3.74 ± 2.55	0.002 ± 0.001	0.08 ± 0.05	146.5 ± 81.8
VAPO	18.18 ± 5.04	0.005 ± 0.002	0.24 ± 0.06	631.7 ± 138.8
VGTOT	21.92 ± 5.24	0.007 ± 0.002	0.32 ± 0.07	778.2 ± 154.5
PVAR	55.79 ± 2.99	0.023 ± 0.001	0.59 ± 0.03	1198.8 ± 73.5
VGPO	18.12 ± 4.66	0.005 ± 0.001	0.25 ± 0.05	639.9 ± 131.3
PVARPO	55.04 ± 3.05	0.022 ± 0.001	0.58 ± 0.03	1177.0 ± 71.4

[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.

503 Table 4. Ratios of posterior means of variances and variance ratios from actual-imputed
504 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

505 [a]2,641 actual Illumina3k SNP plus 44,198 imputed Illumina50k SNP.

506 [b]2,899 Illumina3k SNP (Elzo et al., 2013).

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

509 [d]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTOT =
510 VAGO + VAPO; PVAR = phenotypic variance.

511

512 Table 5. Ratios of posterior means of variances and variance ratios from genomic-
513 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

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

520 Table 6. Spearman rank correlations for animals evaluated using genomic-polygenic,
521 genomic, and polygenic models

	Trait[a]			
Correlation[b]	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

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

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

526

527 Table 7. Spearman rank correlations for animals evaluated using genomic-polygenic,
528 genomic, and polygenic models with actual-imputed Illumina50k and Illumina3k SNP
529 datasets[a]

	Trait[b]			
Correlation[c]	UREA	UBF	UPIMF	UW
GPEBV50k, GPEBV3k	0.91	0.90	0.92	0.95
GEBV50k, GEBV3k	0.71	0.78	0.72	0.62
PEBV50k, PEBV3k	0.88	0.90	0.89	0.94

530 [a]Spearman rank correlations were computed using a subset of 615 animals in common
531 between this study and Elzo et al. (2013).

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

534 [c]GPEBV= genomic-polygenic EBV; GEBV = genomic EBV; PEBV= polygenic EBV. All
535 correlations were significant ($P < 0.0001$).
536

537 Table 8. Predictive abilities and accuracies of genomic-polygenic, genomic, and polygenic
538 models in the validation dataset

	Trait[a]			
Model	UREA	UBF	UPIMF	UW
Heritabilities	0.39	0.31	0.55	0.65
Predictive abilities				
Genomic-Polygenic	-0.06	-0.20	0.17	0.03
	P < 0.3992	P < 0.0069	P < 0.0257	P < 0.6447
Genomic	0.01	0.09	0.17	0.06
	P < 0.8455	P < 0.2084	P < 0.0245	P < 0.3817
Polygenic	-0.07	-0.20	0.04	0.01
	P < 0.3616	P < 0.0070	P < 0.5862	P < 0.9283
Accuracies				
Genomic-Polygenic	-0.10	-0.32	0.27	0.05
Genomic	0.02	0.14	0.27	0.10
Polygenic	-0.11	-0.32	0.06	0.02

539 [a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent
540 intramuscular fat; UW = ultrasound weight.
541
542

543 Table 9. Number and percentage of standardized predicted SNP values from the genomic-
544 polygenic model

	Trait[a]							
	UREA		UBF		UPIMF		UW	
SDSNP Range[b]	N	%	N	%	N	%	N	%
-0.3 to -0.4	0	0	0	0	0	0	2	0
-0.2 to -0.3	0	0	2	0	77	0.16	140	0.30
-0.1 to -0.2	395	0.84	459	0.98	2626	5.61	2910	6.21
0 to -0.1	22767	48.61	22468	47.97	21785	46.51	19305	41.22
0 to 0.1	23145	49.41	23350	49.85	20140	43.00	20791	44.39
0.1 to 0.2	531	1.13	560	1.20	2160	4.61	3560	7.60
0.2 to 0.3	1	0	0	0	51	0.11	128	0.27
0.3 to 0.4	0	0	0	0	0	0	3	0.01

545 [a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent
546 intramuscular fat; UW = ultrasound weight.
547 [b]SDSNP = additive SNP standard deviation.

548 Table 10. Linear regression coefficients for genomic-polygenic, genomic, and polygenic
549 predictions on Brahman fraction of calf

	Trait[a]			
Prediction	UREA	UBF	UPIMF	UW
Genomic-Polygenic	-0.0124	-0.0005	0.0000	-0.1288
	P < 0.0573	P < 0.0002	P < 0.9934	P < 0.0364
Genomic	-0.0148	-0.0005	-0.0010	-0.1212
	P < 0.0001	P < 0. 0001	P < 0.2399	P < 0.0047
Polygenic	-0.0073	-0.0001	0.0006	-0.1345
	P < 0.1204	P < 0.2375	P < 0.5399	P < 0.0032

550 [a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent
551 intramuscular fat; UW = ultrasound weight.
552