Growth and reproduction genomic-polygenic and polygenic parameters and prediction trends as Brahman fraction increases in an Angus-Brahman multibreed population

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Abstract

The objectives of this research were to estimate genomic-polygenic and polygenic parameters and to evaluate prediction trends as Brahman fraction increased from 0% to 100% in a subtropical multibreed Angus-Brahman (MAB) population for four growth and reproduction traits using single-step genomic-polygenic (GPM) and polygenic models (PM). Traits were 365-d yearling weight (YW), yearling reproductive tract score (RTS), age at first calving (AFC), and first calving interval (FCI). Numbers of phenotypic records were 1,758 for YW, 381 for RTS, 1,385 for AFC, and 985 for FCI. The pedigree file had 6,869 calves, sires, and dams, and genotype file contained 115,711 actual and imputed GGPHD150k SNP markers from 1,547 animals. The 4-trait GPM and PM included contemporary group, age of dam (YW only), sex of calf (YW only), direct heterosis, maternal heterosis (YW only) as fixed effects, and animal and residual as random effects. Genetic parameters were estimated using REML procedures and computed using AIREMLF90. Heritabilities were slightly higher for GPM than PM (0.47 vs. 0.45 for YW, 0.31 vs. 0.30 for RTS, 0.14 vs. 0.12 for AFC, and 0.31 vs. 0.29 for FCI). Genetic correlations were positive between YW and RTS (GPM: 0.55; PM: 0.60), negative between RTS and AFC (GPM: -0.22; PM: -0.55) and between AFC and FCI (GPM: -0.68; PM: -0.67), and near zero for all other trait pairs. The similarity between GPM and PM heritabilities and genetic correlations indicated that the 115,711 GGPHD150k SNP markers added little additional information to that contained in the pedigree. Regression coefficients of breed group EBV means on Brahman fraction were negative ($P = 0.0005$) for YW, RTS, and FCI, and positive ($P < 0.0001$) for AFC as Brahman fraction increased. This indicated that heifers with higher Brahman percentages tended to be lighter and less mature as yearlings, older at first calving, and have shorter FCI than heifers with higher Angus

percentages under the subtropical environmental conditions of the MAB population. Regression coefficients of individual animal EBV on Brahman fraction showed similar trends, although absolute values were smaller. However, there was a high degree of variation in EBV values within breed groups. Consequently, animals with high, medium, and low EBV existed across all Brahman percentages, thus allowing the selection of replacement animals of all Brahman percentages based on a common set of objectives.

Key words: Beef; Genomic; Growth; Multibreed; Polygenic; Reproduction

1. Introduction

Beef cattle operations routinely perform the task of choosing replacement heifers to be added to the breeding cow herd. Identification of sexually mature heifers is particularly important for reproduction strategies involving estrous synchronization and seasonal matings that require cows to calve once a year. Reproductive tract score is an indirect measure of sexual maturity that can be used instead of directly measuring age at puberty to identify replacement heifers (Andersen et al., 1991). According to the National Animal Health Monitoring System (NAHMS), approximately 8% of beef cattle operations in the US utilized estrous synchronization and artificial insemination primarily because of time constraints, labor costs, implementation complexity, and lack of facilities (USDA, 2009). The NAHMS estimated that 1.2% of US cow-calf producers utilized reproductive tract scores to choose replacement heifers (USDA, 1994).

Reproductive tract score was positively correlated with yearling weight (0.31; Andersen et al., 1991). Concomitantly, yearling weight was negatively correlated with age at first calving (-0.16; Snelling et al., 2012), and age at first calving was negatively

correlated with rebreeding (-0.35; Cavani et al., 2015), a trait similar to first calving interval. Utilization of reproductive tract score in the US southern region would help identify fertile replacement heifers and reduce age at first calving in the *Bos taurus-Bos indicus* cattle prevalent in this region. Unfortunately, estimates of heritability for reproductive tract score and of genetic correlations between reproductive tract score and yearling weight, age at first calving, and first calving interval needed to perform genetic evaluation and selection are currently unavailable. However, phenotypic and genotypic data for these four traits exists in the Angus-Brahman multibreed herd of the University of Florida. Estimation of genetic parameters and genetic predictions from the Angus-Brahman multibreed herd would provide a reasonable assessment of *Bos taurus-Bos indicus* reproductive ability and potential as replacement cows in Florida and the subtropical Southern region of the US. Thus, the objectives of this research were to estimate genomic-polygenic and polygenic parameters and to evaluate prediction trends as Brahman fraction increased from 0% to 100% for 365-d yearling weight, yearling reproductive tract score, age at first calving, and first calving interval using single-step genomic-polygenic and traditional polygenic models in an Angus-Brahman multibreed population with a breeding protocol that included estrous synchronization and artificial insemination followed by exposure to natural service sires.

2. Materials and methods

2.1. Animals and traits

The research protocol was approved by the University of Florida Institutional Animal Care and Use Committee (IACUC protocol number 201003744). Calves were progeny of a long-term multibreed Angus-Brahman (MAB) project of the University of

Florida, Gainesville. Animals in the MAB herd were generated using a diallel mating plan that involved sires and dams from six breed groups (Elzo and Wakeman, 1998). Breed groups were defined according to their Angus (A) and Brahman (B) fractions as follows: BG1 = (1.0 to 0.80) A (0.0 to 0.20) B, BG2 = (0.79 to 0.60) A (0.21 to 0.40) B, BG3 = (0.625) A (0.375) B, BG4 = (0.59 to 0.40) A (0.41 to 0.60) B, BG5 = (0.39 to 0.20) A (0.61 to 0.80) B, and BG6 = (0.19 to 0.0) A (0.81 to 1.00) B. Calves were born from 2006 to 2015 at the Beef Unit of the University of Florida, Gainesville. These animals were the progeny of 125 sires (18 BG1, 17 BG2, 21 BG3, 16 BG4, 13 BG5, and 40 BG6) and 701 dams (106 BG1, 118 BG2, 89 BG3, 134 BG4, 75 BG5, and 179 BG6). The dataset included information on yearling weights adjusted to 365 d age (YW, kg) from 1,758 male and female calves, reproductive tract scores (RTS, units; Andersen et al., 1991; Table A1, Appendix) from 381 yearling heifers, ages at first calving (AFC, d) from 1,385 first-calf heifers, and first calving intervals (FCI, d) from 985 second-calf cows.

2.2. Feeding and management

Preweaning, calves were managed with their dams on bahiagrass pastures (*Paspalum notatum*) with access to a complete mineral supplement (UF University Special Hi-Cu Mineral, University of Florida, Gainesville, Florida) at the Beef Research Unit of the University of Florida. Birth occurred from December to March and weaning either in late August or early September. Calves also received a supplement of bermudagrass (*Cynodon dactylon*) hay and cotton seed (*Gossypium spp.*) meal during winter (mid-December to mid-March).

Postweaning, calves were either transported to the University of Florida Feed Efficiency Facility (UFFEF; mid-September; 2006 to 2010), or kept at the Beef Research

Unit (2011 to 2015). Calves sent to UFFEF were randomly allocated to pens within sire group (BG1 to BG6) by sex category (bull, heifer, and steer) and remained in these pens for the length of the feed efficiency trial plus the adjustment period (approximately 3 mo). Feed at UFFEF consisted of 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). Calves that remained at the Beef Research Unit continued to graze bahiagrass pastures supplemented with bahiagrass hay, concentrate (1.6 kg to 3.6 kg per day; 14.0 % CP; 488 Pellet Medicated Weaning Ration, Lakeland Animal Nutrition, Lakeland, Florida; soy hull pellets), and free access to a mineral supplement.

The breeding protocol was the same for heifers and cows. It consisted of an initial period of estrous synchronization (ES) and artificial insemination (AI) followed by a natural service period. The steps of the breeding protocol were as follows: 1) Day 0: intravaginal insertion of a CIDR (1.38 g progesterone CIDR, Zoetis, Florham Park, NJ); 2) Day 7: removal of CIDR and injection of 25 mg i.m. Lutalyse (dinoprost tromethamine) Sterile Solution (Zoetis, Florham Park, NJ); 3) Days 8 to 10: Breed on observed heat using the AM/PM rule (i.e., if a cow was observed in estrous in the morning, she was artificially inseminated in the afternoon, and if a cow was observed in estrous in the afternoon, she was artificially inseminated in the next morning); 4) Day 10: approximately 77 to 79 hr after CIDR removal, heifers and cows not observed in heat were artificially inseminated, and injected with GnRH (Cystorelin (gonadorelin diacetate tetrahydrate), 100 mcg, 2 ml, i.m.; Merial LLC, Duluth, GA); 5) Day 14 to 35: rebreeding of heifers and cows showing estrous; and 6) Day 38: heifers and cows were placed with natural service sires in single-

sire pastures for 60 d. This ES-AI breeding protocol is commonly used for beef cattle in the US, hence the need to conduct genomic-polygenic analyses for AFC and FCI under these reproductive management conditions.

2.3. Tissue sampling, genotyping, and imputation

Blood and (or) semen samples from 1,514 MAB animals housed at the UF Beef Research Unit were collected, processed, and stored at -80 °C between 2006 to 2015. Two sets of samples were genotyped by GeneSeek (GeneSeek, Inc., Lincoln, NE, USA). White blood cells from 1,288 samples (95 sires, 144 dams, 75 bulls, 596 heifers, and 378 steers; BG1 = 200, BG2 = 249, BG3 = 204, BG4 = 315, BG5 = 140, and BG6 = 180) in the first set were isolated using the procedure outlined by Beauchemin et al. (2006) and sent to GeneSeek for genotyping with the Illumina3k beadchip in 2010 (Illumina, 2011). Genomic DNA from the second set was extracted from whole blood or semen of 238 animals (29 sires, 36 bulls, 173 steers; BG1 = 35, BG2 = 41, BG3 = 40, BG4 = 46, BG5 = 30, and BG6 = 46) using a commercial kit (QIAamp DNA mini kit, Qiagen, Valencia, CA) and genotyped with GeneSeek GGPHD150k chip (Neogen, 2015).

Multibreed animals genotyped with the Illumina3k chip were imputed to the GGPHD150k chip with program findhap4 (VanRaden et al., 2013; VanRaden, 2015) using the second set of 238 animals from the MAB herd as a reference population (RP). The accuracy of imputation was 59% (measured as concordance rate; Piccoli et al., 2014) using the oldest 80% of the animals genotyped with GGPHD150k (n = 190) and an imputed group containing the remaining 20% (n = 48) with all GGPHD150k SNP masked, except for the 2,252 SNP in common with the Illumina3k. Output file “haplotypes” from findhap4 was utilized by an in-house FORTRAN program to construct genotypic files for the

computation of genomic-polygenic variance components and parameters with the BLUPF90 family of programs (Misztal, 1999; Misztal et al., 2002; Tsuruta, 2014). The SNP with minor allele frequencies lower than 0.04 were discarded (n = 8,707). Consequently, the edited genotype file contained 1,547 MAB animals, each with 115,711 actual or partially imputed SNP marker genotypes (2,252 SNP in common between Illumina3k and GGPHD150k and 113,459 unique to GGPHD150k).

2.4. Variance components, heritabilities, and correlations

A 4-trait single-step genomic-polygenic model (GPM; Aguilar et al., 2010) and a polygenic model (PM) were used to obtain variance components, heritabilities, and genetic, environmental and phenotypic correlations for YW, RTS, AFC, and FCI. The fixed effects for GPM and PM were: 1) contemporary group (location-year; all traits); 2) age of dam (YW only); 3) sex of calf (YW only); 4) direct heterosis as a function of calf heterozygosity (i.e., the probability of having Angus and Brahman alleles in 1 locus; all traits); and 5) maternal heterosis as a function of dam heterozygosity (YW only). Random effects were direct additive genetic and residual. The mean for random direct additive genetic and residual effects was assumed to be zero for the GPM and PM models.

The GPM variance-covariance matrix among direct additive genetic effects for YW, RTS, AFC, and FCI was equal to $\mathrm{H}_1 \otimes \mathrm{V}_{\mathrm{dm}}$, where matrix H_1 was the genomic-polygenic relationship matrix (Legarra et al., 2009), i.e.,

$\begin{bmatrix} A_{11} + A_{12}A_{22}^{-1}(G_{22} - A_{22})A_{22}^{-1}G_{21} & A_{12}A_{22}^{-1}G_{22} \\ G_{22}A_{22}^{-1}A_{21} & G_{22} \end{bmatrix}$, A_{ij} = submatrix ij of the additive relationship matrix, subscript 1 corresponds to non-genotyped animals, and subscript 2 to genotyped animals, $A_{22}^{-1} =$ inverse of the additive relationship submatrix for genotyped

177 animals, $G_{22} = ZZ'/2\sum p_j\,(1-p_j)$ = matrix of genomic relationships for genotyped
178 animals (VanRaden, 2008; Aguilar et al., 2010), p_j = frequency of the "second" allele in
179 locus j, and $z_{ij} = (0 - 2p_j)$ if genotype for locus j was 11, $z_{ij} = (1 - 2p_j)$ if genotype for
180 locus j was 12 or 21, and $z_{ij} = (2 - 2p_j)$ if genotype for locus j was 22. Matrix V_{dm} was a 4
181 × 4 matrix of variances and covariances among direct additive genetic effects for YW,
182 RTS, AFC, and FCI, and "⊗" represented the Kronecker product. Matrices G_{22} and A_{22}
183 were weighted and scaled using the default parameters specified by program PREGSF90 from
184 BLUPF90 Family of programs (Misztal et al., 2002). The default weights were: tau=1, alpha
185 =0.95, beta = 0.05, gamma=0, delta=0, and omega=1. The default scaling of matrices G_{22} and
186 A_{22} required the mean of the diagonal elements of G_{22} and A_{22} to be equal and the mean of
187 the off-diagonal elements of G_{22} and A_{22} to be equal. The PM variance-covariance matrix
188 among direct additive genetic effects for YW, RTS, AFC, and FCI was equal to $A \otimes V_{dm}$,
189 where A was the additive relationship matrix among animals, and "⊗" and V_{dm} were as
190 defined for GPM. The residual variance-covariance matrix for the GPM and PM models
191 was equal to the Kronecker product of an identity matrix times a 4 × 4 matrix of
192 covariances among residual effects for YW, RTS, AFC, and FCI.

193 Restricted maximum likelihood procedures (Corbeil and Searle, 1971; Patterson and
194 Thompson, 1971; Harville, 1977) were used to estimate variance components using an
195 average information algorithm (Gilmour et al., 1995). Computations were carried out with
196 the BLUPF90 family of programs (Misztal, 1999; Misztal et al., 2002; Tsuruta, 2014).
197 Program RENUMF90 was used to renumber animals sequentially and construct input
198 phenotype and pedigree files for subsequent BLUPF90 programs. The REML estimates of
199 variance components, heritabilities, correlations (genetic, environmental, phenotypic) and

200 their standard errors were computed with program AIREMLF90 (Tsuruta, 2014) using a
201 convergence criterion = 10^{-12}. Standard errors for direct additive genetic and environmental
202 variance and covariance components were computed as square roots of diagonal elements
203 of the inverse of the average information matrix. Standard errors of functions of variance
204 components (i.e., phenotypic variances and covariances, heritabilities, and genetic,
205 environmental and phenotypic correlations) were obtained using the repeated sampling
206 procedure of Meyer and Houle (2013). This procedure involved drawing samples of
207 additive direct genetic and environmental variance and covariance components their
208 asymptotic multivariate distribution (n = 5,000), obtaining functions of variance
209 components for each sample, and computing means and SD for each variance component
210 function using values from all samples. The SD of the variance components functions were
211 by definition approximate SE of the corresponding REML estimates of these functions.
212 Computations were performed following convergence of estimation of variance and
213 covariance components using program AIREMLF90.
214
215 *2.5. Genomic-polygenic and polygenic predictions*
216 Estimated breeding values (EBV) were computed for YW, RTS, AFC, and FCI for
217 6,851 pedigree animals (genotyped = 1,547, non-genotyped = 5,304) using GPM and PM
218 and REML variances and covariances estimated with AIREMLF90. Spearman rank
219 correlations were used to compare rankings of animal EBV from GPM and PM for each
220 trait. Regressions of individual animal EBV and breed group mean EBV on Brahman
221 fraction were computed to assess EBV trends for YW, RTS, AFC, and FCI as Brahman
222 fraction increased from 0% to 100% Brahman. Breed group mean EBV was defined as the
223 mean of the EBV of all animals with a specific 32nd Brahman fraction, ranging from 0

(100% Angus) to 32 (100% Brahman). Rank correlations were computed using the CORR procedure whereas regressions were computed using the REG procedure of SAS (SAS Institute Inc., Cary, NC).

3. Results and discussion

Table 1 shows numbers of animals, means, and SD for YW, RTS, AFC, and FCI by breed group and total. The total number of records for RTS was substantially fewer than for YW, AFC, and FCI because measurements for this trait started to be recorded in 2011. Breed group 2 and BG4 had the highest YW means, followed closely by the means for BG1, BG3, and BG5, while BG6 had the lowest YW mean. The two breed groups with the highest RTS means were BG1 and BG2, BG4 had a somewhat lower RTS mean, BG3 (Brangus) and BG5 had nearly the same RTS mean, and the lowest RTS mean was for BG6. Means for AFC and FCI tended to be similar across breed groups because of the estrous synchronization strategy in the MAB herd. Means for AFC were somewhat lower for BG1 and BG6 than for the other four breed groups. Lastly, the lowest FCI mean was for BG5, the FCI mean for BG4 was somewhat higher, and the remaining four breed groups had higher and similar FCI means. Thus, the two breed groups with the highest A fractions (BG1 and BG2) had higher RTS than the other four breed groups. Conversely, the breed group with the highest B fraction (BG6) had the lowest YW and RTS means, and was tied with BG1 for the lowest AFC mean and the largest FCI mean.

3.1. Variance components, heritabilities, and correlations

Restricted maximum likelihood estimates and SE of additive genetic and environmental variances for YW, RTS, AFC, and FCI as well as additive genetic and

248 environmental covariances between pairs of traits obtained with GPM and PM are shown in
249 Table 2. Similarly, Table 3 contains GPM and PM REML estimates and SE of phenotypic
250 variances and heritabilities for these four traits plus phenotypic covariances and additive
251 genetic correlations between pairs of traits. Lastly, Table 4 presents REML estimates and
252 SE of environmental and phenotypic correlations between pairs of traits also computed
253 using GPM and PM.

254 Restricted maximum likelihood estimates of additive genetic, environmental, and
255 phenotypic variance components, heritabilities, and correlations from GPM and PM were
256 broadly similar for all traits. Estimates of additive genetic variances from GPM were, on
257 the average, 9.2 % larger and covariances were 23 % smaller whereas environmental
258 variances were, on the average, 1.8 % smaller and covariances were 6.9% larger than those
259 from PM (Table 2). Phenotypic variances were only slightly larger (0.6 %) and phenotypic
260 covariances slightly smaller (0.5%). Heritabilities were 7.8 % larger and additive genetic
261 correlations, excluding near-zero correlations between YW and AFC and between YW and
262 FCI, were 37.1 % smaller for GPM than for PM (Table 3). Lastly, environmental
263 correlations were 7.2 % larger and phenotypic correlations 3.3 % smaller for GPM than for
264 PM (Table 4). The largely similar additive genetic, environmental, and phenotypic
265 variance components, heritabilities, and genetic correlations from GPM and GP indicated
266 that the 115,711 GGPHD150k SNP markers added little additional information to that
267 contained in the pedigree of this Angus-Brahman dataset. The low impact of genotypic
268 information on estimates of variance components and genetic parameters here may have
269 been largely determined by the low accuracy of imputation (59%) from Illumina3k 2,252
270 SNP to GGPHD150k 115,711 SNP. Further, estimates of linkage disequilibrium in the
271 MAB population, measured in windows of 10 SNP, were 0.15 for r^2 and 0.63 for D'

(PLINK 1.9; Chang et al., 2015; Purcell and Chang, 2016) likely the outcome of repeated crossing over between Angus and Brahman haplotype blocks over twenty-eight years of diallel mating in the MAB herd involving sires and dams of more than thirty Angus and Brahman percentages. The combination of low levels of linkage disequilibrium in the MAB herd and the direct imputation from SNP in the 3k chips (constructed for dairy cattle) to the GGPHD150k (constructed for beef cattle) resulted in a substantially lower imputation accuracy than in other multibreed (76.79% to 93.94% from 8k to 18k; Holstein-upgraded Thai population; Jattawa et al., 2016) and single-breed (88% to 98% from 3k to 50k SNP; Holstein; Sargolzaei et al., 2011; Wiggans et al., 2012; 86% from 3k to 50k; Hereford and Braford; Piccoli et al., 2014) cattle populations.

Heritabilities were medium for YW (GPM: 0.47; PM: 0.45), RTS (GPM: 0.31; PM: 0.30), and FCI (GPM: 0.31; PM: 0.29), and low for AFC (GPM: 0.14; PM: 0.12). The GPM and PM estimates of heritability for YW were somewhat lower than previous estimates for YW in this MAB population (GPM: 0.54; PM: 0.50; Elzo et al., 2015). Possible reasons for different estimates include larger number of animals with YW here (n = 1,758) than in the previous study (n = 812), and adjustment to 365 d of age and imputation to 115,711 SNP from GGPHD150k here versus unadjusted YW and imputation to 46,839 SNP from the Illumina50k in Elzo et al. (2015). The GPM and PM heritabilities for YW were within the range of values found in previous studies in various countries. Values of YW heritabilities here were lower than estimates for Angus (0.49 ± 0.05; Knights et al., 1984) and Brangus cattle (0.53; Stelzleni et al., 2002) in the US and *Bos taurus* composite cattle in Canada (0.69; Crews and Kemp, 2002), similar to Simmental in the US (0.47 ± 0.05; Crews et al., 2003) and higher than estimates for Brangus heifers in the US

295 (0.38 ± 0.10; Peters et al., 2012) and Nellore cattle in Brazil (0.34 ± 0.01; Shiotsuki et al.,
296 2009).

297 The GPM and PM heritabilities for RTS here were nearly identical to the value of
298 0.32 reported by Andersen et al. (1991) in the beef cattle herd of Colorado State University.
299 This was the only heritability value found in the literature. Conversely, the GPM and PM
300 heritability estimates for AFC in the MAB population were roughly in the middle of
301 estimates from a variety of studies involving *Bos taurus* and *Bos indicus* breeds. The AFC
302 heritabilities here were lower than Angus cattle estimates in the US (0.28 ± 0.06; Bormann
303 and Wilson, 2010) and in Great Britain (0.22 ± 0.06; Roughsedge et al., 2005), and from
304 Brahman and several other *Bos indicus* cattle breeds in Mexico (0.46 ± 0.15; Magaña and
305 Segura, 1997). Similar AFC heritabilities were obtained in Nelore cattle in Brazil (0.17 ±
306 0.01; Boligon et al., 2010) and Angus-Blanco Orejinegro-Zebu multibreed cattle in
307 Colombia (0.15 ± 0.13; Vergara et al., 2009). Lastly, heritabilities for AFC here were
308 substantially higher than estimates from Angus, Red Angus, and Hereford (0.07 ± 0.09;
309 Bourdon and Brinks, 1982) and purebred and crossbred *Bos taurus* cattle in the US (0.08 ±
310 0.04; Martinez-Velazquez et al., 2003) and from Brahman (0.10; Cavani et al., 2015) and
311 Tabapua cattle in Brazil (0.09 ± 0.02; Bernardes et al., 2015).

312 The GPM and PM heritability estimates for FCI here were substantially higher than
313 values obtained in Angus cattle in Great Britain (0.09 ± 0.04; Roughsedge et al., 2005),
314 Angus-Blanco Orejinegro-Zebu cattle in Colombia (0.11 ± 0.06; Vergara et al., 2009), and
315 Brahman (0.02; Cavani et al., 2015) and Tabapua cattle (0.05 ± 0.03; Bernardes et al.,
316 2015) in Brazil. The higher heritability values for FCI here may have occurred because the
317 highly controlled mating system in a single season (estrous synchronization followed by at
318 most two artificial inseminations and a short breeding season of 60 d) allowed additive

319 genetic differences to be expressed in animals from the MAB herd while at the same time
320 reducing the environmental variance. In contrast, the other four cattle populations were
321 field datasets representing cattle populations with several herds and matings throughout the
322 year that had substantially larger environmental variances than the MAB herd (4 to 27
323 times) and additive genetic variances ranging from 0.8 to 2.6 times those from the GPM
324 and PM here, hence their small FCI heritability estimates.

325 Additive genetic correlations were positive between YW and RTS (GPM: 0.53; PM:
326 0.60), negative between AFC and FCI (GPM: -0.67; PM: -0.67), and with SE higher than
327 their estimates or near zero values for all other trait pairs (Table 3). Environmental
328 correlations were close to zero for all trait combinations except for the negative
329 environmental correlation between AFC and FCI (GPM: -0.45; PM: -0.47; Table 4).
330 Phenotypic correlations showed a pattern similar to additive genetic correlations, albeit
331 with smaller values. Phenotypic correlations were positive between YW and RTS (GPM:
332 0.25; PM: 0.26), negative between RTS and AFC (GPM: -0.21; PM: -0.22) and between
333 AFC and FCI (GPM: -0.49; PM: -0.49), and close to zero for other pairs of traits (Table 4).

334 Andersen et al. (1991) estimated a lower additive genetic correlation (0.31), a higher
335 environmental correlation (0.94), and a higher phenotypic correlation (0.44) between YW
336 and RTS in the Colorado State University beef cattle herd than the GPM and PM values
337 obtained in the MAB herd here. No other correlation estimates between YW and RTS were
338 found in the literature. The positive additive genetic correlations between YW and RTS
339 here indicated that selection for heavier YW would be expected to also increase RTS and
340 vice versa. However, because the additive genetic correlation estimates were moderate to
341 low, a selection objective that aimed primarily at increasing RTS while maintaining or
342 minimally increasing YW would be achievable by selecting animals with high EBV for

343 RTS within a desired range of EBV for YW. This may be an appropriate alternative for
344 lower-maturing Brahman and high-percentage Brahman calves in the MAB herd here and
345 *Bos taurus*-Brahman herds elsewhere.

346 Despite the positive impact on pregnancy rates on first-calf heifers and throughout
347 the lifetime of cows (Andersen et al., 1991; Holm et al., 2009; Gutierrez et al., 2014), only
348 a small percentage of US cow-calf herds utilize RTS as a management tool to help choose
349 replacement heifers (1.2%; USDA, 1994). Reasons for this low adoption rate of RTS have
350 been probably similar to those indicated for the low rate of use of estrous synchronization
351 and AI in cow-calf herds (i.e., time constraints, labor costs, implementation complexity,
352 and lack of facilities). The medium-sized heritability of RTS indicated that it would be
353 advantageous to use RTS as a genetic management and selection tool to improve pregnancy
354 rates in the MAB herd, and likely other Angus-Brahman crossbred herds under subtropical
355 conditions in the US and elsewhere. However, implementation in private herds will
356 probably remain an issue for most beef cattle producers, except perhaps for those that have
357 already implemented estrous synchronization and AI protocols.

358 The negative GPM and PM additive genetic correlations between AFC and FCI here
359 were higher than an estimate in Brahman cattle in Brazil (-0.13; Cavani et al., 2015), but
360 disagreed with positive values in Angus-Blanco Orejinegro-Zebu cattle in Colombia (0.33
361 ± 0.41; Vergara et al., 2009) and Tabapua cattle in Brazil (0.92 ± 0.33; Bernardes et al.,
362 2015). Positive additive genetic correlations between AFC and FCI indicate that animals
363 with older AFC had longer recovery periods after the first calving in these two populations
364 perhaps due to the extensive nature of their pasture production systems. In contrast, the
365 negative GPM and PM additive genetic correlations between AFC and FCI in this study
366 were likely a consequence of the use of estrous synchronization, artificial insemination, and

a short natural service breeding season (60 d) that forced heifers with older AFC that calved later in the calving season to be bred after a shorter postpartum period than heifers that calved earlier in the season, resulting in a negative association between AFC and FCI. This was a positive outcome that would facilitate selection of heifers that calve at younger ages (and earlier in the calving season) and culling of heifers that calve at older ages (and later in the calving season), resulting in a more efficiently managed breeding herd with shorter breeding and calving seasons. Lastly, the values of heritabilities and additive genetic correlations between YW, RTS, AFC, and FCI obtained in this MAB population indicated that a selection index aimed at increasing YW and RTS and decreasing AFC and FCI would be feasible and likely to produce changes in the desired directions (i.e., higher YW and RTS and lower AFC and FCI).

3.2. Ranking of animals evaluated with the genomic-polygenic and polygenic models

Ranges for EBV and standard errors of prediction (SEP) from GPM and PM were similar for all traits. The GPM EBV ranges were -62.1 kg to 70.2 kg for YW, -1.0 units to 1.6 units for RTS, -58.9 d to 31.8 d for AFC, and -30.2 d to 98.9 d for FCI, and the GPM SEP ranges were 9.5 kg to 30.8 kg for YW, 0.4 units to 0.8 units for RTS, 8.6 d to 15.7 d for AFC, and 10.6 d to 20.0 d for FCI. The EBV for PM ranged from -63.6 kg to 67.6 kg for YW, -1.1 units to 1.6 units for RTS, -51.4 d to 20.8 d for AFC, and -31.2 d to 96.2 d for FCI, and the SEP for PM ranged from 9.7 kg to 30.3 kg for YW, 0.4 units to 0.8 units for RTS, 9.1 d to 14.3 d for AFC, and 11.9 d to 19.6 d for FCI.

Rank correlations between EBV from GPM and PM for all evaluated animals were reasonably high for all traits (0.95 for YW, 0.94 for RTS, 0.91 for AFC, and 0.93 for FCI; $P < 0.0001$) indicating that animal EBV rankings were fairly similar for both models. Rank

391 correlations ($P < 0.0001$) for the 10 animals with the lowest SEP for each of the traits were
392 similar to the overall ranking for YW (0.95) and higher for the other traits (0.98 for RTS,
393 0.95 for AFC, and 0.98 for FCI). These higher rank correlation values indicated that the
394 similarity between GPM and PM rankings increased as the SEP decreased. Further, rank
395 correlation values in this MAB population suggested that the information provided by the
396 115,711 GGPHD150k SNP markers from the 1,547 animals with genotype information
397 modified the additive relationship matrix only to a small extent, hence the similarity in
398 EBV rankings from GPM and PM.
399
400 *3.3. Trends in genomic-polygenic and polygenic EBV as Brahman percentage increased*
401 *from 0% to 100%*
402 Estimates of regression coefficients from individual animal EBV on Brahman
403 fraction (Table 5) were low and negative for YW and RTS ($P < 0.0001$ for GPM and PM),
404 low and positive for AFC ($P < 0.0001$ for GMP; $P = 0.0303$ for PM), and non-significant
405 for FCI (GPM and PM). A similar pattern of regression coefficients, but with lower
406 negative values and higher positive values was obtained for breed group mean EBV (Table
407 6). The GPM and PM regression coefficients for breed group mean EBV on Brahman
408 fraction were negative for YW, RTS, and FCI ($P = 0.0005$ to $P < 0.0001$) and positive for
409 AFC ($P < 0.0001$). Due to the similarity of GPM and PM EBV only GPM graphs of
410 individual animal EBV on 32nd Brahman fraction (Fig. 1) and of breed group mean EBV on
411 32nd Brahman fraction (Fig. 2) are presented. Breed group mean regression coefficients
412 indicated that heifers with higher Brahman percentages tended to be lighter and less mature
413 as yearlings, older at first calving, and have shorter FCI than heifers with higher Angus
414 percentages under the subtropical environmental conditions of the MAB population.

However, the high degree of variation in EBV values within breed groups and the low absolute values of regression coefficients of individual animal EBV on 32nd Brahman fraction determined the existence of animals with high, medium, and low EBV values for all traits across breed groups. This implied that choosing replacement heifers based on higher EBV for RTS within an acceptable range of YW would lower AFC and FCI, thus improving the reproductive performance of the MAB herd. Further, replacement sires could also be chosen based on a similar strategy (phenotypic information for males would come from female relatives). Utilization of a single set of selection objectives for replacement sires and heifers of all Angus and Brahman percentages in the MAB herd would be particularly helpful to decrease the percentage of lower maturing Brahman and high-percentage Brahman animals. This strategy would be expected to increase the growth and reproductive performance similarity among cattle of all Angus and Brahman breed compositions and facilitate feeding and management programs in the MAB herd.

4. Conclusions

The REML estimates of additive genetic, environmental, and phenotypic variance components, heritabilities, and genetic, environmental, and phenotypic correlations from the genomic-polygenic and the polygenic models were similar for all traits. High rank correlations existed between EBV from both models for all traits. These EBV indicated that heifers with higher Brahman percentages tended to be lighter and less mature as yearlings, older at first calving, and have shorter FCI than heifers with higher Angus percentages under the subtropical environmental conditions of this multibreed population. High EBV variation within breed groups and low regression coefficients of individual animal EBV on Brahman fraction determined the existence of cattle with high, medium,

and low EBV in all breed groups, thus allowing the selection of replacement animals of all Brahman percentages based on a common set of objectives.

Conflict of interest

No conflicts of interest influenced this research.

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579 1552-1558.

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

	Trait[a]											
	YW, kg			RTS, units			AFC, d			FCI, d		
Breed group[b]	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
BG1	251	354	56	62	3.6	1.3	180	1078	40	143	390	28
BG2	286	366	58	42	3.5	1.3	218	1083	41	162	388	32
BG3	250	358	58	37	2.8	1.3	164	1081	55	116	389	26
BG4	380	364	55	63	3.2	1.1	363	1084	45	263	385	31
BG5	196	355	52	46	2.7	1.1	205	1087	40	129	379	28
BG6	395	322	48	131	2.4	1.0	255	1078	46	172	390	44
Total	1758	352	57	381	2.9	1.2	1385	1082	45	985	387	33

581 [a]YW = 365-d yearling weight; RTS = reproductive tract score; AFC = age at first calving; FCI =
582 first calving interval.
583 [b]Breed group: BG1 = 100% A to (80% A 20% B); 2) BG2 = (60% A 40% B) to (79% A 21% B); 3)
584 BG3 = Brangus = (62.5% A 37.5% B); 4) BG4 = (40% A 60% B) to (59% A 41% B); 5) BG5 =
585 (20% A 80% B) to (39% A 61%B); and 6) BG6 = (19% A 81% B) to 100% B; A = Angus, B =
586 Brahman.
587

588 Table 2. REML estimates of direct additive genetic and environmental covariances for yearling
589 weight and reproductive traits using genomic-polygenic and polygenic models

	Additive genetic covariances				Environmental covariances			
Trait pair[a]	GPM	SE	PM	SE	GPM	SE	PM	SE
YW, YW; kg^2	773.4	112.8	729.5	107.3	864.6	81.1	886.9	78.8
YW, RTS; kg*u	0.8	4.0	10.7	3.0	-1.7	3.8	2.0	3.4
YW, AFC, kg*d	-4.4	82.3	-6.6	74.6	76.4	88.0	48.6	85.2
YW, FCI; kg*d	-2.4	84.5	-22.1	78.5	-104.0	83.9	-106.1	80.9
RTS, RTS; u*u	0.58	0.19	0.43	0.11	1.00	0.17	1.02	0.14
RTS, AFC; u*d	4.5	3.5	-4.6	2.7	-7.3	4.9	-5.2	4.8
RTS, FCI; u*d	-1.8	3.8	-0.5	2.9	4.6	4.2	4.1	3.9
AFC, AFC; d^2	133.3	80.6	164.6	74.0	1231.7	85.5	1264.5	83.8
AFC, FCI; d^2	-55.7	70.8	-149.0	64.9	-429.1	68.9	-450.6	65.9
FCI, FCI; d^2	348.1	94.0	303.9	89.0	725.3	85.0	736.8	81.4

590 [a]YW = 365-d yearling weight; RTS = reproductive tract score; AFC = age at first calving; FCI =
591 first calving interval; u = units; GPM = genomic-polygenic model; PM = polygenic model.

592 Table 3. REML estimates of phenotypic covariances, heritabilities, and additive genetic correlations
593 for yearling weight and reproductive traits using genomic-polygenic and polygenic models

	Phenotypic covariances				Heritabilites and additive genetic correlations			
Trait pair[a]	GPM	SE	PM	SE	GPM	SE	PM	SE
YW, YW; kg^2	1633.4	66.1	1616.4	64.2	0.47	0.06	0.45	0.06
YW, RTS; kg*u	12.3	3.2	12.7	2.9	0.53	0.32	0.60	0.16
YW, AFC, kg*d	54.1	76.9	42.0	74.7	0.05	0.24	-0.02	0.28
YW, FCI; kg*d	-131.1	71.6	-128.2	69.9	0.04	0.18	-0.01	0.17
RTS, RTS; u*u	1.46	0.11	1.45	0.10	0.31	0.12	0.30	0.08
RTS, AFC; u*d	-9.4	4.3	-9.9	4.2	-0.22	0.55	-0.55	0.58
RTS, FCI; u*d	2.6	3.4	3.5	3.2	-0.16	0.41	-0.05	0.29
AFC, AFC; d^2	1430.3	55.8	1429.1	53.8	0.14	0.05	0.12	0.05
AFC, FCI; d^2	-600.0	44.5	-599.6	42.9	-0.67	0.24	-0.67	0.32
FCI, FCI; d^2	1046.9	52.3	1040.7	51.1	0.31	0.09	0.29	0.08

594 [a]YW = 365-d yearling weight; RTS = reproductive tract score; AFC = age at first calving; FCI = first
595 calving interval; u = units; GPM = genomic-polygenic model; PM = polygenic model; SE = standard
596 deviation of 5,000 samples.
597

598 Table 4. REML estimates of environmental and phenotypic correlations for yearling weight and
599 reproductive traits using genomic-polygenic and polygenic models

	Environmental correlations				Phenotypic correlations			
Trait pair[a]	GPM	SE	PM	SE	GPM	SE	PM	SE
YW, RTS; kg*u	0.08	0.13	0.07	0.11	0.25	0.06	0.26	0.06
YW, AFC, kg*d	0.04	0.09	0.05	0.08	0.04	0.05	0.03	0.05
YW, FCI; kg*d	-0.13	0.11	-0.13	0.10	-0.07	0.10	-0.09	0.10
RTS, AFC; u*d	-0.21	0.14	-0.15	0.13	-0.21	0.10	-0.22	0.09
RTS, FCI; u*d	0.17	0.16	0.15	0.15	0.07	0.09	0.09	0.08
AFC, FCI; d^2	-0.45	0.05	-0.47	0.05	-0.49	0.03	-0.49	0.03

600 [a]YW = 365-d yearling weight; RTS = reproductive tract score; AFC = age at first calving; FCI = first
601 calving interval; u = units; GPM = genomic-polygenic model; PM = polygenic model; SE = standard
602 deviation of 5,000 samples.
603

Table 5. Linear regression coefficients of individual animal EBV on Brahman fraction for yearling weight and reproductive traits using genomic-polygenic and polygenic models

	Linear regression coefficient					
Trait[a]	GPM	SE	P-value	PM	SE	P-value
YW, kg/32nds	-0.3077	0.0147	P < 0.0001	-0.2205	0.0149	P < 0.0001
RTS, units/32nds	-0.0066	0.0003	P < 0.0001	-0.0041	0.0004	P < 0.0001
AFC, d/32nds	0.0235	0.0062	P < 0.0001	0.0115	0.0053	P = 0.0303
FCI, d/32nds	-0.0055	0.0081	P = 0.4993	0.0059	0.0079	P = 0.4546

[a]YW = 365-d yearling weight; RTS = reproductive tract score; AFC = age at first calving; FCI = first calving interval; u = units; GPM = genomic-polygenic model; PM = polygenic model; 32nds = Brahman fraction of animal in 32nds.

Table 6. Linear regression coefficients of breed group mean EBV on Brahman fraction for yearling weight and reproductive traits using genomic-polygenic and polygenic models

	Linear regression coefficient					
Trait[a]	GPM	SE	P-value	PM	SE	P-value
YW, kg/32nds	-0.5299	0.0419	P < 0.0001	-0.4378	0.0437	P < 0.0001
RTS, units/32nds	-0.0120	0.0012	P < 0.0001	-0.0099	0.0013	P < 0.0001
AFC, d/32nds	0.1209	0.0206	P < 0.0001	0.1022	0.0167	P < 0.0001
FCI, d/32nds	-0.0878	0.0191	P < 0.0001	-0.0795	0.0203	P = 0.0005

[a]YW = 365-d yearling weight; RTS = reproductive tract score; AFC = age at first calving; FCI = first calving interval; u = units; GPM = genomic-polygenic model; PM = polygenic model; 32nds = Brahman fraction of animal in 32nds.

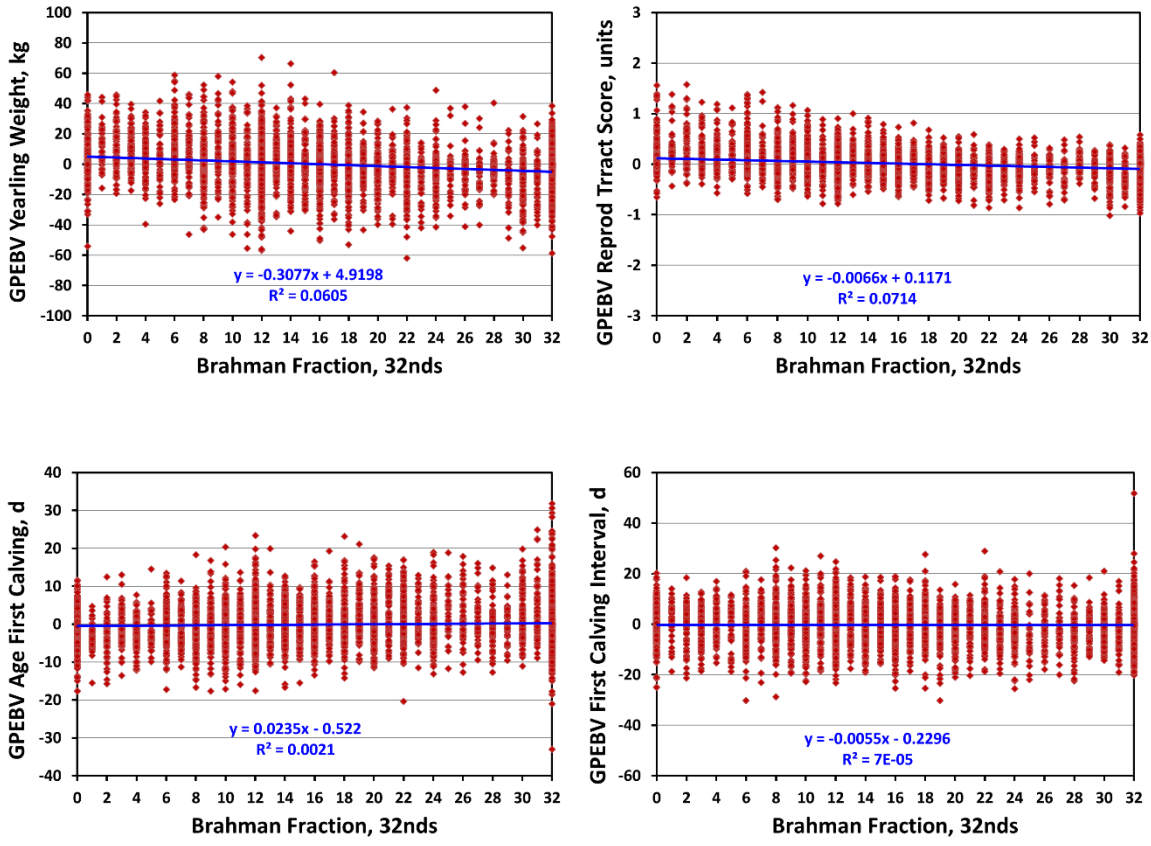

Fig. 1. Genomic-polygenic additive direct genetic predictions for yearling weight, reproductive tract score, age at first calving, and calving interval as Brahman fraction increased from 0 to 100%

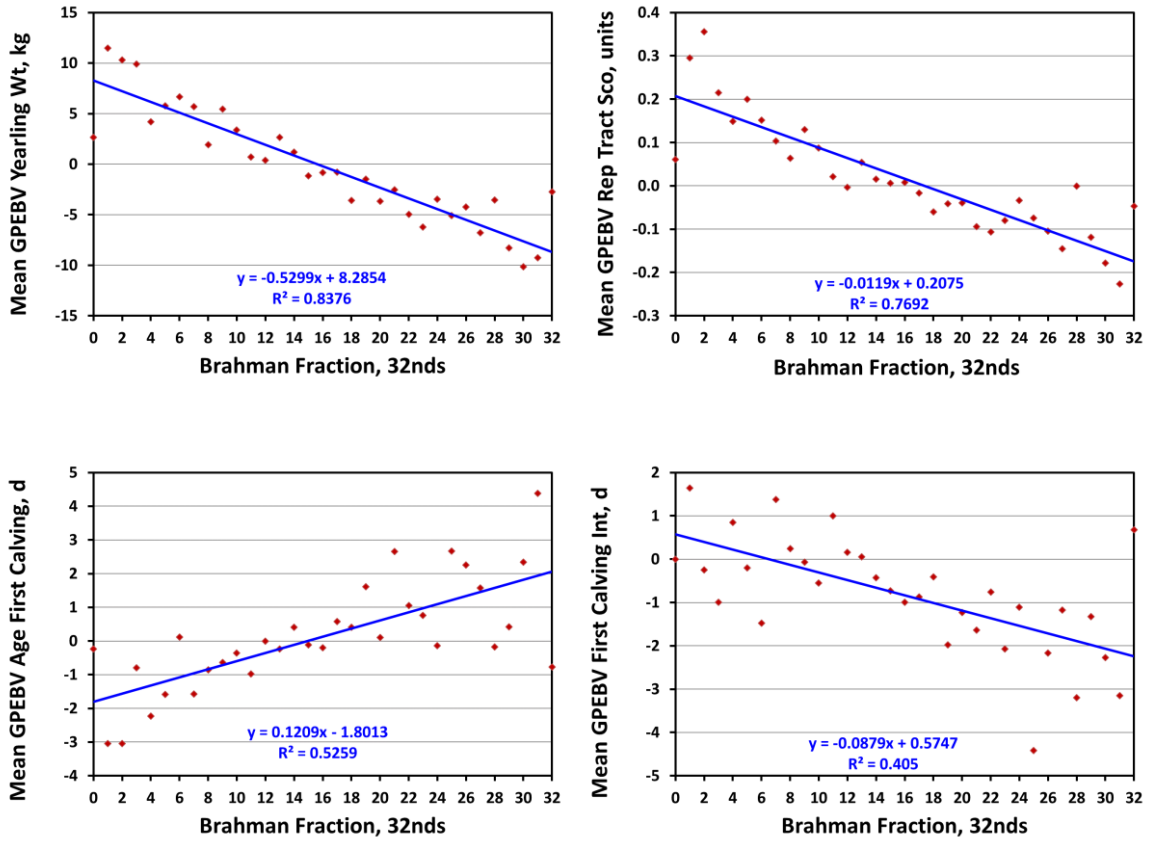

Fig. 2. Mean genomic-polygenic additive direct genetic predictions for yearling weight, reproductive tract score, age at first calving, and calving interval as Brahman fraction increased from 0 to 100%

Appendix

Table A1. Reproductive tract scores (RTS; Andersen et al., 1991)

		Ovaries			
RTS	Uterine horns	Length, mm	Height, mm	Width, mm	Ovarian structures
1	Immature < 20 mm diameter, no tone	15	10	8	No palpable structures
2	20 to 25 mm diameter, no tone	18	12	10	8 mm follicles
3	25 to 30 mm diameter, slight tone	22	15	10	8 to 10 mm follicles
4	30 mm diameter, good tone	30	16	12	> 10 mm follicles, corpus luteum possible
5	>30 mm diameter, good tone, erect	> 32	20	15	> 10 mm follicles, corpus luteum present