Genomic-polygenic and polygenic predictions for nine ultrasound and carcass traits in Angus-Brahman multibreed cattle using three sets of genotypes

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Abstract

The objectives of this study were to estimate variance components, genetic parameters, EBV, accuracies, and rankings for nine ultrasound and carcass traits in a multibreed Angus-Brahman population using three genomic-polygenic models and one polygenic model (PM). The genomic-polygenic models used the complete GeneSeek GPF250k SNP set (GPM), top 5% SNP (GPMR1), and 5% SNP evenly spread across the genome (GPMR2). Yearling ultrasound traits were weight (UW), ribeye area (UREA), backfat (UFAT), and percent intramuscular fat (UPIMF). Carcass traits were slaughter age (SLA), hot carcass weight (HCW), ribeye area (REA), backfat thickness (FAT), and marbling score (MAR). The 9-trait GPM, GPMR1, GPMR2, and PM contained fixed contemporary group, age of calf (ultrasound traits only), sex of calf, and direct heterosis effects, and random animal and residual effects. Variance components and genetic parameters were computed using AIREMLF90. Comparable heritabilities were obtained with GPM and PM for UW (GPM: 0.54 ± 0.05; PM: 0.51 ± 0.05), UREA (GPM: 0.36 ± 0.03; PM: 0.34 ± 0.03), UFAT (GPM: 0.12 ± 0.02; PM: 0.11 ± 0.02), UMPIMF (GPM: 0.34 ± 0.03; PM: 0.30 ± 0.03), SLA (GPM: 0.59 ± 0.07, PM: 0.61 ± 0.06), HCW (GPM: 0.58 ± 0.06, PM: 0.52 ± 0.07), REA (GPM: 0.48 ± 0.04, PM: 0.45 ± 0.05), FAT (GPM: 0.41 ± 0.05, PM: 0.30 ± 0.05), and MAR (GPM: 0.56 ± 0.07, PM: 0.51 ± 0.08). Additive genetic correlations between pairs of ultrasound and carcass traits were all between -0.31 and 0.81. The highest positive additive genetic correlations were between UW and UREA, UW and HCW, UW and REA, UREA and HCW, UREA and REA, UFAT and FAT, and between HCW and REA. The largest negative additive genetic correlations were between UREA and UPIMF, UFAT and SLA, UFAT and HCW, UPIMF and REA, and between REA and MAR. High similarity existed among predicted EBV and accuracies from GPM,

GPMR1, and GPMR2 as well as high-rank correlations for sires, dams, and progenies. This indicated that the two reduced genotype sets were appropriate alternatives to the complete GPF250k set for genomic-polygenic evaluation and selection in this multibreed Angus-Brahman population. High EBV variability existed among animals of all Angus and Brahman percentages and no specific breed composition was overwhelmingly better or worse for any of the nine traits. This indicated that optimization of genetic progress through selection in multibreed Angus-Brahman populations should be based solely on genetic merit regardless of breed composition.

Key words: Beef; Carcass; Genomic; Multibreed; Polygenic; Ultrasound

1. Introduction

Carcass traits constitute a major set of target traits for genetic evaluation and selection in beef cattle. However, they are expensive to measure and mostly collected on steer progeny of sires and dams considered as potential parents of subsequent generations. Yearling ultrasound carcass traits have been found to have high genetic correlations with carcass traits (Crews et al., 2003; Kemp et al., 2002; Moser et al., 1998; Reverter et al., 2000). Thus, ultrasound carcass traits have been used to increase the accuracy and to lower the cost of national genetic evaluations of slaughterhouse carcass traits (Crews and Kemp, 2002; Crews et al., 2004; MacNeil et al., 2010; MacNeil and Northcutt, 2008). Additionally, genomic information has also been used to increase the accuracy of both ultrasound and carcass traits while simultaneously reducing generation interval (Fernandes Junior et al., 2016; MacNeil et al., 2010; Magnabosco et al., 2016).

Genetic evaluation and selection of animals with desirable carcass characteristics is particularly important in Brahman and Brahman-*Bos taurus* crossbreds with high Brahman content because these cattle tend to have more variation in tenderness, smaller ribeye areas, and lower marbling ability than *Bos taurus* animals (Elzo et al., 2012; Johnson et al., 1990; Pringle et al., 1997). However, animal genomic-polygenic and polygenic evaluations for yearling ultrasound traits (ribeye area, fat over the ribeye, marbling) in an Angus-Brahman multibreed population showed large variability among EBV for animals of breed fractions that ranged from 100% Angus to 100% Brahman indicating the existence of animals with favorable EBV for ultrasound traits across the full spectrum of breed compositions (Elzo et al., 2013, 2015).

High-accuracy animal EBV could conceivably be obtained for carcass traits by utilizing all available ultrasound and carcass phenotypic data, pedigree, and genotypic information traits in Brahman-*Bos taurus* multibreed populations prevalent in subtropical and tropical areas. However, the elevated cost of high-density and low-density chips continues to deter many beef producers from genotyping their cattle. Consequently, there is a need to compare rankings and accuracies of genomic-polygenic EBV obtained using the complete set of SNP from a high-density chip with those obtained using small subsets of SNP from these chips that could be construed as low-cost low-density chips. Thus, the objectives of this research were: 1) To estimate heritabilities for and genetic correlations between nine ultrasound and carcass traits using multiple-trait single-step genomic-polygenic and polygenic models; 2) To assess values, accuracies, and rankings of animal genomic-polygenic EBV computed using the complete set of SNP and two small SNP subsets from GeneSeek GGPHD250k as well as animal polygenic EBV in a multibreed Angus-Brahman cattle population from subtropical US.

2. Materials and methods

2.1. Animals, feeding and management

The protocol for this research (number 201003744) was approved by the University of Florida Institutional Animal Care and Use Committee. Animals were from the multibreed Angus-Brahman (MAB) herd of the University of Florida (UF). Mating in the MAB herd followed a diallel design where sires from six breed groups were mated to dams of these same breed groups (Elzo and Wakeman, 1998). The Angus (A) and Brahman (B) composition of the six breed groups was as follows: BG1 = 100% A to (80% A 20% B), BG2 = (60% A 40% B) to (79% A 21% B), BG3 = Brangus = (62.5% A 37.5% B), BG4 = (40% A 60% B) to (59% A 41% B), BG5 = (20% A 80% B) to (39% A 61%B), and BG6 = (19% A 81% B) to 100% B. Calves (n = 1,981; 285 BG1, 316 BG2, 271 BG3, 426 BG4, 216 BG5, and 467 BG6) were born at the UF Beef Unit between 2006 and 2015. They were the offspring of 125 sires (21 BG1, 16 BG2, 22 BG3, 16 BG4, 14 BG5, and 36 BG6) and 691 dams (101 BG1, 106 BG2, 87 BG3, 135 BG4, 75 BG5, and 181 BG6).

Calves were born between December and March and kept with their dams on bahiagrass pastures (*Paspalum notatum*) at the UF Beef Unit until weaning in late August or early September. During this period, calves received a complete mineral supplement (UF University Special Hi-Cu Mineral, University of Florida, Gainesville, Florida) and were also given bermudagrass (*Cynodon dactylon*) hay and cotton-seed (*Gossypium spp.*) meal in the winter months (mid-December to mid-March). Calves born between 2006 and 2010 were transported to the UF Feed Efficiency Facility (UFFEF) in September, where they were randomly allocated to pens within sire group (BG1 to BG6) by sex (bull, heifer, steer) subclass. Calves stayed in these pens for the 90 d feed efficiency trial. While at

UFFEF, calves were fed whole corn or corn gluten, cottonseed hulls, molasses, chopped grass hay, and a vitamin-mineral-protein supplement (FRM, Bainbridge, GA; mean dry matter = 12.9%, mean crude protein = 98.2%, mean net energy for maintenance = 1.6 mcal/kg DM, and mean net energy for gain = 1.0 mcal/kg DM). Conversely, calves born from 2011 to 2015 remained at the UF Beef Unit on bahiagrass pastures and additionally fed bahiagrass hay, concentrate (1.6 kg to 3.6 kg of soy hull pellets per day; 14.0 % CP; 488 Pellet Medicated Weaning Ration, Lakeland Animal Nutrition, Lakeland, Florida), and a mineral supplement. Subsequently, yearling steers were transported to a contract feeder (2006 to 2009: King Ranch Feedyard, Kingsville, Texas; 2010 to 2014: Suwannee Farms, O Brien, Florida; 2015: Quincey Farms, Chiefland, Florida), where they were provided a standard feedlot diet consisting of corn, protein, vitamins, and minerals until they reached a subcutaneous fat thickness over the ribeye of approximately 1.27 cm.

2.2. Traits

Traits were yearling ultrasound weight (UW, kg), yearling ultrasound ribeye area (UREA, cm^2), yearling ultrasound backfat (UFAT, cm), yearling ultrasound percent intramuscular fat (UPIMF, %), slaughter age (SLA, d), hot carcass weight (HCW, kg), ribeye area (REA, cm^2), backfat thickness (FAT, cm), and marbling score (MAR, units; 100 to 199 = practically devoid, 200 to 299 = traces, 300 to 399 = slight, 400 to 499 = small, 500 to 599 = modest, 600 to 699 = moderate, 700 to 799 = slightly abundant, 800 to 899 = moderately abundant, and 900 to 999 = abundant).

A certified technician recorded ultrasound images from yearling male and female calves using an Aloka 500 ultrasound system (Hitachi Aloka Medical, Ltd., Wallinford, Connecticut, USA) in December. Yearling weights (UWT) were collected prior to

acquiring ultrasound images. Analysis of the ultrasonic images with UICS Scanning Software by Walter and Associates, LLC (Ames, 106 Iowa, USA) yielded UREA, UBF, and UPIMF phenotypes.

Steers at the contract feeder were transported to a commercial packing plant after approximately reaching 1.27 cm over the ribeye (2006 to 2010; Sam Kane Beef Processors, Corpus Christi, Texas; 2011 to 2012: FPL Food, LLC, Augusta, Georgia; 2013 to 2014: Central Beef Industries, Bushnell, Florida; 2015: Adena Meat Products, Fort McCoy, Florida, and UF Meats Laboratory, Gainesville, Florida) and harvested using established USDA-FSIS procedures. Carcass data (HCW, REA, FAT, and MAR) were collected 24 hr postmortem (USDA, 1997). Slaughter age (SLA) was computed as the number of days between birth and slaughter.

2.3. Tissue sampling and genotyping

Tissue samples (blood, semen) from 782 animals were collected for this study between 2006 and 2015 and stored at -80 °C. There were 70 sires, 696 steers, and 16 heifers (BG1 = 126, BG2 = 120, BG3 = 123, BG4 = 159, BG5 = 83, and BG6 = 171) represented in these samples. A commercial kit (QIAamp DNA mini kit, Qiagen, Valencia, CA) was used to extract DNA from blood and semen samples. The DNA samples were sent to Neogen for genotyping with GeneSeek Genomic Profiler F250 (number of SNP in autosomes and X chromosome = 221,049; Neogen, 2016). All SNP with minor allele frequencies lower than 0.05 were discarded (n = 94,033). Thus, the genotype files contained 127,016 SNP autosomal and X chromosome markers for each genotyped animal.

2.4. Variance components, heritabilities, and correlations

Variance components, heritabilities, and genetic, environmental and phenotypic correlations for UW, UREA, UFAT, UPIMF, SLA, HCW, REA, FAT, and MAR were obtained using a 9-trait single-step genomic-polygenic model (GPM; Aguilar et al., 2010) and a 9-trait polygenic model (PM). The single-step procedure was utilized here because it permits the utilization of phenotypes, pedigree, and genotypes to obtain the most accurate genomic-polygenic predictions for animals when only a fraction of animals evaluated have genotypic records. Fixed effects for GPM and PM were contemporary group (location-year), age of calf (ultrasound traits only), sex of calf, and direct heterosis as a function of calf heterozygosity (i.e., the probability of one Angus and one Brahman allele in 1 locus). Random effects for all traits in GPM and PM were animal direct additive genetic and residual. Mean of random direct additive genetic and residual effects for all traits in GPM and PM were equal to zero. The variance-covariance matrices among direct genetic effects for UW, UREA, UFAT, UPIMF, SLA, HCW, REA, FAT, and MAR were equal to $H_1 \otimes V_{dm}$ for GPM and $A \otimes V_d$ for PM, where $H_1 = \begin{bmatrix} A_{11} + A_{12}A_{22}^{-1}(G_{22} - A_{22})A_{22}^{-1}G_{21} & A_{12}A_{22}^{-1}G_{22} \\ G_{22}A_{22}^{-1}A_{21} & G_{22} \end{bmatrix}$, the genomic-polygenic relationship matrix among animals with and without genotypes (Legarra et al., 2009), A was the additive relationship matrix among all animals, V_d was a 9 × 9 matrix of variances and covariances among direct additive genetic effects for UW, UREA, UFAT, UPIMF, SLA, HCW, REA, FAT, and MAR, and "⊗" was the Kronecker product. The submatrices within matrix H_1 were defined as follows: A_{ij} was the ijth submatrix of the additive relationship matrix, i, j = 1, 2, where subscript 1 referred to non-genotyped animals and subscript 2 to genotyped animals, A_{22}^{-1} was the inverse of the additive relationship submatrix for genotyped animals, $G_{22} = ZZ'/2\sum p_j(1-p_j)$, was the matrix of genomic relationships for genotyped

175 animals (Aguilar et al., 2010; VanRaden, 2008), p_j = frequency of "2" alleles in locus j, and
176 the elements of matrix Z were equal to $(0 - 2p_j)$ if the genotype in locus j was equal to 11,
177 $(1 - 2p_j)$ if the genotype in locus j was equal to either 12 or 21, and $(2 - 2p_j)$ if the
178 genotype in locus j was equal to 22. The default weights (tau = 1, alpha = 0.95, beta = 0.05,
179 gamma = 0, delta = 0, and omega = 1) and scaling for G_{22} and A_{22} (mean of diagonal
180 elements of G_{22} = mean of diagonal elements of A_{22}, and mean of off-diagonal elements of
181 G_{22} = mean of off-diagonal elements of A_{22}) were used for the computation of the inverse of
182 matrix H_1 when solving the mixed model equations with the BLUPF90 Family of programs
183 (Misztal et al., 2002). The variance-covariance matrix among residuals for GPM and PM
184 was equal to $I \otimes V_e$, I was an identity matrix, V_e was a 9 × 9 matrix of variances and
185 covariances among residual effects for UW, UREA, UFAT, UPIMF, SLA, HCW, REA,
186 FAT, and MAR, and "⊗" was the Kronecker product.

187 Variance and covariance components for GPM and PM were estimated using
188 restricted maximum likelihood procedures (Corbeil and Searle, 1971; Harville, 1977;
189 Patterson and Thompson, 1971) via an average information algorithm (Gilmour et al.,
190 1995) within the BLUPF90 family of programs (Misztal, 1999; Misztal et al., 2002;
191 Tsuruta, 2014). Specifically, program AIREMLF90 (Tsuruta, 2014) of the BLUPF90
192 family of programs was used to obtain estimates of variance and covariance components,
193 heritabilities, genetic correlations, environmental correlations, and phenotypic correlations,
194 as well as their corresponding standard errors using a convergence criterion of 10^{-11}. The
195 diagonal elements of the inverse of the information matrix computed at convergence
196 contained the estimation error variances of variance and covariance components. Thus,
197 standard errors of direct additive genetic and environmental variances and covariances for

198 the nine traits were computed as square roots of their estimation error variances. The
199 repeated sampling procedure of Meyer and Houle (2013) programmed within AIREMLF90
200 was utilized to compute SE for functions of estimated variances and covariances after
201 convergence using 5,000 samples of additive direct genetic and environmental variance and
202 covariance components from their asymptotic multivariate normal distribution. Values of
203 all functions (i.e., phenotypic variances and covariances, heritabilities, genetic correlations,
204 environmental correlations, and phenotypic correlations) were computed for each sample,
205 and then means and SD for each function were computed using all samples. These SD
206 were approximate SE of the corresponding REML estimates of variance component
207 functions.
208
209 *2.5. Genomic-polygenic and polygenic EBV, accuracies, and rankings*
210 The REML estimates of variance and covariance components at convergence were
211 utilized to compute genomic-polygenic estimated breeding values (GPEBV) and polygenic
212 EBV (PEBV) for UW, UREA, UFAT, UPIMF, SLA, HCW, REA, FAT, and MAR using
213 GPM and PM models that contained the same fixed and random effects as those used for
214 variance component estimation. To assess the impact of utilizing low-cost low-density
215 chips on genomic-polygenic predictions, accuracies, and rankings, GPEBV were also
216 computed with GPM that used genotype files containing two reduced SNP sets of
217 GeneSeek Genomic Profiler F250. The first GPM (GPMR1) utilized a reduced SNP set
218 (R1) that contained only SNP in the top 5% by absolute value of their Best Predictor
219 (Henderson, 1973; Wang et al., 2012) across all nine traits (n = 24,761) computed with
220 program POSTGSF90 (Aguilar and Misztal, 2014). A total of 18,405 SNP (74.3%) were
221 from chromosomes 11, 23, 24, 25, and 26, eight chromosomes (8, 9, and 16 to 21) had no

SNP represented, and the remaining 16 chromosomes contributed with 6,356 SNP (25.7%) of the top 5% SNP. The second GPM (GPMR2) used a reduced SNP set (R2) that was constructed using 24,761 SNP (5%) chosen evenly across the genome regardless of their predicted value. Genomic-polygenic EBV for all traits were computed for all animals using GPMR1 (GPEBVR1) and GPMR2 (GPEBVR2). Accuracies of GPEBV, GPEBVR1, GPEBVR2, and PEBV for all animals and traits were computed using the expression $\left[1 - \mathrm{PEV_{ij}}/\mathrm{AGV_j}\right]^{1/2} * 100$, where $\mathrm{PEV_{ij}}$ is the prediction error variance for trait j within animal i, and $\mathrm{AGV_j}$ is the additive genetic variance for trait j. Means and SD of accuracies for GPEBV, GPEBVR1, GPEBVR2, and PEBV were computed for sires, dams, progenies, and all animals using the TABULATE procedure of SAS (SAS Institute Inc., Cary, NC). Rankings of sires (n = 292), dams (n = 1,238), progeny (n = 2,103), and all animals (n = 3,633) with GPEBV, GPEBVR1, GPEBVR2, and PEBV were compared using Spearman rank correlations computed using the CORR procedure of SAS. The GPEBV from all evaluated animals (n = 3,633) were also plotted against Brahman fraction to visualize variation and trends in EBV in animals ranging in Brahman fraction from 0% (Angus) to 100% (Brahman).

3. Results and discussion

Table 1 presents numbers of calves with records, means, and SD per trait (UW, UREA, UFAT, UPIMF, SLA, HCW, REA, FAT, and MAR) and breed group (BG1 to BG6) and total. Numbers of records for yearling ultrasound traits (UW, UREA, UFAT, and UPIMF) were over twice the number of carcass-trait records (SLA, HCW, REA, FAT, and MAR) because ultrasound traits were taken from bulls, heifers, and steers, whereas carcass

245 traits were obtained almost exclusively from steers (720 steers and 36 culled heifers).
246 Means and SD for UW and UREA were lower for BG6 than for the other five breed groups
247 likely a reflection of the younger age of Brahman calves when ultrasound measures were
248 taken. Means for UFAT were similar but SD differed substantially across breed groups.
249 The UPIMF was higher for BG1 (Angus and high percent Angus calves) than for all other
250 breed groups, and the SD tended to be higher for breed groups with higher Angus
251 percentages. Means for SLA differed little among breed groups, but SD were lower for
252 BG1 and BG5 and higher for BG6 than for the other three breed groups. Means and SD for
253 HCW, REA, and FAT were substantially lower for BG6 (Brahman and high percent
254 Brahman) than for any other breed group. The highest HCW and REA means were those
255 for BG3 (Brangus). The smallest MAR means and SD were those for BG5 and BG6 and
256 the highest values were for BG1 with BG2, BG3, and BG4 having values closer to BG1
257 than to BG6.
258
259 *3.1. Variance components, heritabilities, and correlations*
260 Genomic-polygenic and polygenic estimates of additive genetic and environmental
261 variances and covariances for UW, UREA, UFAT, UPIMF, SLA, HCW, REA, FAT, and
262 MAR are shown in Table 2, phenotypic variances and covariances as well as heritabilities
263 and additive genetic correlations in Table 3, and environmental and phenotypic correlations
264 in Table 4. Similar estimates of additive genetic, environmental, and phenotypic variances
265 and covariances were obtained with GPM and PM. On the average, GPM additive genetic
266 variances were 11.4% higher, additive genetic covariances were 25.6% higher,
267 environmental variances were 2.3% lower, environmental covariances were 11.3% higher,
268 phenotypic variances 4.5% higher, and phenotypic covariances were 8.5% higher than

269 those from PM. The somewhat higher values of genetic variances and covariances from
270 GPM may have been due to additional information provided by SNP markers from
271 GeneSeek Genomic Profiler 250F in linkage disequilibrium with QTL affecting these traits.
272 The resemblance between GPM and PM variances and covariances resulted in similar
273 average values of heritabilities (GPM values were 9.4% higher than PM values), genetic
274 correlations (18.4% smaller for GPM than for PM, excluding near zero values),
275 environmental correlations (13.3% smaller for GPM than for PM, excluding near zero
276 values), and phenotypic correlations (0.03% higher for GPM than for PM). Consequently,
277 the information from the 127,016 SNP markers from GeneSeek Genomic Profiler 250F
278 from the 782 genotyped animals had little impact on the estimates of variance components
279 and variance ratios for these nine ultrasound and carcass traits in the UF multibreed Angus-
280 Brahman population. The low levels of linkage disequilibrium (0.15 for r^2 and 0.63 for D'
281 for 10 SNP windows; PLINK 1.9; Chang et al., 2015; Purcell and Chang, 2016) estimated
282 for this MAB population (Elzo et al., 2016) may have reduced the impact of genotypic
283 information on the combined genomic-expected relationship matrix H_1 (used in GPM)
284 resulting in cell values similar to those in additive relationship matrix A (used in PM),
285 hence the resemblance between EBV from GPM and PM. Thus, similar REML estimates
286 of additive genetic variances and covariances were the outcome of comparable GPMEBV
287 and PEBV that were used as inputs for their estimation.
288 Yearling ultrasound trait heritabilities (Table 3) were moderate for UW (GPM: 0.54
289 ± 0.05; PM: 0.51 ± 0.05); UREA (GPM: 0.36 ± 0.03; PM: 0.34 ± 0.03), and UMPIMF
290 (GPM: 0.34 ± 0.03; PM: 0.30 ± 0.03) and low for UFAT (GPM: 0.12 ± 0.02; PM: 0.11 ±
291 0.02). Conversely, all carcass traits had moderate heritabilities (SLA, GPM: 0.59 ± 0.07,
292 PM: 0.61 ± 0.06; HCW, GPM: 0.58 ± 0.06, PM: 0.52 ± 0.07; REA, GPM: 0.48 ± 0.04, PM:

293 0.45 ± 0.05; FAT, GPM: 0.41 ± 0.05, PM: 0.30 ± 0.05; MAR, GPM: 0.56 ± 0.07, PM: 0.51
294 ± 0.08; Table 3). Yearling ultrasound heritabilities in the MAB population were
295 comparable to estimated obtained in multibreed Angus-Brahman (Elzo et al., 1998), Angus
296 (Kemp et al., 2002; Reverter et al., 2000), Brangus (Moser et al., 1998; Peters et al., 2012;
297 Stelzleni et al., 2002), Nellore (Yokoo et al., 2015), and Simmental (Crews et al., 2003).
298 Similarly, carcass heritabilities here were also within the range of values estimated for
299 Angus (MacNeil and Northcutt, 2008; Reverter et al., 2000), Brangus (Moser et al., 1998),
300 Nellore (Caetano et al., 2013), and Simmental (Crews et al., 2003).
301 Additive genetic correlations between pairs of ultrasound and(or) carcass traits were
302 all between -0.31 and 0.81 (Table 3). The highest positive additive genetic correlations
303 were between UW and UREA (GPM: 0.65 ± 0.06, PM: 0.69 ± 0.06), UW and HCW (GPM:
304 0.67 ± 0.07, PM: 0.63 ± 0.07), UW and REA (GPM: 0.42 ± 0.09, PM: 0.36 ± 0.09), UREA
305 and HCW (GPM: 0.41 ± 0.10, PM: 0.37 ± 0.10), UREA and REA (GPM: 0.67 ± 0.08, PM:
306 0.58 ± 0.09), UFAT and FAT (GPM: 0.81 ± 0.05, PM: 0.69 ± 0.08), and between HCW and
307 REA (GPM: 0.57 ± 0.08, PM: 0.70 ± 0.07). The largest negative correlations were between
308 UREA and UPIMF (GPM: -0.30 ± 0.08, PM: -0.24 ± 0.08), UFAT and SLA (GPM: -0.31 ±
309 0.12, PM: -0.30 ± 0.13), UFAT and HCW (GPM: -0.27 ± 0.11, PM: -0.28 ± 0.12), UPIMF
310 and REA (GPM: -0.28 ± 0.11, PM: -0.16 ± 0.12), and between REA and MAR (GPM: -
311 0.27 ± 0.09, PM: -0.23 ± 0.09). The vast majority of the remaining additive genetic
312 correlations were either near zero or below ± 0.20. Although specific values differed,
313 additive genetic correlations between ultrasound traits (UW, UREA, UFAT, UPIMF)
314 tended to be in agreement with reported estimates in Angus (Kemp et al., 2002; MacNeil
315 and Northcutt, 2008; Reverter et al., 2000), Brangus (Moser et al., 1998; Stelzleni et al.,
316 2002), and Nellore (Yokoo et al., 2015). Similarly, there was reasonable agreement

between estimates of additive genetic correlations between carcass traits here (CWT, REA, FAT, MAR) and those obtained in multibreed Angus-Brahman (Elzo et al., 1998), Angus (Kemp et al., 2002; MacNeil and Northcutt, 2008; Reverter et al., 2000), Brangus (Moser et al., 1998), and Nellore (Caetano et al., 2013). Lastly, estimates of additive genetic correlations between ultrasound and carcass traits reported for Angus (Crews et al., 2003; Kemp et al., 2002; MacNeil and Northcutt, 2008; Reverter et al., 2000), Brangus (Moser et al., 1998), and Simmental (Crews et al., 2003) ranged from moderately to strongly positive as corresponding values estimated here.

Environmental and phenotypic correlations showed similar patterns of values for all traits (Table 4). Most GPM and PM environmental and phenotypic correlations were close to zero. The largest positive environmental and phenotypic correlations were those between UW and UREA (environmental, GPM: 0.47 ± 0.04, PM: 0.44 ± 0.04, and phenotypic, GPM: 0.54 ± 0.02, PM: 0.54 ± 0.02), UW and HCW (environmental, GPM: 0.45 ± 0.05, PM: 0.49 ± 0.05, and phenotypic, GPM: 0.57 ± 0.03, PM: 0.56 ± 0.03), UREA and HCW (environmental, GPM: 0.23 ± 0.06, PM: 0.26 ± 0.06, and phenotypic, GPM: 0.31 ± 0.04, PM: 0.30 ± 0.03), and between HCW and FAT (environmental, GPM: 0.37 ± 0.08, PM: 0.29 ± 0.07, and phenotypic, GPM: 0.24 ± 0.04, PM: 0.26 ± 0.04). The largest negative environmental and phenotypic correlations were between UW and SLA (environmental, GPM: -0.39 ± 0.07, PM: -0.35 ± 0.08, and phenotypic, GPM: -0.28 ± 0.04, PM: -0.29 ± 0.04) and between REA and FAT (environmental, GPM: -0.27 ± 0.05, PM: -0.33 ± 0.05, and phenotypic, GPM: -0.17 ± 0.04, PM: -0.17 ± 0.04). Environmental and phenotypic correlations here tended to be somewhat lower than values obtained previously in multibreed Angus-Brahman (Elzo et al., 1998), Angus (Kemp et al., 2002; Reverter et

al., 2000), Brangus (Moser et al., 1998), Nellore (Caetano et al., 2013), and Simmental (Crews et al., 2003).

The high ultrasound and carcass heritabilities as well as the high level of association between ultrasound and carcass traits found in this multibreed Angus-Brahman population reaffirmed previous suggestions on the advantages of utilizing both ultrasound and carcass phenotypic measurements to improve the accuracy of genetic evaluation and selection of cattle for carcass traits (Crews et al., 2003; MacNeil et al., 2010; Moser et al., 1998; Reverter et al., 2000). Utilization of ultrasound information would be particularly important for genetic improvement programs involving Brahman-*Bos taurus* multibreed populations in tropical and subtropical regions where phenotypic information on carcass traits is limited.

3.2. Genomic-polygenic and polygenic EBV, accuracies, and rankings

Means and SD of differences between genomic-polygenic EBV obtained with reduced genotype sets 1 (GPEBVR1) and 2 (GPEBVR2) and with the complete set of genotypes (GPEBV), and between PEBV and GPEBV were computed for sires, dams, progenies, and all animals. Similar patterns of means and SD existed for sires, dams, progenies, and all animals; thus, only means and SD of differences for all animals are presented in Table 5. Means and SD of differences between GPEBVR1 and GPEBV, and between GPEBVR2 and GPEBV for sires, dams, progenies, and for all animals were smaller than differences between PEBV and GPEBV for all traits. Although small, absolute values of mean and(or) SD differences between GPEBVR1 and GPEBV tended to be larger than corresponding GPEBVR2 minus GPEBV for UW, UREA, SLA, HCW, REA, and MAR. However, mean and SD of differences between GPEBVR1 and

GPEBVR2 relative to GPEBV were either zero or near zero for UFAT, UPIMF, and FAT. Thus, utilization of the top 5% of SNP markers across the nine ultrasound and carcass traits (n = 24,761) yielded values of genomic-polygenic EBV that were close to those obtained with a set of 24,761 SNP markers spread across the genome, and to those predicted using the full set of SNP markers. In fact, rank correlations between GPEBVR1 and GPEBVR2, GPEBV and GPEBVR1, and between GPEBV and GPEBVR2 were above 0.99 for all traits in sires (all traits, except for SLA; mean = 0.994; range = 0.982 to 0.998; $P < 0.0001$), dams (all traits; mean = 0.998; range = 0.993 to 0.999; $P < 0.0001$), progenies (all traits; mean = 0.997; range = 0.992 to 0.999; $P < 0.0001$), and all animals (all traits; mean = 0.997; range = 0.992 to 0.999; $P < 0.0001$) indicating a high degree of agreement among EBV from these models. Rank correlations between EBV from the three genomic-polygenic models and PEBV were somewhat lower for sires (mean = 0.941; range: 0.879 to 0.970), dams (mean = 0.963; range: 0.911 to 0.989), progenies (mean = 0.954; range: 0.901 to 0.978), and all animals (mean = 0.956; range: 0.902 to 0.981). Patterns of rank correlations between GPEBV, GPEBVR1, GPEBVR2, and PEBV for sires, dams, progenies, and all animals were comparable. Thus, Table 6 shows rank correlations only for all animals.

Accuracies of EBV for all traits differed little among the three genomic-polygenic models and the polygenic model for sires, dams, progenies, and all animals. Further, similar patterns existed for means of accuracy differences between these models for sires, dams, and progenies. Thus, percentage differences between accuracies of GPEBVR1 and GPEBV, GPEBVR2 and GPEBV, and PEBV and GPEBV are shown only for all animals in Table 7. Mean percentage differences in accuracy relative to GPEBV (Table 7) for GPEBVR1 (mean = 0.00 %; range = -0.04 % to 0.06 %) were more similar to those for

388 GPEBVR2 (mean = 0.07 %; range = 0.04 % to 0.10 %) than for PEBV (mean = -5.93 %;
389 range = -9.71 % to -2.64 %). The high degree of similarity among predicted EBV and
390 accuracies from GPM, GPMR1, and GPMR2 as well as their high rank correlation values
391 for sires, dams, and progenies indicated that reduced genotype sets 1 and 2 would be
392 appropriate alternatives to the utilization of the complete set of genotypes in GeneSeek
393 Genomic Profiler F250. Further, the closeness between GPEBVR1 and GPEBVR2 values
394 and accuracies of prediction indicated that there was virtually no difference between
395 choosing SNP markers from the top 5% for UW, UREA, UFAT, UPIMF, SLA, HCW,
396 REA, FAT, and MAR and choosing them from across the genome regardless of their
397 predicted value.

398 The variability among GPEBV as a function of Brahman fraction is shown in Figure
399 1 for two ultrasound traits (UREA and UPIMF) and their corresponding carcass traits (REA
400 and MAR). Each diamond in this figure represents the GPEBV of an animal in the
401 multibreed herd. Similar plots existed for UW, UFAT, SLA, HCW, and FAT. All figures
402 showed that large amounts of variation existed among animals of all Angus and Brahman
403 breed compositions and that no specific breed composition was overwhelmingly better or
404 worse for any of these traits. Comparable figures were obtained for all traits with EBV
405 from the two reduced genomic-polygenic models (GPEBVR1 and GPEBVR2) and the
406 polygenic model.

407 The MAB population represents a structured version of Angus-Brahman multibreed
408 populations in tropical and subtropical regions of the US and other countries. Assuming
409 that field MAB populations in these regions and the UFMAB population share a reasonable
410 degree of similarity, GPEBV variation, accuracy of EBV, and EBV rankings here indicated
411 that it would be desirable for these populations to evaluate and select animals from all

412 breed compositions if their aim were to optimize genetic progress. Further, the similarity
413 between GPEBV, GPEBVR1, and GPEBVR2 indicated that these populations could utilize
414 a lower density rather than a high-density chip for genomic-polygenic predictions with little
415 impact on rankings and selection of desirable animals for the ultrasound and carcass traits
416 considered here. However, it is doubtful that the genomic-polygenic models using the two
417 reduced sets of SNP markers identified in the UF multibreed Angus-Brahman population
418 will yield EBV as close to those of the complete genomic-polygenic model in other
419 multibreed Angus-Brahman populations in the US or elsewhere because of differences in
420 population structure and linkage disequilibrium patterns. Thus, identifying appropriate
421 reduced sets of SNP markers from GeneSeek GPF250k or other high-density genotyping
422 chips in these populations will require genomic-polygenic analyses similar to the ones
423 conducted in this research. The need to conduct these analyses to identify representative
424 SNP marker subsets across related multibreed Angus-Brahman populations may decrease in
425 the future if commercial chips are populated with biologically relevant SNP markers (e.g.,
426 SNP markers inside exons of structural or regulatory genes). However, field multibreed
427 populations tend to change in an unstructured fashion due to multiple selection objectives
428 across herds and changes in selection objectives and mating plans over time. Thus, it
429 would be advisable to verify the effectiveness of both complete and reduced sets of SNP
430 markers for traits targeted by selection across these related multibreed Angus-Brahman
431 populations at regular intervals over time.
432

433 **4. Conclusions**

434 Comparable additive genetic, environmental, and phenotypic variance and
435 covariances, heritabilities, genetic correlations, environmental correlations, and phenotypic

correlations were estimated using three genomic-polygenic models using a complete high-density set and two reduced sets of SNP, and a polygenic model. Genomic-polygenic EBV and accuracies from the three genomic-polygenic models were highly similar and had high pairwise rank correlations for all traits in sires, dams, and progenies. Conversely, polygenic EBV were less similar, had lower rank correlations, and their EBV accuracies were lower than those of genomic-polygenic models. The similarity between EBV, accuracies, and rankings among the three genomic-polygenic models indicated that either one of the reduced SNP sets would be a feasible alternative to the complete high-density SNP set in this population, and perhaps in other multibreed Angus-Brahman populations in subtropical and tropical environments.

Conflict of interest

No conflicts of interest influenced this research.

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Table 1. Numbers of calves, means and standard deviations per breed group and total for yearling ultrasound and carcass traits

		Breed group[b]						
Trait[a]		BG1	BG2	BG3	BG4	BG5	BG6	Total
UW	N	285	316	271	426	216	462	1976
	Mean, kg	347	356	344	351	341	301	338
	SD, kg	52	58	51	57	53	50	57
UREA	N	284	315	269	426	216	456	1966
	Mean, cm^2	56	58	57	57	58	51	56
	SD, cm^2	12	12	12	12	12	11	12
UFAT	N	284	316	271	426	216	459	1972
	Mean, cm	0.6	0.6	0.6	0.6	0.6	0.5	0.6
	SD, cm	0.7	0.3	0.3	1	0.5	1.1	0.8
UPIMF	N	285	315	271	425	214	460	1970
	Mean, %	3.4	3.1	3	2.9	2.7	2.9	3
	SD, %	1.4	1.4	1.3	1.3	1.3	1.2	1.3
SLA	N	115	110	132	169	78	152	756
	Mean, d	527	524	521	524	530	526	525
	SD, d	34	39	40	39	37	43	39
HCW	N	111	109	128	166	78	152	744
	Mean, kg	339	335	346	331	334	308	331
	SD, kg	48	41	47	45	41	31	44
REA	N	111	109	128	166	78	152	744
	Mean, cm^2	80	80	82	79	78	74	79
	SD, cm^2	10	9	12	10	10	7	10
FAT	N	111	109	128	166	78	152	744
	Mean, cm	1.5	1.4	1.5	1.4	1.4	1.2	1.4
	SD, cm	0.5	0.5	0.5	0.6	0.5	0.4	0.5
MAR	N	111	109	128	165	78	152	743
	Mean, units	487	438	427	426	385	362	420
	SD, units	103	87	88	91	63	48	91

[a]UW = yearling ultrasound weight; UREA = yearling ultrasound ribeye area; UFAT = yearling ultrasound backfat; UPIMF = yearling ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score.

[b]Breed group: BG1 = 100% A to (80% A 20% B); 2) BG2 = (60% A 40% B) to (79% A 21% B); 3) BG3 = Brangus = (62.5% A 37.5% B); 4) BG4 = (40% A 60% B) to (59% A 41% B); 5) BG5 = (20% A 80% B) to (39% A 61%B); and 6) BG6 = (19% A 81% B) to 100% B; A = Angus, B = Brahman.

571

Table 2. REML estimates of additive genetic and environmental covariances for yearling ultrasound and carcass traits using genomic-polygenic and polygenic models

	Additive genetic covariances				Environmental covariances			
Trait pair[a]	GPM	SE	PM	SE	GPM	SE	PM	SE
UW,UW; kg^2	**723.35**	**88.94**	**655.15**	**82.04**	**621.92**	**55.86**	**627.92**	**56.23**
UW,UREA; kg*cm^2	82.19	13.15	78.90	12.13	72.24	8.07	68.35	8.08
UW,UFAT; kg*cm	-0.24	0.31	-0.14	0.29	0.86	0.27	0.80	0.28
UW,UPIMF; kg*%	-1.82	0.93	-1.58	0.82	-1.26	0.37	-1.41	0.27
UW,SLA; kg*d	-132.94	67.51	-156.56	61.36	-192.45	39.07	-163.07	40.54
UW,HCW; kg*kg	445.62	67.04	368.44	59.56	236.44	32.91	266.82	34.77
UW,REA; kg*cm^2	65.97	15.44	50.95	13.39	-2.48	7.30	4.28	6.83
UW,FAT; kg*cm	0.90	0.97	2.34	0.81	2.24	0.64	0.75	0.64
UW,MAR; kg*units	-96.69	144.86	46.11	131.30	-74.91	69.19	-188.11	72.08
UREA,UREA; cm^4	**22.13**	**2.60**	**19.69**	**2.44**	**38.54**	**1.27**	**38.95**	**1.39**
UREA,UFAT; cm^2*cm	-0.02	0.05	0.01	0.05	0.26	0.04	0.23	0.04
UREA,UPIMF; cm^2*%	-0.70	0.18	-0.49	0.17	-0.18	0.06	-0.30	0.06
UREA,SLA; cm^2*d	-26.99	11.50	-25.73	10.53	-17.30	5.28	-16.56	6.19
UREA,HCW; cm^2*kg	48.37	12.07	37.67	10.65	30.33	7.21	34.92	7.67
UREA,REA; cm^2*cm^2	18.55	2.79	14.20	2.53	4.74	0.86	6.53	1.08
UREA,FAT; cm^2*cm	-0.02	0.16	0.15	0.13	0.31	0.09	0.18	0.10
UREA,MAR; cm^2*units	-35.37	30.05	-24.23	24.81	-2.38	16.91	-9.70	7.83
UFAT,UFAT; cm^2	**0.01**	**0.00**	**0.01**	**0.00**	**0.09**	**0.00**	**0.09**	**0.00**
UFAT,UPIMF; cm*%	0.01	0.01	0.01	0.01	-0.03	0.01	-0.03	0.01
UFAT,SLA; cm*d	-0.83	0.33	-0.73	0.32	-0.17	0.35	-0.20	0.34
UFAT,HCW; cm*kg	-0.73	0.31	-0.67	0.30	0.08	0.29	0.12	0.32
UFAT,REA; cm*cm^2	-0.10	0.07	0.02	0.07	-0.03	0.08	-0.13	0.08
UFAT,FAT; cm*cm	0.03	0.01	0.02	0.00	0.01	0.01	0.01	0.01
UFAT,MAR; cm*units	0.95	0.79	0.90	0.73	-1.01	0.69	-1.09	0.66
UPIMF,UPIMF; %^{2}	**0.25**	**0.03**	**0.21**	**0.03**	**0.47**	**0.02**	**0.49**	**0.02**
UPIMF,SLA; %*d	-1.87	1.33	-1.71	1.24	0.72	0.86	0.75	0.92
UPIMF,HCW; %*kg	-1.26	1.23	-1.16	1.09	-1.17	0.80	-0.96	0.79
UPIMF,REA; %*cm^2	-0.80	0.31	-0.38	0.29	0.00	0.21	-0.32	0.23
UPIMF,FAT; %*cm	-0.01	0.02	-0.01	0.01	0.04	0.01	0.05	0.01
UPIMF,MAR; %*units	18.27	3.03	14.46	2.75	2.95	1.03	5.71	0.99
SLA,SLA; d^2	**587.32**	**97.60**	**565.90**	**73.83**	**404.50**	**60.04**	**351.91**	**43.56**
SLA,HCW; d*kg	171.45	68.98	157.28	58.71	49.06	43.14	41.67	40.59
SLA,REA; d*cm^2	18.83	14.41	16.68	13.46	6.09	6.84	5.15	7.87
SLA,FAT; d*cm	0.41	1.01	0.49	0.90	0.41	0.67	0.32	0.72
SLA,MAR; d*units	-48.53	163.17	-64.78	159.49	291.92	97.99	318.58	114.41
HCW,HCW; kg^2	**622.79**	**90.65**	**524.28**	**82.14**	**446.10**	**54.31**	**480.03**	**61.50**
HCW,REA; kg*cm^2	83.03	15.12	88.76	14.02	22.90	6.90	7.78	7.84
HCW,FAT; kg*cm	0.94	0.99	1.35	0.84	2.91	0.66	2.52	0.69
HCW,MAR; kg*units	-114.50	135.75	7.77	121.94	159.16	64.01	71.14	72.07
REA,REA; cm^4	**34.81**	**4.96**	**30.74**	**4.42**	**37.10**	**1.96**	**36.78**	**2.15**
REA,FAT; cm^2*cm	-0.08	0.20	0.14	0.17	-0.60	0.10	-0.80	0.12
REA,MAR; cm^2*units	-97.91	32.70	-73.59	27.70	20.36	11.00	13.68	8.22
FAT,FAT; cm^2	**0.10**	**0.02**	**0.07**	**0.01**	**0.14**	**0.01**	**0.16**	**0.01**
FAT,MAR; cm*units	3.66	2.37	3.75	2.04	3.05	1.53	2.90	1.44
MAR,MAR; units^2	**3753.50**	**640.78**	**3270.80**	**628.49**	**2898.50**	**415.29**	**3101.90**	**475.02**

[a]UW = ultrasound weight; UREA = ultrasound ribeye area; UFAT = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score; GPM = genomic-polygenic model; PM = polygenic model.

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Table 3. REML estimates of phenotypic covariances, heritabilities, and additive genetic correlations for yearling ultrasound and carcass traits using genomic-polygenic and polygenic models

	Phenotypic covariances				Heritabilities and additive genetic correlations			
Trait pair[a]	GPM	SE	PM	SE	GPM	SE	PM	SE
UW,UW; kg^2	**1345.30**	**56.52**	**1283.10**	**50.97**	**0.54**	**0.05**	**0.51**	**0.05**
UW,UREA; kg*cm^2	154.42	9.30	147.24	8.50	0.65	0.06	0.69	0.06
UW,UFAT; kg*cm	0.61	0.27	0.66	0.26	-0.08	0.11	-0.05	0.11
UW,UPIMF; kg*%	-3.09	0.86	-2.99	0.79	-0.14	0.07	-0.14	0.07
UW,SLA; kg*d	-325.39	53.23	-319.63	47.25	-0.20	0.10	-0.26	0.09
UW,HCW; kg*kg	682.07	54.51	635.26	47.86	0.67	0.07	0.63	0.07
UW,REA; kg*cm^2	63.49	13.56	55.23	12.05	0.42	0.09	0.36	0.09
UW,FAT; kg*cm	3.13	0.75	3.10	0.68	0.11	0.12	0.35	0.11
UW,MAR; kg*units	-171.59	127.49	-142.00	114.67	-0.06	0.09	0.03	0.09
UREA,UREA; cm^4	**60.66**	**2.34**	**58.64**	**2.15**	**0.36**	**0.03**	**0.34**	**0.03**
UREA,UFAT; cm^2*cm	0.23	0.06	0.24	0.06	-0.05	0.11	0.02	0.11
UREA,UPIMF; cm^2*%	-0.88	0.18	-0.79	0.16	-0.30	0.08	-0.24	0.08
UREA,SLA; cm^2*d	-44.29	10.84	-42.29	9.88	-0.24	0.10	-0.24	0.10
UREA,HCW; cm^2*kg	78.71	10.33	72.59	9.29	0.41	0.10	0.37	0.10
UREA,REA; cm^2*cm^2	23.29	2.75	20.74	2.45	0.67	0.08	0.58	0.09
UREA,FAT; cm^2*cm	0.29	0.15	0.32	0.14	-0.02	0.11	0.13	0.12
UREA,MAR; cm^2*units	-37.75	26.54	-33.92	23.83	-0.12	0.11	-0.10	0.10
UFAT,UFAT; cm^2	**0.10**	**0.00**	**0.10**	**0.00**	**0.12**	**0.02**	**0.11**	**0.02**
UFAT,UPIMF; cm*%	-0.02	0.01	-0.02	0.01	0.25	0.10	0.26	0.12
UFAT,SLA; cm*d	-1.00	0.38	-0.94	0.36	-0.31	0.12	-0.30	0.13
UFAT,HCW; cm*kg	-0.65	0.34	-0.55	0.33	-0.27	0.11	-0.28	0.12
UFAT,REA; cm*cm^2	-0.13	0.09	-0.11	0.09	-0.15	0.11	0.03	0.13
UFAT,FAT; cm*cm	0.04	0.01	0.03	0.01	0.81	0.05	0.69	0.08
UFAT,MAR; cm*units	-0.05	0.85	-0.19	0.81	0.15	0.13	0.16	0.13
UPIMF,UPIMF; %^{2}	**0.72**	**0.03**	**0.70**	**0.02**	**0.34**	**0.03**	**0.30**	**0.03**
UPIMF,SLA; %*d	-1.15	1.16	-0.97	1.05	-0.16	0.11	-0.16	0.12
UPIMF,HCW; %*kg	-2.43	1.07	-2.12	0.95	-0.10	0.10	-0.11	0.11
UPIMF,REA; %*cm^2	-0.80	0.29	-0.70	0.26	-0.28	0.11	-0.16	0.12
UPIMF,FAT; %*cm	0.03	0.02	0.04	0.01	-0.05	0.11	-0.09	0.13
UPIMF,MAR; %*units	21.22	2.90	20.18	2.60	0.60	0.08	0.56	0.09
SLA,SLA; d^2	**991.83**	**63.01**	**917.81**	**54.04**	**0.59**	**0.07**	**0.61**	**0.06**
SLA,HCW; d*kg	636.39	93.56	607.57	79.22	0.28	0.10	0.29	0.10
SLA,REA; d*cm^2	24.92	11.95	21.84	10.37	0.13	0.10	0.13	0.10
SLA,FAT; d*cm	0.82	0.67	0.81	0.57	0.05	0.14	0.08	0.15
SLA,MAR; d*units	243.40	115.32	253.81	100.23	-0.03	0.11	-0.05	0.12
HCW,HCW; kg^2	**1068.90**	**65.29**	**1004.30**	**55.98**	**0.58**	**0.06**	**0.52**	**0.07**
HCW,REA; kg*cm^2	105.93	12.93	96.54	11.37	0.57	0.08	0.70	0.07
HCW,FAT; kg*cm	3.85	0.70	3.88	0.59	0.12	0.13	0.23	0.14
HCW,MAR; kg*units	44.66	116.11	78.92	101.24	-0.08	0.09	0.00	0.10
REA,REA; cm^4	**71.90**	**4.42**	**67.52**	**3.77**	**0.48**	**0.04**	**0.45**	**0.05**
REA,FAT; cm^2*cm	-0.69	0.17	-0.65	0.15	-0.04	0.11	0.10	0.13
REA,MAR; cm^2*units	-77.55	30.65	-59.92	27.03	-0.27	0.09	-0.23	0.09
FAT,FAT; cm^2	**0.24**	**0.01**	**0.22**	**0.01**	**0.41**	**0.05**	**0.30**	**0.05**
FAT,MAR; cm*units	6.72	1.69	6.64	1.50	0.19	0.12	0.25	0.14
MAR,MAR; units^2	**6651.90**	**414.78**	**6372.70**	**369.02**	**0.56**	**0.07**	**0.51**	**0.08**

[a]UW = yearling ultrasound weight; UREA = yearling ultrasound ribeye area; UFAT = yearling ultrasound backfat; UPIMF = yearling ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score; GPM = genomic-polygenic model; PM = polygenic model.

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Table 4. REML estimates of environmental and phenotypic correlations for yearling ultrasound and carcass traits using genomic-polygenic and polygenic models

	Environmental correlations				Phenotypic correlations			
Trait pair[a]	GPM	SE	PM	SE	GPM	SE	PM	SE
UW,UREA; kg*cm^2	**0.47**	**0.04**	**0.44**	**0.04**	**0.54**	**0.02**	**0.54**	**0.02**
UW,UFAT; kg*cm	0.12	0.04	0.11	0.04	0.05	0.02	0.06	0.02
UW,UPIMF; kg*%	-0.07	0.02	-0.08	0.01	-0.10	0.03	-0.10	0.03
UW,SLA; kg*d	-0.39	0.07	-0.35	0.08	-0.28	0.04	-0.29	0.04
UW,HCW; kg*kg	0.45	0.05	0.49	0.05	0.57	0.03	0.56	0.03
UW,REA; kg*cm^2	-0.02	0.05	0.03	0.05	0.20	0.04	0.19	0.04
UW,FAT; kg*cm	0.24	0.07	0.08	0.06	0.18	0.04	0.18	0.04
UW,MAR; kg*units	-0.06	0.05	-0.14	0.05	-0.06	0.04	-0.05	0.04
UREA,UFAT; cm^2*cm	**0.14**	**0.02**	**0.12**	**0.02**	**0.10**	**0.02**	**0.10**	**0.02**
UREA,UPIMF; cm^2*%	-0.04	0.01	-0.07	0.01	-0.13	0.03	-0.12	0.02
UREA,SLA; cm^2*d	-0.14	0.04	-0.14	0.05	-0.18	0.04	-0.18	0.04
UREA,HCW; cm^2*kg	0.23	0.06	0.26	0.06	0.31	0.04	0.30	0.03
UREA,REA; cm^2*cm^2	0.13	0.02	0.17	0.03	0.35	0.04	0.33	0.03
UREA,FAT; cm^2*cm	0.14	0.04	0.07	0.04	0.08	0.04	0.09	0.04
UREA,MAR; cm^2*units	-0.01	0.05	-0.03	0.02	-0.06	0.04	-0.06	0.04
UFAT,UPIMF; cm*%	**-0.15**	**0.03**	**-0.15**	**0.03**	**-0.06**	**0.02**	**-0.07**	**0.02**
UFAT,SLA; cm*d	-0.03	0.06	-0.04	0.06	-0.10	0.04	-0.10	0.04
UFAT,HCW; cm*kg	0.01	0.05	0.02	0.05	-0.06	0.03	-0.06	0.03
UFAT,REA; cm*cm^2	-0.02	0.05	-0.08	0.05	-0.05	0.04	-0.04	0.04
UFAT,FAT; cm*cm	0.08	0.05	0.13	0.05	0.24	0.04	0.23	0.04
UFAT,MAR; cm*units	-0.06	0.04	-0.07	0.04	0.00	0.03	-0.01	0.03
UPIMF,SLA; %*d	**0.05**	**0.06**	**0.06**	**0.07**	**-0.04**	**0.04**	**-0.04**	**0.04**
UPIMF,HCW; %*kg	-0.08	0.06	-0.06	0.05	-0.09	0.04	-0.08	0.04
UPIMF,REA; %*cm^2	0.00	0.05	-0.08	0.06	-0.11	0.04	-0.10	0.04
UPIMF,FAT; %*cm	0.16	0.04	0.18	0.04	0.08	0.04	0.10	0.03
UPIMF,MAR; %*units	0.08	0.03	0.15	0.03	0.31	0.04	0.30	0.03
SLA,HCW; d*kg	**0.11**	**0.10**	**0.10**	**0.10**	**0.21**	**0.04**	**0.21**	**0.04**
SLA,REA; d*cm^2	0.05	0.06	0.05	0.07	0.09	0.04	0.09	0.04
SLA,FAT; d*cm	0.05	0.09	0.04	0.10	0.05	0.04	0.06	0.04
SLA,MAR; d*units	0.27	0.09	0.31	0.11	0.09	0.04	0.10	0.04
HCW,REA; kg*cm^2	**0.18**	**0.05**	**0.06**	**0.06**	**0.38**	**0.04**	**0.37**	**0.03**
HCW,FAT; kg*cm	0.37	0.08	0.29	0.07	0.24	0.04	0.26	0.04
HCW,MAR; kg*units	0.14	0.06	0.06	0.06	0.02	0.04	0.03	0.04
REA,FAT; cm^2*cm	**-0.27**	**0.05**	**-0.33**	**0.05**	**-0.17**	**0.04**	**-0.17**	**0.04**
REA,MAR; cm^2*units	0.06	0.03	0.04	0.02	-0.11	0.04	-0.09	0.04
FAT,MAR; cm*units	**0.15**	**0.08**	**0.13**	**0.07**	**0.17**	**0.04**	**0.18**	**0.04**

[a]UW = yearling ultrasound weight; UREA = yearling ultrasound ribeye area; UFAT = yearling ultrasound backfat; UPIMF = yearling ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score; GPM = genomic-polygenic model; PM = polygenic model.

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Table 5. Means and SD of differences between GPEBVR1, GPEBVR1, and PEBV relative to GPEBV for yearling ultrasound and carcass traits[a]

		GPEBVR1		GPEBVR2		PEBV	
Trait[b]	N	Mean	SD	Mean	SD	Mean	SD
UW	3,633	-0.01	0.99	0.06	0.58	-0.29	3.52
UREA	3,633	0.01	0.18	0.00	0.10	-0.07	0.56
UFAT	3,633	0.00	0.00	0.00	0.00	0.00	0.01
UPIMF	3,633	0.00	0.02	0.00	0.01	0.02	0.06
SLA	3,633	0.01	1.26	0.03	0.63	-1.18	3.21
HCW	3,633	-0.03	1.17	0.03	0.61	-1.21	4.18
REA	3,633	0.00	0.26	0.00	0.14	-0.31	1.17
FAT	3,633	0.00	0.01	0.00	0.01	0.00	0.06
MAR	3,633	-0.33	3.10	0.00	1.48	3.08	13.93

[a]GPEBV = EBV from genomic-polygenic model with all SNP markers; GPEBVR1 = EBV from genomic-polygenic model with reduced SNP marker set 1; GPEBVR2 = EBV from genomic-polygenic model with reduced SNP marker set 2; PEBV = EBV from polygenic model.

[b]UW = yearling ultrasound weight; UREA = yearling ultrasound ribeye area; UFAT = yearling ultrasound backfat; UPIMF = yearling ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score.

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Table 6. Rank correlations between GPEBV, GPEBVR1, GPEBVR2, and PEBV for yearling ultrasound and carcass traits[a]

Trait[b]	N	GPEBV, GPEBVR1	GPEBV, GPEBVR2	GPEBV, PEBV	GPEBVR1, GPEBVR2	GPEBVR1, PEBV	GPEBVR2, PEBV
UW	3,633	0.998	0.999	0.981	0.998	0.980	0.980
UREA	3,633	0.997	0.999	0.976	0.996	0.975	0.976
UFAT	3,633	0.994	0.999	0.946	0.992	0.944	0.946
UPIMF	3,633	0.997	0.999	0.978	0.996	0.978	0.977
SLA	3,633	0.993	0.998	0.960	0.992	0.955	0.957
HCW	3,633	0.997	0.999	0.967	0.997	0.966	0.966
REA	3,633	0.997	0.999	0.932	0.996	0.932	0.932
FAT	3,633	0.994	0.999	0.905	0.993	0.902	0.905
MAR	3,633	0.998	0.999	0.964	0.998	0.963	0.963
Mean	**3,633**	**0.996**	**0.999**	**0.957**	**0.995**	**0.955**	**0.956**

[a]GPEBV = EBV from genomic-polygenic model with all SNP markers; GPEBVR1 = EBV from genomic-polygenic model with reduced SNP marker set 1; GPEBVR2 = EBV from genomic-polygenic model with reduced SNP marker set 2; PEBV = EBV from polygenic model; All rank correlations were significant ($P < 0.0001$).

[b]UW = yearling ultrasound weight; UREA = yearling ultrasound ribeye area; UFAT = yearling ultrasound backfat; UPIMF = yearling ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score.

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Table 7. Percentages of differences in accuracy of GPEBVR1, GPEBVR2, and PEBV relative to accuracies of GPEBV for yearling ultrasound and carcass traits[a]

		GPEBVR1	GPEBVR2	PEBV
Trait[b]	N	% Difference	% Difference	% Difference
UW	3,633	-0.01	0.04	-2.92
UREA	3,633	-0.04	0.05	-5.29
UFAT	3,633	-0.03	0.07	-9.71
UPIMF	3,633	0.06	0.05	-8.06
SLA	3,633	0.06	0.10	-2.64
HCW	3,633	0.00	0.06	-4.66
REA	3,633	-0.04	0.06	-8.39
FAT	3,633	-0.04	0.07	-3.84
MAR	3,633	0.00	0.09	-7.87
Mean	**3,633**	**0.00**	**0.07**	**-5.93**

[a]GPEBV = EBV from genomic-polygenic model with all SNP markers; GPEBVR1 = EBV from genomic-polygenic model with reduced SNP marker set 1; GPEBVR2 = EBV from genomic-polygenic model with reduced SNP marker set 2; PEBV = EBV from polygenic model.
[b]UW = yearling ultrasound weight; UREA = yearling ultrasound ribeye area; UFAT = yearling ultrasound backfat; UPIMF = yearling ultrasound percent intramuscular fat; SLA= slaughter age; HCW = hot carcass weight; REA = ribeye area; FAT = backfat thickness; MAR = marbling score.

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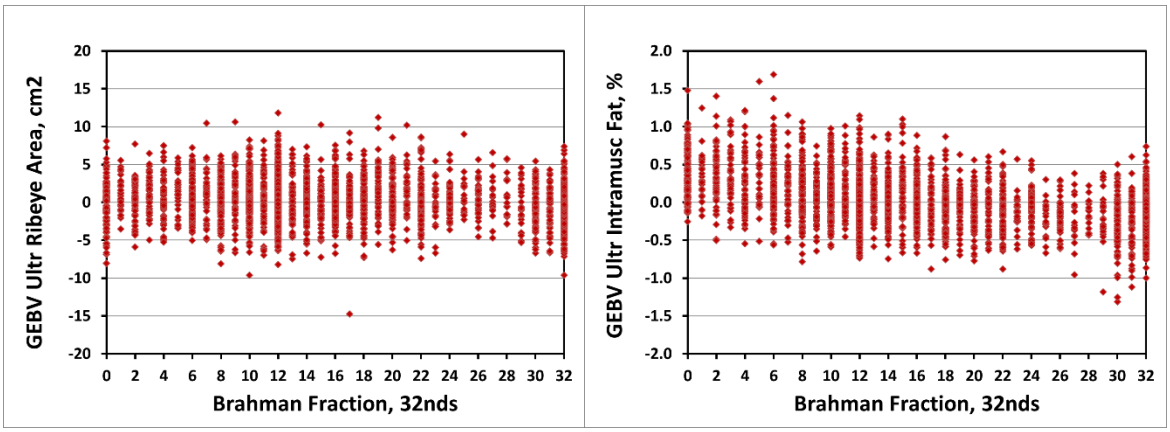

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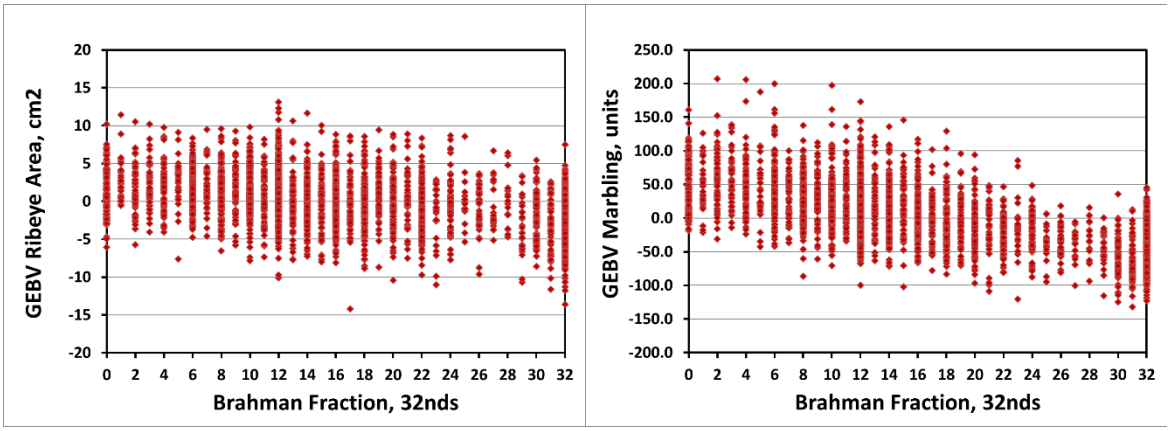

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582 **Fig. 1.** Genomic-polygenic EBV for ultrasound ribeye area, ultrasound percent

583 intramuscular fat, ribeye area, and marbling in animals from the Angus-Brahman

584 multibreed population

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