Genetic parameters and predictions for direct and maternal growth traits in a multibreed Angus-Brahman cattle population using genomic-polygenic and polygenic models

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Abstract

The objectives of this research were to compare variance components, genetic parameters, and EBV rankings for birth weight (BW) direct and maternal, weaning weight (WW) direct and maternal, and postweaning gain from 205 d to 365 d (PWG) direct using three genomic-polygenic and one polygenic model representing four plausible beef cattle genetic evaluation scenarios for growth traits under subtropical conditions in the US southern region. In addition, EBV trends as percentage Brahman increased from 0% to 100% were evaluated for each trait and model. The dataset included 5,264 animals from a multibreed Angus-Brahman population born from 1987 to 2013. Genomic-polygenic models 1 (GP1; pedigree relationships for all animals; genomic relationships for genotyped animals), 2 (GP2; pedigree relationships for non-genotyped animals; genomic relationships for genotyped animals), and 3 (GP3; no pedigree relationships; genomic relationships for genotyped animals) used actual and imputed genotypes from 46,768 SNP markers. Variance components and genetic parameters were estimated using REML procedures. Variance component and genetic parameter estimates from GP1 were the most similar to those from the polygenic model, followed by those from GP2, and the least similar (especially for maternal traits) were those from GP3. Similarly, the highest rank correlations were those between animal EBV from the polygenic model and GP1, followed by those between animal EBV from GP1 and GP2 and between the polygenic model and GP2. Model GP3 performed poorly for maternal traits due to ignoring calf-dam relationships. These results indicated that the polygenic model and genomic-polygenic model 1 should be preferred. However, high genotyping costs still make the polygenic model preferable for commercial beef cattle operations. Brahman animals tended to have higher EBV for BW direct and WW direct, and lower EBV for PWG direct, BW maternal,

and WW maternal. However, low regression coefficients for EBV on Brahman fraction ensured that high, medium, and low EBV animals from all breed compositions existed in this multibreed population.

Key words: Beef; Direct; Genomic; Growth; Maternal; Multibreed

1. Introduction

Utilization of genotype information for genetic evaluation of cattle has become widespread in beef and dairy cattle. Genomic evaluations are currently routinely conducted in dairy cattle in the US and other countries (VanRaden 2008; Harris and Johnson, 2010; VanRaden et al., 2011, 2013; Legarra and Ducrocq, 2012). Conversely, the US beef industry has only recently begun to implement national genomic evaluations that combine phenotypic, pedigree, and genotypic information (Fernando and Garrick, 2013). Purebred breeders and commercial cattle producers have been encouraged by breed associations and private companies to genotype their animals with one or more chips of various densities. Genotyping animals from purebred cattle operations that submit phenotypes, pedigree, and genotypes to breed associations conducting national genetic evaluations will likely enhance the ability of individual cattle breeders to identify superior animals. However, the potential usefulness of genotyping to enhance genetic selection within commercial cattle operations that do in-house genetic evaluations seems less clear. Increases in prediction accuracies will depend on the extent of genotyping (and density of genotyping chips), the availability of individual phenotypes, and the completeness of pedigree information.

Implementation of genomic evaluation methodology has been greatly facilitated by the development of the single-step genomic evaluation procedure (Aguilar et al., 2010).

The integration of the unified procedure into the freely available BLUPF90 family of programs has increased the feasibility of utilizing of genomic procedures to analyze traits that are not only affected by direct genetic effects, but also by maternal effects such as preweaning weights in beef cattle. Estimates of genetic parameters, prediction accuracies, and animal rankings for these types of traits using genomic and polygenic models have yet to be evaluated. Further, considering the multibreed nature of the current beef cattle national genetic evaluation system in the US, genomic and polygenic models for growth traits need to be compared using information from multibreed populations. The only reported work on this subject was a comparison of various genomic evaluation models using simulated weaning direct and maternal QTL effects (Lourenco et al., 2013).

This research was aimed at comparing multibreed beef cattle evaluations for growth traits using four scenarios defined in terms of availability of phenotypic, pedigree, and genotypic information to represent genetic evaluations in purebred and in commercial cattle herds. The four scenarios represented genetic evaluations using: 1) all available phenotypic, pedigree, and genotypic data (genomic-polygenic model 1; 2) all available phenotypic data, pedigree from non-genotyped animals only, and all available genotypic data (genomic-polygenic model 2); and 2) all available phenotypic and genotypic data, but no pedigree information (genomic-polygenic model 3); and 4) all available phenotypic and pedigree data and no genotypic information (polygenic model). Scenarios 1 and 4 represent purebred cattle breeders and commercial producers that keep all feasible records and scenarios 2 and 3 represent two cases of commercial operations with incomplete information. These four scenarios were constructed using information from the multibreed Angus-Brahman population of the University of Florida. The diallel-mating design of this population has created a continuum of breed compositions ranging from 100% Angus to

100% Brahman over its 26 years of existence (1987 to 2013). Most beef cattle in the southern region of the US, and Florida in particular, span the range from completely Brahman to completely *Bos taurus*, where Angus is the most represented *Bos taurus* breed. This makes the multibreed Angus-Brahman population of the University of Florida well-suited to study these four scenarios under the subtropical conditions of the US southern region. Thus, the objectives of this research were: 1) to compare variance components and genetic parameters (heritabilities, genetic correlations) for birth weight direct and maternal, weaning weight direct and maternal, and postweaning gain direct computed under scenarios 1, 2, 3, and 4; 2) to compare rankings of animals for birth weight direct and maternal, weaning weight direct and maternal, and postweaning gain direct across scenarios 1, 2, 3, and 4; and 3) to evaluate EBV trends for each trait computed in scenarios 1, 2, 3, and 4 as percentage Brahman increased from 0% to 100% in a multibreed Angus-Brahman population under subtropical environmental conditions.

2. Materials and methods

2.1. Animals and traits

The University of Florida Institutional Animal Care and Use Committee approved the research protocol for animals involved in this project (IACUC protocol number 201003744). Animals used in this research belonged to the long-term multibreed Angus-Brahman (MAB) project of the University of Florida, Gainesville. The mating plan 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 mating breed groups were defined in terms of ranges of Angus (A) and Brahman (B) percentages as follows: 1) 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. The dataset included information on preweaning and postweaning growth from calves born between 1987 and 2013. There were 5,264 calves with birth weights (BW, kg; 2,689 bulls and 2,575 heifers), 5,262 calves with weaning weights adjusted to 205 d of age (WW, kg; 614 bulls, 2,573 heifers, and 2,075 steers), and 3,846 calves with postweaning gains from 205 d to 365 d of age (PWG, kg; 209 bulls, 1,784 heifers, and 1,853 steers). These calves were the progeny of 293 sires (54 BG1, 37 BG2, 60 BG3, 35 BG4, 38 BG5, and 69 BG6) and 1,725 dams (291 BG1, 249 BG2, 254 BG3, 349 BG4, 200 BG5, and 282 BG6). Number of calves per breed group, means, and SD for BW, WW, and PWG are presented in Table 1. Except for two, all calves with BW had WW records, and 73% of calves with WW information had PWG data. Culling and sale of excess calf inventory at weaning were responsible for the lower number of animals with postweaning gain phenotypes.

2.2. Feeding and management

Calves stayed at the Pine Acres Research Station (1987 to 1994) and at the Beef Research Unit (1995 to 2013) of the University of Florida from birth (December to March) to weaning (August, September). Preweaning, cows and calves were kept in bahiagrass pastures (*Paspalum notatum*) with access to a complete mineral supplement (UF University Special Hi-Cu Mineral, University of Florida, Animal Science Department, Gainesville, Florida). They 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 kept at their birth location (Pine Acres Research Station and at the Beef Research Unit), except from 2006 to 2010 when they were kept at the University

of Florida Feed Efficiency Facility (UFFEF). When calves remained at their respective birth locations (1987 to 2005 and 2011 to 2013), they were kept in 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 mineral supplement. During the years (2006 to 2010) that calves were taken to the University of Florida Feed Efficiency Facility (UFFEF), they were randomly allocated to pens within sire group (BG1 to BG6) by sex category (bull, heifer, and steer). Calves at UFFEF were fed a diet 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).

2.3. Tissue sampling, genotyping, and imputation

Tissue samples (blood, semen) from 1,232 animals from the MAB herd were collected at the Beef Research Unit of the University of Florida from 2006 to 2010. A total of 161 parents (20 sires and 141 dams), and 1,071 progeny (109 bulls, 613 heifers, and 349 steers) were represented in these samples. Tissue samples were processed and stored at -80 °C at New Mexico State University. Samples were centrifuged for 30 min at 1,875 g at 4°C, followed by retrieval of the white blood cell supernatant, and addition of sterile phosphate-buffered saline up to a volume of 1.0 mL (Beauchemin et al., 2006). The processed samples were forwarded to GeneSeek (Gene Seek, Inc., Lincoln, NE, USA) in 2010 for genotyping with the Illumina3k genotyping beadchip (Illumina, 2011a).

Multibreed animals genotyped with the Illumina3k chip were imputed to Illumina50k (Illumina, 2011b) with software findhap2 (VanRaden, 2011) using a reference

156 population (RP) of 828 Brangus heifers previously genotyped with version 1 of the
157 Illumina50k chip (Fortes et al., 2012; Peters et al., 2012). Animal relationships within the
158 RP and MAB subpopulations were available. However, pedigree data linking RP heifers
159 with MAB animals were unavailable, thus animals from RP and MAB were assumed to be
160 unrelated. The resulting RP-MAB pedigree file for findhap2 contained 8,720 animals
161 (2,046 from RP and 6,674 from MAB). Because the locations of SNP markers in the
162 Illumina3k (n = 2,900) corresponded to version 2 of the Illumina50k chip, only those SNP
163 markers found both in versions 1 and 2 of the Illumina50k chip and their locations in
164 version 2 (n = 50,276) were used for imputation. The number of Illumina3k SNP markers
165 present among the 50,276 Illumina50k SNP markers was 2,816. Input files for findhap2
166 were: 1) genotype file with gene content data (0, 1, 2 = number of "second" alleles, 5 =
167 unknown) for 1,300 MAB animals genotyped for 2,816 Illumina3k SNP markers, and 828
168 RP heifers genotyped for 50,276 Illumina50k SNP markers; 2) chromosome data file (SNP
169 name, chromosome number, SNP number within and across chromosomes, SNP location in
170 base pairs, SNP number for Illumina50k and 3k chips); and 3) combined RP-MAB pedigree
171 file.

172 The output file "haplotypes" from Findhap2 was subsequently utilized as input file
173 for an in-house FORTRAN program used to construct phenotypic, genotypic, and pedigree
174 files for the computation of variance components and genetic parameters with the
175 BLUPF90 family of programs (Misztal, 1999; Misztal et al., 2002). The SNP with minor
176 allele frequencies lower than 0.04 were discarded (n = 3,508). Consequently, the edited
177 genotype file contained 1,232 MAB animals, each with 46,768 SNP markers (2,639 actual
178 Illumina3k SNP and 44,129 imputed Illumina50k SNP).
179

180 *2.4. Variance Components and Variance Ratios*

181 Variance components, heritabilities, and genetic, environmental and phenotypic
182 correlations for BW direct, BW maternal, WW direct, WW maternal, and PWG direct were
183 computed using three multiple-trait genomic-polygenic models (VanRaden, 2008; Aguilar
184 et al., 2010) in scenarios 1, 2, and 3, and a multiple-trait polygenic model in scenario 4.
185 The multiple-trait genomic-polygenic model for scenario 1 was a single-step model
186 (Aguilar et al., 2010) that utilized all available phenotypic and genotypic data and
187 accounted for pedigree relationships among all animals (i.e., genotyped and non-
188 genotyped). The multiple-trait genomic-polygenic model for scenario 2 was a single-step
189 model that used all available phenotypic and genotypic information and pedigree
190 relationships only for animals without genotypic information. The multiple-trait genomic-
191 polygenic model for scenario 3 was a single-step model that utilized all phenotypic and
192 genotypic information and ignored all pedigree relationships among animals in the MAB
193 population. Genomic-polygenic model 1 corresponded to the original idea of combining
194 pedigree and molecular marker information (Legarra et al., 2009; Aguilar et al., 2010).
195 Genomic-polygenic model 2 was chosen to assess the ability of genomic relationships to
196 account for additive relationships among genotyped animals. Pedigree relationships
197 between non-genotyped and genotyped animals were set to zero to avoid computational
198 problems. Direct substitution of a submatrix of genomic relationships for its corresponding
199 submatrix of pedigree relationships was found to produce an indefinite genomic-polygenic
200 relationship matrix (i.e., a matrix with positive and negative eigenvalues; Legarra et al.,
201 2009). Genomic-polygenic model 3 represented a “worst case scenario” where a fraction of
202 the population was genotyped, and animals have phenotypes but no pedigree information.
203 This scenario represents the case of a commercial cattle producer that genotyped a fraction

204 of the herd, collects phenotypic records from individual animals, but kept no pedigree
205 records. The polygenic model was considered to be the comparison base. Thus, estimates
206 of variance components and genetic parameters from genomic-polygenic models used in
207 scenarios 1, 2, and 3 were compared to those from the polygenic model in scenario 4.
208 The fixed effects for the three genomic-polygenic models and the polygenic model
209 were: 1) contemporary group (location-year for BW and WW direct and maternal; location-
210 year-pen subclass for PWG); 2) age of dam (all traits); 3) sex of calf (males and females for
211 BW, and bulls, heifers, and steers for WW and PWG; 4) direct heterosis for all traits as a
212 function of calf heterozygosity (i.e., the probability of having Angus and Brahman alleles in
213 1 locus); and 5) maternal heterosis for BW and WW as a function of dam heterozygosity.
214 Random effects were direct additive genetic for BW, WW, and PWG, maternal additive
215 genetic for BW and WW, and residual (assumed to contain only environmental effects) for
216 BW, WW, and PWG. The mean for random animal, dam, and residual effects was assumed
217 to be zero in all models. The variance-covariance matrices among direct and maternal
218 additive genetic effects for the single-step models used in scenarios 1, 2, and 3 were equal
219 to:
220 1) $H_1 \otimes V_{dm}$ for single-step model 1 (scenario 1), where matrix H_1 was the complete
221 genomic-polygenic relationship matrix, i.e.,
222 $\begin{bmatrix} A_{11} + A_{12}A_{22}^{-1}(G_{22} - A_{22})A_{22}^{-1}G_{21} & A_{12}A_{22}^{-1}G_{22} \\ G_{22}A_{22}^{-1}A_{21} & G_{22} \end{bmatrix}$, A_{ij} is submatrix ij of the
223 additive relationship matrix, subscript 1 corresponds to non-genotyped animals, and
224 subscript 2 to genotyped animals, A_{22}^{-1} is the inverse of the additive relationship submatrix for
225 genotyped animals, $G_{22} = ZZ'/2\sum p_j\,(1 - p_j)$ is the matrix of genomic relationships for
226 genotyped animals (VanRaden, 2008; Aguilar et al., 2010), where p_j is the frequency of the

227 "second"allele in locus j, and $z_{ij} = (0 - 2p_j)$ if the genotype for locus j is 11, $z_{ij} = (1 -$

228 $2p_j)$ if the genotype for locus j is 12 or 21, and $z_{ij} = (2 - 2p_j)$ if the genotype for locus j is

229 22. Matrix V_{dm} was a 5 × 5 matrix of variances and covariances among direct and maternal

230 additive genetic effects for BW, WW, and PWG, i.e.,

231 $V_{dm} = \begin{bmatrix} \sigma_{d1d1} & \sigma_{d1d2} & \sigma_{d1d3} & \sigma_{d1m1} & \sigma_{d1m2} \\ \sigma_{d2d1} & \sigma_{d2d2} & \sigma_{d2d3} & \sigma_{d2m1} & \sigma_{d2m2} \\ \sigma_{d2d1} & \sigma_{d3d2} & \sigma_{d3d3} & \sigma_{d3m1} & \sigma_{d3m2} \\ \sigma_{m1d1} & \sigma_{m1d2} & \sigma_{m1d3} & \sigma_{m1m1} & \sigma_{m1m2} \\ \sigma_{m2d1} & \sigma_{m2d2} & \sigma_{m2d3} & \sigma_{m2m1} & \sigma_{m2m2} \end{bmatrix}$, where subscripts d = direct, m = maternal, 1 =

232 BW, 2 = WW, and 3 = PWG. Lastly, "⊗" was the Kronecker product.

233 2) $H_2 \otimes V_{dm}$ for single-step model 2 (scenario 2), where matrix H_2 considered

234 pedigree relationships only among non-genotyped animals and only genomic relationships

235 among genotyped animals, i.e., it assumed $A_{22} = 0$ and off-diagonal submatrices of H_2

236 equal to zero, i.e., $H_2 = \begin{bmatrix} A_{11} & 0 \\ 0 & G_{22} \end{bmatrix}$, where A_{11}, G_{22}, V_{dm}, and "⊗" were as defined above.

237 3) $H_3 \otimes V_{dm}$ for single-step model 3 (scenario 3), where matrix H_3 considered only

238 genomic relationships among animals in the population (thus A_{22} and off-diagonal

239 submatrices of H_3 were equal to zero) and assumed non-genotyped animals to be unrelated,

240 i.e., $H_3 = \begin{bmatrix} I_{11} & 0 \\ 0 & G_{22} \end{bmatrix}$, where I_{11} = identity matrix of dimension equal to the number of non-

241 genotyped animals, and G_{22} , V_{dm}, and "⊗" were as defined previously.

242 The variance-covariance matrix among direct and maternal additive genetic effects

243 for the polygenic model (scenario 4) was equal to $A \otimes V_{dm}$, where A was the additive

244 relationship matrix among all animals in the population, and "⊗" and V_{dm} were as defined

245 for the single-step models. The residual variance-covariance matrix for all models was the

246 Kronecker product of a 3 × 3 matrix of covariances among residual effects for BW, WW,
247 and PWG times an identity matrix.

248 Variance components were estimated using restricted maximum likelihood (REML)
249 procedures (Corbeil and Searle, 1971; Patterson and Thompson, 1971; Harville, 1977) with
250 an average information algorithm (Gilmour et al., 1995). Computations were carried out
251 with the BLUPF90 family of programs (Misztal, 1999; Misztal et al., 2002). Program
252 RENUMF90 was utilized to renumber animals sequentially and construct input files for
253 subsequent BLUPF90 programs. Program AIREMLF90 (Tsuruta, 2014) was utilized to
254 compute REML estimates of variance components, heritabilities, correlations (genetic,
255 environmental, phenotypic) and their standard errors (convergence criterion = 10^{-12}).
256 Standard errors for all direct additive genetic, maternal additive genetic and environmental
257 variance and covariance components were computed as square roots of diagonal elements
258 of the inverse of the average information matrix.

259 Phenotypic covariances were computed as linear combinations of additive direct and
260 maternal variances and covariances. For example, the phenotypic covariance between traits
261 i and j, $\sigma_{pipj} = \sigma_{didj} + \frac{1}{2}\sigma_{dimj} + \frac{1}{2}\sigma_{djmi} + \sigma_{mimj} + \sigma_{eiej}$, where subscripts p =
262 phenotypic, d = direct, m = maternal, and e = environmental. Heritabilities for all traits and
263 effects as well as correlations between pairs of traits and effects were computed using the
264 usual expressions. Standard deviations for these functions of variance components were
265 obtained using the repeated sampling approach suggested by Meyer and Houle (2013).
266 First, 5,000 samples of direct, maternal, and environmental variances and covariance
267 components were obtained from their asymptotic multivariate distribution. Second,
268 functions of variance components (i.e., phenotypic covariances, heritabilities, and

269 correlations) were computed for each sample. Third, means and SD were computed for
270 each function using values from all samples. These computations were performed with one
271 additional round of iteration of AIREMLF90 after convergence. Code used to compute
272 sample means and SD for phenotypic variances and covariances, direct and maternal
273 heritabilities and genetic, environmental and phenotypic correlations using program
274 AIREMLF90 is shown in Appendix 1.
275
276 *2.5. Genomic-Polygenic and Polygenic Predictions*
277 Estimated breeding values (EBV) were computed for all traits (BW and WW direct
278 and maternal, and PWG direct) for 5,190 animals (genotyped = 1,232, non-genotyped =
279 3,958) and genotyped animals using genomic-polygenic model 1 (GP1_EBV), model 2
280 (GP2_EBV), model 3 (GP3_EBV), and the polygenic model (PEBV). The EBV were
281 computed during the additional iteration of AIREMLF90 after convergence (convergence
282 criterion = 10^{-12}) using the variances and covariances estimated with AIREMLF90.
283 Spearman rank correlations were used to compare rankings of animal EBV for each trait in
284 the top 5%, 10%, 25%, and for all evaluated animals. Lastly, regressions of EBV on
285 Brahman fraction of animal were computed for each trait to assess EBV trends as
286 percentage Brahman increased from 0% to 100% Brahman.
287
288 **3. Results and discussion**
289 Table 1 shows descriptive statistics (numbers of animals, means, and SD) for BW,
290 WW, and PWG per breed group and for the complete dataset. Calves with Brahman
291 fractions over 80% had higher BW and lower WW and PWG than calves with Brahman
292 fractions 20% or lower. Crossbred calves with Brahman fractions between 40% and 60%

293 had the highest WW, whereas calves with Brahman fractions between 37.5% and 60% had
294 the highest PWG.
295
296 *3.1. Variance components and variance ratios*
297 Table 2 presents REML estimates and SE of additive genetic variances for and
298 covariance components between direct and maternal BW, direct and maternal WW, and
299 direct PWG genetic effects obtained using genomic-polygenic models 1, 2, and 3, and the
300 polygenic model. Estimates of additive genetic variances and covariances from genomic-
301 polygenic model 1 were, on the average, slightly larger than those from the polygenic
302 model (mean difference = 3.25 kg^2), thus the inclusion of genotypic information had little
303 effect on estimates of variance components for growth traits in this multibreed population.
304 Exclusion of pedigree information from genotyped animals (genomic-polygenic model 2)
305 and from all animals (genomic-polygenic model 3) yielded lower estimates of variance and
306 covariance components than estimates from the polygenic model (mean difference = -9.15
307 kg^2 for model 2 and -27.27 kg^2 for model 3). Thus, compared to estimates from the
308 polygenic model, partially (genomic-polygenic model 2) or completely ignoring (genomic-
309 polygenic models 3) additive relationships among animals underestimated the additive
310 genetic variation for growth traits in this population.
311 The opposite trend occurred for environmental variances and covariances across
312 models (Table 3). Estimates of environmental variances and covariances for BW, WW,
313 and PWG were, on the average, slightly lower for genomic-polygenic model 1 (mean
314 difference = -2.32 kg^2), and higher for genomic-polygenic models 2 (mean difference =
315 12.56 kg^2) and 3 (mean difference = 46.33 kg^2) than estimates from the polygenic model.
316 The higher average additive genetic variances and covariances and lower environmental

317 variances from genomic-polygenic model 1 may be an indication that the additional
318 genotypic information included in genomic-polygenic model 1 accounted for additive
319 genetic variability more fully than the polygenic model. Perhaps the portion of the additive
320 genetic variation unaccounted for by ignoring additive relationships in part (genomic-
321 polygenic model 2) or completely (genomic-polygenic model 3) was captured by the
322 residual component resulting in overestimation of environmental variances and
323 covariances.

324 Estimates of phenotypic variances and covariances followed the same pattern across
325 models (Table 4) as additive genetic variance components (Table 2). Estimates of
326 phenotypic variances and covariances for BW, WW, and GW from genomic-polygenic
327 model 1 were slightly higher (mean difference = 4.25 kg^2), whereas those from genomic-
328 polygenic models 2 (mean difference = -11.92 kg^2) and 3 (mean difference = -19.92 kg^2)
329 were lower than those from the polygenic model. Thus, ignoring pedigree relationships
330 among genotyped animals (genomic-polygenic model 2) or all pedigree relationships
331 (genomic-polygenic model 3) resulted in underestimation of phenotypic variances and
332 covariances relative to those of the polygenic model.

333 The pattern for estimates of variance ratios across models mimicked the one for
334 estimates of additive variance components. Estimates of heritabilities and genetic
335 correlations (Table 5) from genomic-polygenic model 1 and the polygenic model were very
336 similar (mean difference = 0.01), while mostly lower estimates were obtained with
337 genomic-polygenic models 2 (mean difference = -0.04) and 3 (mean difference = -0.06).
338 Environmental correlations (Table 6) from genomic-polygenic model 1 were nearly
339 identical to those of the polygenic model (mean difference = -0.003), whereas those from
340 genomic-polygenic models 2 (mean difference = 0.05) and 3 (mean difference = 0.18)

341 tended to be somewhat higher than estimates from the polygenic model. Nearly identical
342 phenotypic correlations (Table 7) were obtained with genomic-polygenic model 1 and the
343 polygenic model (mean difference = 0.003), but slightly lower estimates were computed
344 with genomic-polygenic models 2 (mean difference = -0.013) and 3 (mean difference = -
345 0.020) than with the polygenic model.

346 All available phenotypic, pedigree, and genotypic data from the Angus-Brahman
347 multibreed herd were used to estimate variance components and genetic parameters in this
348 research. Estimates from the polygenic model represented the best estimates for this herd
349 given the fixed and random effects included in this model and the available phenotype and
350 pedigree information. Similarly, estimates from the genomic-polygenic model 1
351 represented the best estimates considering the fixed and random effects included in this
352 model and the available phenotypes, pedigree, and genotype information. The remaining
353 two genomic-polygenic models represented approximations to genomic-polygenic model 1.
354 Genomic-polygenic model 2 evaluated the effect of ignoring pedigree data from genotyped
355 animals, and model 3 assessed the effect of ignoring all relationships on variance
356 components and genetic parameters. Ignoring pedigree relationships (genomic-polygenic
357 model 2) among genotyped animals had a small impact on variance components and
358 genetic parameters. The impact of ignoring all pedigree relationships (genomic-polygenic
359 model 3) was more severe resulting in underestimation of most variance components and
360 genetic parameters. The similarity between estimates of variance components and genetic
361 parameters from the polygenic model and genomic-polygenic model 1 indicated that
362 genotypes provided little additional information on additive genetic (co)variability beyond
363 that supplied by pedigree data. In addition, the similarity between variance components
364 and genetic parameters from the polygenic model and genomic-polygenic model 2

365 indicated that genotypic and pedigree information from genotyped animals accounted for
366 additive genetic (co)variability for growth traits to a similar extent.
367 Estimates of variance components and genetic parameters for growth traits here
368 were within the range of values obtained for *Bos taurus* (Garrick et al., 1989; Meyer, 1992,
369 1994; Van Vleck et al., 1996; Dodenhoff et al., 1998; Elzo and Wakeman, 1998; Elzo et al.
370 1998, 2001; Montaldo and Kinghorn, 2003; Szabo et al., 2012), *Bos indicus* (Eler et al.,
371 1995; Diop et al., 1999; Elzo and Wakeman, 1998; Elzo et al. 1998, 2001; Montaldo and
372 Kinghorn, 2003), and *Bos taurus* × *Bos indicus* cattle (Meyer, 1992; Elzo and Wakeman,
373 1998; Elzo et al. 1998, 2001; Demeke et al., 2003; Vergara et al., 2009).
374
375 *3.2. Ranking of animals evaluated with genomic-polygenic and polygenic models*
376 Rank correlations between EBV from the three genomic-polygenic and the
377 polygenic models increased as the fraction of the population included in the computations
378 increased from 5% to 10% to 25% to 100% (Table 8).
379 The highest rank correlations were between EBV from genomic-polygenic model 1
380 and the polygenic model (top 5% mean = 0.89; complete population mean = 0.98). The
381 second highest rank correlations were between EBV from genomic-polygenic models 1 and
382 2 (top 5% mean = 0.52; complete population mean = 0.87), and between genomic-
383 polygenic model 2 and the polygenic model (top 5% mean = 0.53; complete population
384 mean = 0.87).
385 The lowest rank correlations were between EBV from genomic-polygenic models 1,
386 2, and the polygenic model and EBV from the genomic-polygenic model 3. The rank
387 correlation for the top 5% of the population ranged from -0.04 (models 3 and polygenic for
388 BW maternal) to 0.49 (models 1 and 3 for WW direct), whereas the range for the complete

389 population was from -0.12 (model 3 and polygenic for BW maternal) to 0.85 (models 1 and
390 3 as well as models 3 and polygenic for WW direct).

391 Rank correlations also tended to be higher for direct BW and WW than for maternal
392 BW and WW across models. The largest mean rank correlations for preweaning traits (i.e.,
393 BW and WW) were between genomic-polygenic model 1 and the polygenic model (mean
394 direct = 0.99; mean maternal = 0.98), followed by those between model 1 and model 2
395 (mean direct = 0.94; mean maternal = 0.84) and between model 2 and polygenic (mean
396 direct = 0.94; mean maternal = 0.83). Rank correlations involving genomic-polygenic
397 model 3 yielded the lowest values (mean direct from 0.82 to 0.87; mean maternal from -
398 0.02 to 0.09).

399 Rank correlations clearly showed a high degree of agreement between animal
400 rankings from the polygenic model and genomic-polygenic model 1. This indicated that
401 these two models not only accounted for direct and maternal additive genetic variation for
402 growth traits similarly, but that they also yielded predicted values that ranked animals
403 similarly. The genomic-polygenic model 2 was a close second, and the genomic-polygenic
404 model 3 showed a lower level of agreement for additive direct genetic effects, but had a
405 dismal performance for maternal effects likely due to assuming calves and dams to be
406 unrelated. These rank correlations indicated that genomic-polygenic evaluation when no
407 pedigree information was available (scenario 3) would yield EBV of limited use to
408 accurately choose animals for direct BW, WW, and PWG and of little or no use to select
409 animals for maternal BW and WW. Thus, commercial producers that genotyped a fraction
410 of their animals, kept individual phenotypic records but have no pedigree data would
411 receive limited or no benefit from their genotyping investment.

412 Considering the cost of genotyping and the short time required for collecting
413 phenotypes for growth traits, the close agreement between the polygenic model and
414 genomic-polygenic model 1 would favor the use of the polygenic model for growth traits.
415 However, genotypes here were a mixture of actual SNP from Illumina3k and imputed
416 genotypes from Illumina50k. Imputation accuracy from the Illumina3k to the Illumina50k
417 has been found to be between 81% and 93% depending on the imputation procedure
418 (Dassonneville et al., 2011; Huang et al., 2012; Mulder et al., 2012). Thus, if animals had
419 been genotyped with the Illumina50k, perhaps larger differences between variance
420 components, genetic parameters, and EBV from the genomic-polygenic model 1 and the
421 polygenic model could have been obtained. However, the issue of genotyping costs would
422 have remained. High genotyping cost is still likely to be the main constraint to widespread
423 use of genotyping for genomic-polygenic evaluation by purebred and commercial cattle
424 producers.
425
426 *3.3. Trends of genomic-polygenic and polygenic EBV from 100% Angus to 100% Brahman*
427 Linear regression coefficients of genomic-polygenic EBV on Brahman fraction of
428 animal were positive for BW and WW direct, and negative for PWG direct and BW and
429 WW maternal for all models, except for genomic-polygenic model 3 (Table 9). Regression
430 coefficients from genomic-polygenic model 1 and the polygenic model were nearly
431 identical for all traits. Regression coefficients from genomic-polygenic model 3 were
432 substantially lower than those from the other models for direct BW and WW, and near zero
433 for direct PWG and maternal BW and WW. Thus, completely ignoring pedigree
434 relationships negatively affected the predictive ability of genomic-polygenic model 3.

435 Values of regression coefficients indicated that Brahman animals tended to have
436 higher EBV for BW direct and WW direct, and lower EBV for PWG direct, BW maternal,
437 and WW maternal. However, although significant ($P < 0.0001$), all regressions were low
438 with all models indicating that animals with high, medium, and low EBV for these growth
439 traits existed in this multibreed population. As examples, Figure 1 show EBV for WW
440 direct and Figure 2 show EBV for WW maternal from genomic-polygenic model 1.
441 It is well-known that beef cattle need to contain a percentage of Brahman genes to
442 survive and produce under the hot and humid subtropical conditions of the US southern
443 region. Results here showed that Brahman and crossbred Angus-Brahman cattle of a
444 variety of Brahman percentages (including Brangus) could have comparable or better EBV
445 for growth traits than less well-adapted purebred Angus cattle under subtropical Florida
446 conditions. Thus, beef cattle producers in Florida and the Southern region of the US could
447 take advantage of crossbred cattle with a wide range of Brahman fractions (i.e., not limited
448 to 5/8 Angus 3/8 Brahman) for their commercial operations.
449

450 **4. Conclusions**

451 Similar estimates of variance components and genetic parameters for birth weight
452 direct, weaning weight direct, postweaning gain direct, birth weight maternal, and weaning
453 weight maternal were obtained using genomic-polygenic model 1 and a polygenic model.
454 Similarly, high rank correlations existed between EBV from these two models for direct
455 and maternal growth traits. Between the two approximate genomic-polygenic models,
456 model 2 was the one closest to genomic-polygenic model 1. Genomic-polygenic model 3
457 performed poorly for maternal traits. These results indicated that the polygenic model and
458 genomic-polygenic model 1 should be preferred. Thus, to obtain the benefit of genotyping

459 a fraction of the herd, commercial producers would need to keep complete pedigree records
460 as well as individual animal phenotypes. However, high genotyping costs still make the
461 polygenic model preferable for commercial beef cattle operations. Brahman animals
462 tended to have higher EBV for BW direct and WW direct, and lower EBV for PWG direct,
463 BW maternal, and WW maternal. However, low regression coefficients of EBV on
464 Brahman fraction were evidence that high, medium, and low EBV animals from all breed
465 compositions existed in this multibreed population.
466

467 **Conflict of interest**

468 No conflicts of interest influenced this research.
469

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478

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

	Trait[a]								
	BW, kg			WW, kg			PWG, kg		
Breed group[b]	N	Mean	SD	N	Mean	SD	N	Mean	SD
BG1	764	31.6	5.6	764	210.5	32.5	576	75.2	62.7
BG2	792	31.9	5.5	792	221.1	30.6	625	83.1	61.2
BG3	730	33.7	6.1	728	217.2	33.3	531	83.1	62.5
BG4	1,338	33.8	6.4	1,338	223.8	29.1	944	79.9	58.9
BG5	722	34.6	6.4	722	221.3	31.5	574	71.4	54.2
BG6	918	33.7	6.1	918	207.6	30.5	596	72.3	53.0
Total	5,264	33.3	6.1	5,262	217.4	31.6	3,846	77.7	59.0

599 [a]BW = Birth weight; WW = Weaning weight adjusted to 205 d of age; PWG = Postweaning gain
600 from 205 d to 365 d of age.
601 [b] Breed group: BG1 = 100% A to (80% A 20% B); 2) BG2 = (60% A 40% B) to (79% A 21% B);
602 3) BG3 = Brangus = (62.5% A 37.5% B); 4) BG4 = (40% A 60% B) to (59% A 41% B); 5) BG5 =
603 (20% A 80% B) to (39% A 61%B); and 6) BG6 = (19% A 81% B) to 100% B; A = Angus, B =
604 Brahman.
605

606 Table 2. REML estimates of direct and maternal additive genetic variance and covariance
607 components for growth traits using genomic-polygenic and polygenic models

	Additive genetic covariances, kg^2							
Trait pair[a]	GPM1	SE	GPM2	SE	GPM3	SE	PM	SE
BWD, BWD	17.90	1.92	20.93	2.20	10.42	0.14	19.56	2.03
BWD,WWD	42.25	6.36	48.06	6.94	18.50	0.45	45.60	5.72
BWD, PWGD	2.47	7.81	-3.23	9.47	-9.85	0.43	0.75	7.86
BWD, BWM	-4.49	1.08	-6.19	1.30	-1.40	0.11	-5.64	1.14
BWD, WWM	-5.64	4.50	-11.07	5.25	5.79	0.29	-8.83	4.38
WWD, WWD	266.10	33.53	246.83	33.52	173.35	2.39	259.32	20.37
WWD, PWGD	139.91	35.35	49.01	39.33	49.76	1.78	132.31	33.89
WWD, BWM	0.63	4.10	-2.22	4.54	15.43	0.48	-1.65	4.00
WWD, WWM	11.02	20.08	-21.18	21.97	-2.00	1.18	11.40	17.22
PWGD, PWGD	274.86	52.77	243.31	55.04	178.72	2.46	266.95	49.58
PWGD, BWM	19.27	5.87	9.06	8.13	-2.39	0.47	19.09	5.65
PWGD, WWM	56.11	28.36	75.07	36.02	9.71	1.20	43.04	26.61
BWM, BWM	8.21	0.92	8.45	1.07	12.72	0.18	8.63	0.93
BWM, WWM	12.41	3.17	12.88	3.61	4.97	0.32	13.47	3.10
WWM, WWM	164.92	19.34	150.16	21.35	84.42	1.16	153.17	17.83

608
609 [a] BWD = birth weight direct, WWD = weaning weight direct, PWGD = postweaning gain
610 direct, BWM = birth weight maternal, WWM = weaning weight maternal; GPM1, GPM2,
611 GPM3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model.

612 Table 3. REML estimates of environmental variance and covariance components for
613 growth traits using genomic-polygenic and polygenic models

	Environmental variances and covariances, kg^2							
Trait pair[a]	GPM1	SE	GPM2	SE	GPM3	SE	PM	SE
BWE, BWE	12.00	1.07	10.308	1.26	10.32	0.20	11.21	1.11
BWE,WWE	19.19	3.61	15.334	4.09	31.72	1.08	17.63	3.03
BWE, PWGE	8.50	5.43	15.314	6.54	26.62	5.68	9.56	5.22
WWE, WWE	300.95	19.88	320.53	21.41	411.40	5.70	307.84	6.59
WWE, PWGE	-38.67	25.05	12.291	28.76	33.10	7.00	-33.02	24.08
PWGE, PWGE	542.96	42.87	560.41	50.18	623.62	12.15	545.61	40.63

614
615 [a] BWE = birth weight environmental, WWE = weaning weight environmental, PWGE =
616 postweaning gain environmental; GPM1, GPM2, GPM3 = genomic-polygenic models 1, 2,
617 and 3; PM = polygenic model.
618

Table 4. REML estimates of phenotypic variance and covariance components for growth traits using genomic-polygenic and polygenic models

	Phenotypic variances and covariances, kg^2							
Trait pair[a]	GPM1	SE	GPM2	SE	GPM3	SE	PM	SE
BWP, BWP	33.62	0.86	33.50	0.82	32.06	0.30	33.75	0.87
BWP,WWP	71.34	3.21	69.63	2.84	65.81	1.26	71.46	3.12
BWP, PWGP	20.61	4.90	16.62	4.74	15.57	5.77	19.86	4.86
WWP, WWP	742.99	20.28	696.34	16.47	667.17	6.37	731.73	19.37
WWP, PWGP	129.30	24.31	98.83	22.16	87.72	7.23	120.81	23.79
PWGP, PWGP	817.82	35.31	803.72	32.94	802.34	12.32	812.56	34.34

[a] BWP = birth weight phenotypic, WWP = weaning weight phenotypic, PWGP = postweaning gain phenotypic; GPM1, GPM2, GPM3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.

Table 5. REML estimates of direct and maternal heritabilities and additive genetic correlations for growth traits using genomic-polygenic and polygenic models

	Heritabilities and Additive Genetic Correlations							
Trait pair[a]	GPM1	SD	GPM2	SD	GPM3	SD	PM	SD
BWD, BWD	0.53	0.05	0.62	0.06	0.32	0.004	0.58	0.05
BWD,WWD	0.61	0.06	0.67	0.06	0.44	0.008	0.64	0.05
BWD, PWGD	0.04	0.11	-0.05	0.14	-0.23	0.009	0.01	0.11
BWD, BWM	-0.37	0.07	-0.47	0.06	-0.12	0.01	-0.43	0.06
BWD, WWM	-0.10	0.08	-0.20	0.09	0.20	0.009	-0.16	0.08
WWD, WWD	0.36	0.04	0.35	0.04	0.26	0.004	0.35	0.02
WWD, PWGD	0.52	0.12	0.20	0.16	0.28	0.009	0.50	0.11
WWD, BWM	0.01	0.09	-0.05	0.10	0.33	0.009	-0.03	0.09
WWD, WWM	0.05	0.10	-0.11	0.11	-0.02	0.01	0.06	0.09
PWGD, PWGD	0.34	0.06	0.30	0.06	0.22	0.004	0.33	0.05
PWGD, BWM	0.41	0.13	0.20	0.19	-0.05	0.01	0.40	0.12
PWGD, WWM	0.26	0.14	0.39	0.20	0.08	0.01	0.21	0.13
BWM, BWM	0.24	0.03	0.25	0.03	0.40	0.005	0.26	0.03
BWM, WWM	0.34	0.07	0.36	0.08	0.15	0.01	0.37	0.07
WWM, WWM	0.22	0.02	0.22	0.03	0.13	0.002	0.21	0.02

[a] BWD = birth weight direct, WWD = weaning weight direct, PWGD = postweaning gain direct, BWM = birth weight maternal, WWM = weaning weight maternal; GPM1, GPM2, GPM3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.

633 Table 6. REML estimates of environmental correlations for growth traits using genomic-
634 polygenic and polygenic models

	Environmental correlations							
Trait pair[a]	GPM1	SD	GPM2	SD	GPM3	SD	PM	SD
BWE,WWE	0.32	0.05	0.27	0.06	0.49	0.01	0.30	0.04
BWE, PWGE	0.11	0.07	0.20	0.09	0.33	0.07	0.12	0.07
WWE, PWGE	-0.10	0.06	0.03	0.09	0.07	0.01	-0.08	0.06

635
636 [a] BWE = birth weight environmental, WWE = weaning weight environmental, PWGE =
637 postweaning gain environmental; GPM1, GPM2, GPM3 = genomic-polygenic models 1, 2,
638 and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.
639

640 Table 7. REML estimates of phenotypic correlations for growth traits using genomic-
641 polygenic and polygenic models

	Phenotypic correlations							
Trait pair[a]	GPM1	SD	GPM2	SD	GPM3	SD	PM	SD
BWP,WWP	0.45	0.01	0.46	0.01	0.45	0.007	0.45	0.01
BWP, PWGP	0.12	0.03	0.10	0.03	0.10	0.04	0.12	0.03
WWP, PWGP	0.17	0.05	0.13	0.03	0.12	0.01	0.16	0.03

642
643 [a] BWP = birth weight phenotypic, WWP = weaning weight phenotypic, PWGP =
644 postweaning gain phenotypic; GPM1, GPM2, GPM3 = genomic-polygenic models 1, 2,
645 and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.
646

647 Table 8. Rank correlations between animal EBV from polygenic and genomic-polygenic
648 models for the top 5%, 10%, 25%, and all evaluated animals

		Rank correlations[b]					
Trait[a]	Top	GPM1, GPM2	GPM1, GPM3	GPM1, PM	GPM2, GPM3	GPM2, PM	GPM3, PM
BWD	5%	0.61	0.40	0.90	0.73	0.66	0.47
	10%	0.69	0.54	0.93	0.75	0.74	0.59
	25%	0.78	0.58	0.96	0.64	0.82	0.59
	100%	0.93	0.78	0.99	0.87	0.94	0.80
WWD	5%	0.72	0.49	0.95	0.47	0.76	0.51
	10%	0.72	0.48	0.96	0.54	0.74	0.49
	25%	0.77	0.57	0.96	0.64	0.79	0.59
	100%	0.94	0.85	0.99	0.87	0.94	0.85
PWGD	5%	0.46	0.35	0.88	0.68	0.47	0.36
	10%	0.55	0.36	0.90	0.67	0.55	0.40
	25%	0.58	0.38	0.91	0.59	0.56	0.41
	100%	0.82	0.56	0.98	0.67	0.81	0.56
BWM	5%	0.45	0.04ns	0.83	-0.08ns	0.46	-0.04ns
	10%	0.38	0.03ns	0.86	-0.11*	0.45	-0.04ns
	25%	0.50	0.06*	0.90	-0.13	0.53	-0.04ns
	100%	0.85	-0.08	0.98	-0.19	0.84	-0.12
WWM	5%	0.38	0.11ns	0.88	-0.04ns	0.28	0.06ns
	10%	0.40	0.15	0.89	-0.01ns	0.34	0.10*
	25%	0.53	0.13	0.92	-0.01ns	0.47	0.06*
	100%	0.83	0.26	0.98	0.15	0.82	0.23

649 [a] BWD = birth weight direct, WWD = weaning weight direct, PWGD = postweaning gain
650 direct, BWM = birth weight maternal, WWM = weaning weight maternal; PM = polygenic
651 model; GPM1, GPM2, GPM3 = genomic-polygenic models 1, 2, and 3.

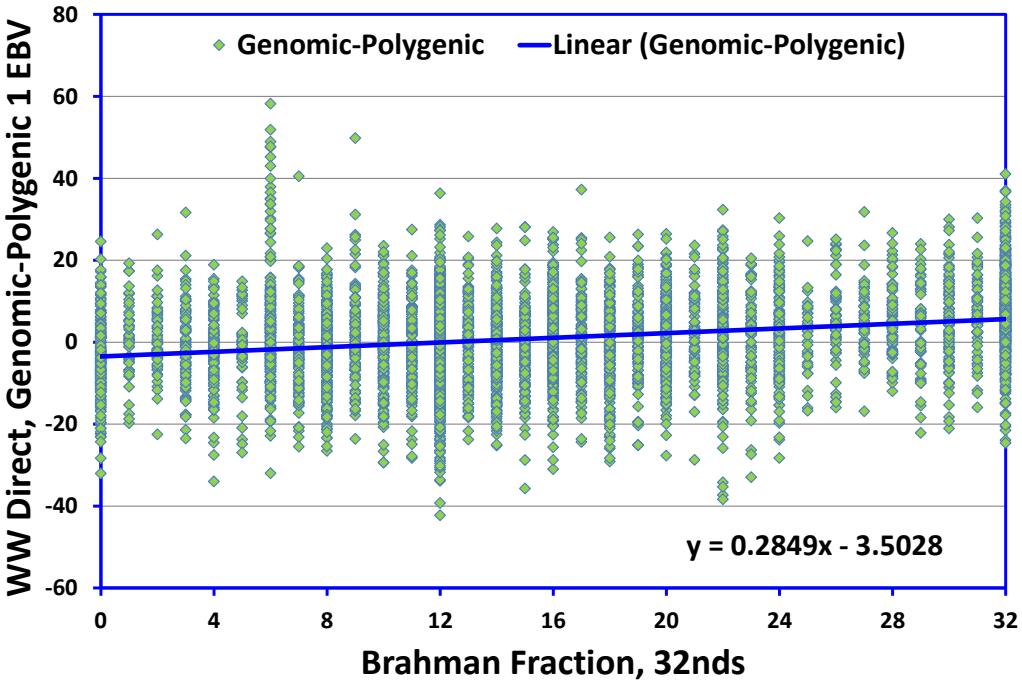
652 [b] ns = non-significant; * = $P < 0.0352$ to $P < 0.0127$; All other rank correlations were
653 significant at $P < 0.0001$, except for one that was significant at $P < 0.0005$.

654

655 Table 9. Linear regression coefficients of EBV from genomic-polygenic and polygenic
656 models on Brahman fraction of animal

	Linear regression coefficient, kg/32nds Brahman fraction[b]							
Trait[a]	GPM1	SE	GPM2	SE	GPM3	SE	PM	SE
BWD	0.18	0.004	0.15	0.005	0.04	0.003	0.17	0.005
WWD	0.29	0.017	0.25	0.016	0.08	0.011	0.27	0.017
PWGD	-0.29	0.014	-0.13	0.011	-0.09	0.008	-0.25	0.014
BWM	-0.12	0.002	-0.10	0.002	0.02	0.002	-0.12	0.002
WWM	-0.13	0.010	-0.09	0.010	0.03	0.003	-0.14	0.010

657
658 [a] BWD = birth weight direct, WWD = weaning weight direct, PWGD = postweaning gain
659 direct, BWM = birth weight maternal, WWM = weaning weight maternal; GPM1, GPM2,
660 GPM3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model.
661 [b] All regression coefficients were significant ($P < 0.0001$).
662



663

664 **Fig. 1.** Direct weaning weight EBV from genomic-polygenic model 1

665

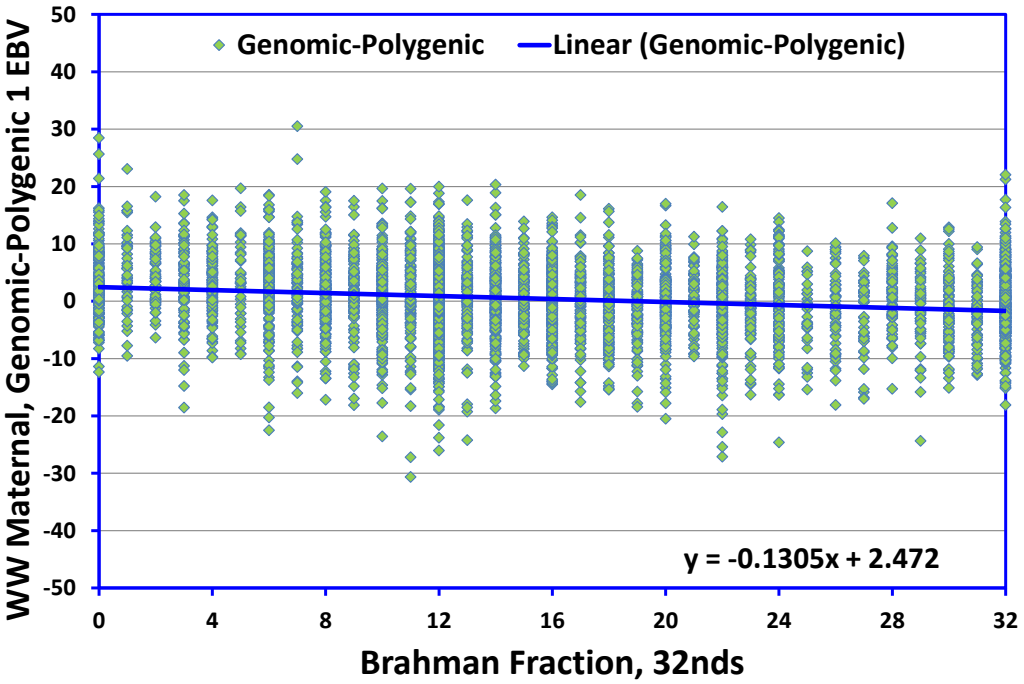


Fig. 2. Maternal weaning weight EBV from genomic-polygenic model 1

Appendix 1

Code used to compute sampling means and SD of phenotypic variance components and genetic parameters with program AIREMLF90

```
#Phenotypic covariances
OPTION se_covar_function cp1p1 G_6_6_1_1+G_6_7_1_1+G_7_7_1_1+R_1_1
OPTION se_covar_function cp1p2
G_6_6_1_2+(0.5)*G_6_7_1_2+(0.5)*G_6_7_2_1+G_7_7_1_2+R_1_2
OPTION se_covar_function cp1p3 G_6_6_1_3+(0.5)*G_6_7_3_1+R_1_3
OPTION se_covar_function cp2p2 G_6_6_2_2+G_6_7_2_2+G_7_7_2_2+R_2_2
OPTION se_covar_function cp2p3 G_6_6_2_3+(0.5)*G_6_7_3_2+R_2_3
OPTION se_covar_function cp3p3 G_6_6_3_3+R_3_3
```

```
680
681  #Heritabilities Direct
682  OPTION se_covar_function h1d
683  G_6_6_1_1/(G_6_6_1_1+G_6_7_1_1+G_7_7_1_1+R_1_1)
684  OPTION se_covar_function h2d
685  G_6_6_2_2/(G_6_6_2_2+G_6_7_2_2+G_7_7_2_2+R_2_2)
686  OPTION se_covar_function h3d G_6_6_3_3/(G_6_6_3_3+R_3_3)
687
688  #Heritabilities Maternal
689  OPTION se_covar_function h1m
690  (G_7_7_1_1)/(G_6_6_1_1+G_6_7_1_1+G_7_7_1_1+R_1_1)
691  OPTION se_covar_function h2m
692  (G_7_7_2_2)/(G_6_6_2_2+G_6_7_2_2+G_7_7_2_2+R_2_2)
693
694  #Genetic Correlations (Direct, Direct)
695  OPTION se_covar_function rd1d2 G_6_6_1_2/(G_6_6_1_1*G_6_6_2_2)**(0.5)
696  OPTION se_covar_function rd1d3 G_6_6_1_3/(G_6_6_1_1*G_6_6_3_3)**(0.5)
697  OPTION se_covar_function rd2d3 G_6_6_2_3/(G_6_6_2_2*G_6_6_3_3)**(0.5)
698
699  #Genetic Correlations (Direct, Maternal)
700  OPTION se_covar_function rd1m1 (G_6_7_1_1)/(G_6_6_1_1*G_7_7_1_1)**(0.5)
701  OPTION se_covar_function rd1m2 (G_6_7_1_2)/(G_6_6_1_1*G_7_7_2_2)**(0.5)
702  OPTION se_covar_function rd2m1 (G_6_7_2_1)/(G_6_6_2_2*G_7_7_1_1)**(0.5)
703  OPTION se_covar_function rd2m2 (G_6_7_2_2)/(G_6_6_2_2*G_7_7_2_2)**(0.5)
```

```
OPTION se_covar_function rd3m1 (G_6_7_3_1)/(G_6_6_3_3*G_7_7_1_1)**(0.5)
OPTION se_covar_function rd3m2 (G_6_7_3_2)/(G_6_6_3_3*G_7_7_2_2)**(0.5)

#Genetic Correlations (Maternal, Maternal)
OPTION se_covar_function rm1m2
(G_7_7_1_2)/(G_7_7_1_1*G_7_7_2_2)**(0.5)G_6_7_1_1+0.25*G_6_6_1_1)*(G_7_7_2_
2-G_6_7_2_2+0.25*G_6_6_2_2))**(0.5)

#Environmental Correlations
OPTION se_covar_function re1e2 R_1_2/(R_1_1*R_2_2)**(0.5)
OPTION se_covar_function re1e3 R_1_3/(R_1_1*R_3_3)**(0.5)
OPTION se_covar_function re2e3 R_2_3/(R_2_2*R_3_3)**(0.5)

#Phenotypic Correlations
OPTION se_covar_function rp1p2
(G_6_6_1_2+(0.5)*G_6_7_1_2+(0.5)*G_6_7_2_1+G_7_7_1_2+R_1_2)/((G_6_6_1_1+G_
6_7_1_1+G_7_7_1_1+R_1_1)*(G_6_6_2_2+G_6_7_2_2+G_7_7_2_2+R_2_2))**(0.5)
OPTION se_covar_function rp1p3
(G_6_6_1_3+(0.5)*G_6_7_3_1+R_1_3)/((G_6_6_1_1+G_6_7_1_1+G_7_7_1_1+R_1_1)*
(G_6_6_3_3+R_3_3))**(0.5)
OPTION se_covar_function rp2p3
(G_6_6_2_3+(0.5)*G_6_7_3_2+R_2_3)/((G_6_6_2_2+G_6_7_2_2+G_7_7_2_2+R_2_2)*
(G_6_6_3_3+R_3_3))**(0.5)
```