1 Genomic-polygenic evaluation of multibreed Angus-Brahman cattle for postweaning feed
2 efficiency and growth using actual and imputed Illumina50k SNP genotypes

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Abstract

The objectives were to estimate the fractions of additive genetic variances for 4 postweaning feed efficiency and growth traits explained by 46,909 actual and imputed SNP genotypes, to compare rankings of calf additive genetic predictions from genomic-polygenic (GP), genomic (G), and polygenic (P) models, and to determine trends of predicted additive genetic values from calves ranging from 100% Angus to 100% Brahman in a multibreed population. Traits were postweaning residual feed intake (RFI), daily feed intake (DFI), feed conversion ratio (FCR), and weight gain (PWG). Phenotypes were from 807 bull, heifer, and steer calves housed at the Feed Efficiency Facility of the University of Florida from 2006 to 2010. Imputation from 2,899 SNP (Illumina3k) to 46,909 SNP (Illumina50k) was done with program findhap2 using a reference population of 828 Brangus heifers. Fixed effects for all models were contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf. Random effects were additive SNP (GP and G models), additive polygenic (GP and P models), and residual. Software GS3 was used to compute variance components and heritabilities, and additive genetic predictions. Heritabilities were 0.30 for RFI, 0.37 for DFI, 0.25 for FCR, and 0.33 for PWG. Fractions of additive variances explained by the 46,909 actual and imputed SNP were 0.48 for RFI, 0.36 for DFI, 0.50 for FCR, and 0.28 for PWG. These fractions were 3.2, 3.2, 2.0, and 1.8 times larger than those previously obtained for these 4 traits using the 2,899 SNP from the Illumina3k chip. Rank correlations between calf additive genetic predictions were high between GP and P and between GP and G models (0.89 to 0.98; $P < 0.0001$), and somewhat lower between G and P models (0.69 to 0.81; $P < 0.0001$). Regressions of additive genetic predictions on Brahman fraction of calf were negative with the G model for DFI ($P < 0.0344$) and with all models for PWG ($P < 0.0171$

to $P < 0.0001$). Imputation from the Illumina3k to 50k substantially increased the explained fraction of additive SNP and total genetic variances resulting in considerably higher rank correlations between calf additive genetic predictions from G and GP, and from G and P models in this Angus-Brahman multibreed population.

Key words: Beef; Crossbred; Genomic; Imputation; Polygenic

1. Introduction

Utilization of chips with SNP markers evenly distributed across the genome to aid genetic evaluation of beef and dairy cattle has increased substantially in recent years. However, although prices of high-density chips (e.g., Illumina50k, Illumina90k, IlluminaHD) have decreased, they are still too high for widespread utilization by the cattle industry. Another option would be to use less expensive low density chips (e.g., Illumina3k, Illumina7k, Illumina9k). However, the amount of additive genetic variation for postweaning feed efficiency, growth, and ultrasound carcass traits explained by the Illumina3k chip in an Angus-Brahman multibreed population was found to be lower than that explained by the Illumina50k chip in other beef cattle populations (Elzo et al., 2012, 2013). It would be desirable to increase both the fraction of additive genetic variation accounted for the set of SNP used for genomic and genomic-polygenic predictions as well as their accuracy without unduly increasing costs. One alternative would be to predict SNP for animals genotyped with a low density chip using SNP from a reference group of animals genotyped with a high density chip using imputation algorithms (Howie et al., 2009; Weigel et al., 2010; Sargolzaei et al., 2011a; VanRaden et al., 2011, 2013). Thus, the objectives of this research were: 1) to estimate the fractions of additive genetic variances

for 4 postweaning feed efficiency and growth traits explained by 46,909 actual and imputed SNP genotypes, 2) to compare the rankings of calf additive genetic predictions from genomic-polygenic (GP), genomic (G), and polygenic (P) models, and 3) to determine GP, G, and P trends of predicted additive genetic values from calves ranging from 100% Angus to 100% Brahman in a multibreed population under subtropical conditions.

2. Materials and methods

2.1. Animals, feeding, and management

The research protocol for this project was approved by the University of Florida Institutional Animal Care and Use Committee (IACUC protocol number 201003744). A total of 807 calves from the multibreed Angus-Brahman (MAB) herd of the University of Florida (UF), Gainesville, were used in this research. Calves were the progeny of 61 sires and 365 dams from 6 breed groups mated according to a diallel design (Elzo and Wakeman, 1998). Breed groups were defined as follows: Angus = (1.0 to 0.80) A (0.0 to 0.20) B, ¾ A ¼ B = (0.79 to 0.60) A (0.21 to 0.40) B, Brangus = (0.625) A (0.375) B, ½ A ½ B = (0.59 to 0.40) A (0.41 to 0.60) B, ¼ A ¾ B = (0.39 to 0.20) A (0.61 to 0.80) B, and Brahman: (0.19 to 0.0) A (0.81 to 1.00) B. Calves were born from 2006 to 2010 (65 bulls, 409 heifers, and 333 steers). Calf numbers by breed group were: 123 Angus, 164 ¾ A ¼ B, 141 Brangus, 190 ½A ½B, 86 ¼ A ¾ B, and 103 Brahman (Table 1).

Calves kept at the Beef Research Unit (BRU) of the University of Florida from birth until they were taken to the Feed Efficiency Facility (UFEF, Marianna, Florida) for the feed efficiency trial. They received a preconditioning diet at the BRU for 3 to 4 weeks prior transport to the UFEF. The preconditioning diet encompassed concentrate (1.6 kg to 3.6 kg per day; 14.0 % CP; 488 Pellet, Medicated Weaning Ration, Lakeland Animal Nutrition,

Lakeland, Florida; and soy hull pellets), ad libitum access to a mineral supplement, and bahiagrass (*Paspalum notatum*) hay.

The postweaning feed efficiency trial at UFEF had an adjustment period of 21 d and a trial period of 70 d. Calves were identified using half-duplex passive transponder ear tags (Allflex USA Inc., Dallas-Fort Worth, TX) at UFEF. Then, calves from each sire group (A, ¾ A ¼ B, Brangus, ½ A ½ B, ¼ A ¾ B, and B) by sex (bull, heifer, and steer) subclass were randomly allocated to pens (108 m^2/pen; 2 GrowSafe nodes per pen; mean stocking rate = 15 calves/pen; 7.5 calves/GrowSafe node). The UFEF ration was offered ad libitum and contained whole corn or corn gluten, cottonseed hulls, molasses, chopped grass hay, and a vitamin-mineral-protein supplement. The UFEF ration supplied from 2006 to 2010 had a mean of 89.2% of dry matter, 12.9% of crude protein, 1.6 mcal/kg DM of net energy for maintenance, and 1.0 mcal/kg DM of net energy for gain. Postweaning individual animal feed intake was measured in real time using a GrowSafe system (GrowSafe Systems, Ltd., Airdrie, Alberta, Canada) and calf weights were collected every 2 weeks.

2.2. Traits

Traits were postweaning phenotypic residual feed intake (RFI, kg DM*day^{-1}), mean daily feed intake (DFI, kg DM*day^{-1}), mean daily feed conversion ratio (FCR, kg DM*day^{-1}/kg weight gain*day^{-1}), and postweaning weight gain during the 70-d feeding trial (PWG, kg). The RFI, DFI, FCR, and PWG were computed as explained in Elzo et al. (2009). The postweaning phenotypic residual feed intake for each calf was equal to the difference between its expected and actual mean DFI during the 70-day feeding trial (Koch et al., 1963; Archer et al., 1997; Arthur et al., 2001). The expected DFI for each calf was obtained as the linear regression of their DFI measurements on their average daily gain and

metabolic mid-weight. The average daily gain for a calf was computed as the regression of a calf weight on weight day (i.e., every two weeks). Metabolic mid-weight was equal to mid-weight (i.e., initial weight regression estimate plus regression estimate for average daily gain times 35 d) raised to the power of 0.75. Mean DFI was the average daily feed intake during the 70-d trial. Mean daily feed conversion ratio was the ratio of DFI to average daily gain. Postweaning weight gain was the difference between individual calf weights at d 70 and d 1 of the feeding trial.

2.3. Tissue sampling and genotyping

Blood samples were collected with EDTA vacutainer tubes at weaning. Samples were kept at 4°C before shipping to Dr. M. Thomas laboratory at New Mexico State University for processing and storage at -80 °C. Tubes were centrifuged at 1,875 x g at 4 °C for 30 min to get the white blood cell supernatant; then, PBS was added to obtain a volume of 1.0 mL (Beauchemin et al., 2006). A volume of 0.05 mL of each sample was forwarded to GeneSeek (GeneSeek, Lincoln, NE) for DNA extraction and genotyping with the Illumina Bovine3K BeadChip (Illumina, 2011a).

2.4. Imputation and datasets

Imputation of from Illumina3k to Illumina50k in animals from the MAB population genotyped with the Illumina3k chip was accomplished using program findhap2 (VanRaden, 2011) using a reference population (RP) of 828 registered Brangus heifers genotyped with version 1 of the Illumina50k chip (Illumina, 2011b). Heifers from RP were raised in Camp Cooley Ranch (Franklin, TX) and the Chihuahuan Desert Rangeland Research Center and Campus Farm of New Mexico State University (Luna-Nevarez et al, 2010; Peters et al.,

2012; Peters et al., 2013). No pedigree information was available to account for relationships between the MAB and the RP populations. Thus, animals from the MAB population were assumed to be unrelated to animals from the reference population. However, relationships among animals within each population (i.e., MAB and RP) were accounted for. This resulted in a combined pedigree file of 7,989 animals (5,864 for MAB and 3,034 for RP). Numbers of animals with genotypes were 1,300 (Illumina3k) in MAB and 828 in RP. The location of SNP markers in the Illumina3k chip corresponded to the location of SNP markers in version 2 of the Illumina50k chip. Thus, SNP markers from version 2 of the Illumina50k chip (n = 54,609) were matched to SNP markers from version 1 of the Illumina50k chip (n = 54,011) to determine the subset of SNP markers present in both chips. Only the subset of SNP markers from autosomal chromosomes and chromosome X present in both chips and their location in version 2 of the Illumina50k chip (n = 50,276) were used for imputation. Subsequently, SNP markers from the Illumina3k chip (n = 2,900) were matched to this subset of 50,276 SNP markers of the Illumina50k chip to identify the subset of SNP markers present in it (n = 2,816). Thus, the input files for findhap2 were: 1) a genotype file containing gene content information (i.e., number of "second alleles" = 0, 1, 2, and 5 for unknown) on 2,816 loci from the Illumina3k chip for 1,300 MAB animals and on 50,276 loci from the Illumina50k version 1 chip for 828 RP heifers; 2) a chromosome data file containing information on 50,276 SNP markers in common in versions 1 and 2 of the Illumina50k chip (i.e., SNP name, chromosome number, location in base pairs (bp) within and across chromosomes, and SNP location in both the Illumina50k and 3k chips); and 3) a pedigree file containing animals, sires and dams from the MAB and RP populations. Program findhap2 was run with the following options: iters = 4, Xchrom = 30, maxlen = 600, minlen = 35, steps = 3, maxhap = 20,000, hapout = 1, and

genout = 1. The output file "haplotypes" from findhap2 contained paternal and maternal actual and imputed SNP data (i.e., 1's and 2's) on 50,276 loci for all animals in the MAB and RP populations. The subset of file "haplotypes" containing SNP marker information on all animals from the MAB population was matched with a file with phenotypic information on RFI, DFI, FCR, and PWG and only calves with information on all 4 traits were kept (n = 807). Minor allele frequencies (MAF) in the subset of the MAB population containing animals with all phenotypes were determined and SNP information from loci with MAF < 0.04 was discarded (n = 3,367), leaving each animal with parental SNP data on 46,909 loci. Phenotypic and parental SNP data were merged to construct a MAB input data file for program GS3. The resulting input data file contained phenotypes for RFI, DFI, FCR, and PWG and actual and imputed parental SNP data on 46,909 loci (2,648 actual SNP from the Illumina3k and 44,261 imputed SNP from the Illumina50k chip) for 807 calves. The MAB pedigree input file for GS3 had 5,864 animals (calves, sires, and dams).

2.5. Genomic-Polygenic Variance Components and Variance Ratios

Estimates of variance components for RFI, DFI, FCR, and PWG were obtained using single-trait genomic-polygenic models (VanRaden, 2008; Legarra et al., 2008; Snelling et al., 2011; Elzo et al., 2012). Fixed effects were contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf. Random effects were additive SNP marker locus effect as a function of the number of "2" alleles in each locus (AS; mean zero; variance = additive SNP variance), calf additive polygenic effect (AP; mean zero; variance = A*Vg; A = additive relationship matrix with 5,864 animals, Vg = additive polygenic variance), and residual effect (mean zero, common variance). Variance components and heritabilities were estimated using Markov Chain

179 Monte Carlo (MCMC) procedures with option VCE of program GS3 (Legarra, 2009;
180 Number of iterations = 120,000; Burn-in = 20,000; Thinning = 100; Correction = 10,000).
181 The starting values for the additive polygenic variance (VAPO) and the residual variance
182 (VRES) for each trait were REML estimates obtained using single-trait polygenic models
183 that included all the effects of the genomic-polygenic model, except for the random
184 additive SNP marker effects. The starting value for the additive SNP variance (VSNP) for
185 each trait was computed using the expression $\frac{\widehat{V}g}{\sum_{i=1}^{46,909} 2p_i q_i}$ (Habier et al., 2007; VanRaden,
186 2008; Gianola et al., 2009), where $\widehat{V}g$ = REML estimate of the additive polygenic variance
187 from a single-trait polygenic model computed using ASREML (Gilmour et al., 2006), and
188 p_i = frequency of allele "1" and q_i = frequency of allele "2" in SNP marker locus i.
189 Program GS3 produced values of VSNP, VAPO, and VRES for 1,200 MCMC samples for
190 each trait. Additive genomic variances (VAGO), total additive genetic variances
191 (VGTOT), phenotypic variances (PVAR), and heritabilities were computed for each sample
192 as follows: 1) VAGO = VSNP × $\sum_{i=1}^{46,909} 2p_i q_i$; 2) VGTOT = VAGO + VAPO; 3) PVAR =
193 VAGO + VAPO + VRES; and 4) heritability = VGTOT/PVAR. Lastly, posterior means
194 and standard deviations for VAGO, VAPO, VGTOT, PVAR, and heritabilities of MCMC
195 samples excluding the burn-in period (n = 1,000) were used to obtain estimates of variances
196 and heritabilities and their dispersion for RFI, DFI, FCR, and PWG.
197 For comparison purposes estimates of VAPO, VRES, PVAR, and heritability values
198 were computed with a polygenic model that contained the same effects as the genomic-
199 polygenic model, except for additive SNP marker locus effects, using the same MCMC
200 procedure and GS3 computer program.
201

2.6. Genomic-polygenic, genomic, and polygenic additive genetic predictions

Program GS3 (Legarra, 2009) was used to compute calf genomic-polygenic, genomic and polygenic predicted values (EBV) for RFI, DFI, FCR, and PWG with option BLUP (Gauss-Seidel iteration; convergence criterion = 10^{-8}) using VAGO, VAPO, and VRES values estimated with the genomic-polygenic model above. Calf genomic-polygenic EBV were computed with the same model used to estimate variance components, the model used to obtain calf genomic EBV ignored polygenic effects, and the model for calf polygenic EBV ignored additive SNP marker locus effects. Thus, 1) Calf genomic-polygenic EBV (GEBV) were computed using a genomic-polygenic model as $\mathrm{GPEBV} = f_B(B-A)^0 + \sum_{i=1}^{46,909} w_i * \widehat{AS}_i + \widehat{AP}$, where f_B = Brahman fraction of calf, and $(B-A)^0$ = generalized least squares solution of the difference between Brahman and Angus breed effects, w_i = number of "2" alleles in locus i, $\widehat{AS}_i$ = BLUP of the difference between allele 2 and allele 1, and $\widehat{AP}$ = calf polygenic value; 2) Calf genomic EBV (GEBV) were computed using a genomic model as $\mathrm{GEBV} = f_B(B-A)^0 + \sum_{i=1}^{46,909} w_i * \widehat{AS}_i$; and 3) Calf polygenic EBV (PEBV) were computed using a polygenic model as $\mathrm{PEBV} = f_B(B-A)^0 + \widehat{AP}$. Calf rankings across models were compared using Spearman's rank correlations computed using the correlation procedure of SAS (SAS Institute Inc., Cary, NC). Calf trends from Angus to Brahman were evaluated using linear regressions of GPEBV, GEBV, and PEBV on calf Brahman fraction computed using the regression procedure of SAS.

Predictive abilities for the genomic-polygenic, genomic and polygenic models for RFI, DFI, FCR, and PWG were obtained using the correlation between predicted genomic-polygenic, genomic and polygenic values and phenotypes in a validation dataset (Legarra et al., 2008) composed of animals with records in 2010 (n = 189; 23% of the dataset). The

training dataset was composed of animals with records from 2006 to 2009 (n = 618; 77% of the dataset). The same models used in the complete dataset to obtain best linear unbiased predictions were used to compute genomic-polygenic, genomic, and polygenic predictions in the training population. Accuracies were computed as predictive abilities divided by the square root of heritabilities (Legarra et al., 2008).

3. Results and discussion

Table 1 presents numbers of calves, means and SD for RFI, DFI, FCR, and PWG by breed group and for the complete dataset. Number of calves per breed group ranged from 86 for ¼ A ¾ B to 190 for ½ A ½ B. Means for the complete dataset were 0.00 kg DM*d^{-1} for RFI, 8.47 kg DM*d^{-1} for DFI, 8.41 kg DM*d^{-1}/kg gain*d^{-1} for FCR, and 74.59 kg for PWG. Means per breed group ranged from -0.25 kg DM*d^{-1} for Brahman to 0.15 kg DM*d^{-1} for ¼ A ¾ B for RFI, from 7.74 kg DM*d^{-1} for Brahman to 8.80 kg DM*d^{-1} for ¼ A ¾ B for DFI, from 7.78 kg DM*d^{-1}/kg gain*d^{-1} for Angus to 9.36 kg DM*d^{-1}/kg gain*d^{-1} for Brahman and from 62.18 kg for Brahman to 78.21 kg for ¾ A ¼ B for PWG.

3.1. Genomic and polygenic variance components and variance ratios

Table 2 presents posterior means and SD for additive genomic (VAGO), additive polygenic (VAPO), total additive (VGTOT) and phenotypic variances (PVAR) from genomic-polygenic models for RFI, DFI, FCR, and PWG computed using MCMC procedures (program GS3, option VCE; Legarra et al., 2009). The last two rows of Table 2 show estimates of additive polygenic (VGPO) and phenotypic variances (PVARPO) from polygenic models for these 4 traits. Similarly, Table 3 shows posterior means and SD for

248 variance ratios from genomic-polygenic models (first 3 rows) and polygenic models (last
249 row) for RFI, DFI, FCR, and PWG.

250 Ratios of PVAR from genomic-polygenic to PVAR from polygenic models were
251 similar for all traits (1.02 to 1.04; Table 4) indicating that both models accounted for
252 similar amounts of phenotypic variation for RFI, DFI, FCR, and PWG. Conversely,
253 estimates of VGTOT were from 32% (PWG) to 76% (RFI) larger for genomic-polygenic
254 than for polygenic models (Table 4). These percentages were larger than the ratios of
255 VGTOT from genomic-polygenic to polygenic models obtained for these 4 traits with the
256 Illumina3k chip (from 10% for DFI to 37% for FCR; Elzo et al., 2012). This suggested that
257 the VAGO accounted for by genomic-polygenic models with 46,909 actual and imputed
258 SNP from the Illumina50k chip was substantially larger than the VAGO explained by 2,899
259 SNP from the Illumina3k. This was supported by the large differences in VAGO/VGTOT
260 and VAGO/PVAR ratios from genomic-polygenic analyses. The VAGO/VGTOT ratios
261 were from 83% (PWG) to 221% (DFI) higher and the VAGO/PVAR ratios were from 64%
262 (PWG) to 433% (RFI) higher with the actual-imputed Illumina50k SNP set than with the
263 Illumina3k SNP set (Table 5). As animals from the reference Brangus population were
264 assumed to be unrelated to animals in the Angus-Brahman population, these increments in
265 VAGO could be attributed to additive variation due to QTL affecting these traits that were
266 in linkage disequilibrium with the imputed SNP markers from the Illumina50k set.
267 Wiggans et al. (2011) indicated that 95.2% of the genotypes were correctly imputed from a
268 3k (2,614 SNP) to a 50k (42,503 SNP) set on the average with program findhap2 in US
269 dairy cattle. A somewhat lower value of correctly imputed genotypes (93.2%) from 3k
270 (2,614 SNP) to 50k (42,503 SNP) was reported by Sargolzaei et al. (2011b) for Canadian
271 dairy cattle. Imputation errors for animals were likely higher here than in the US and

Canadian dairy cattle populations because heifers from the Brangus reference population were assumed to be unrelated to calves from the multibreed population, and lower levels of linkage disequilibrium in calves from the Angus-Brahman multibreed herd compared to those of dairy breeds due to the diallel crossbred mating structure of the multibreed population. Because genotyping errors due to imputation likely occurred, VAGO increments here were probably lower than those that could have been estimated if animals from the Angus-Brahman population had been genotyped with an actual Illumina50k chip.

Imputation from Illumina3k to 50k not only increased the amount of VAGO, but also tended to increase heritability values relative to values obtained with the Illumina3k (Elzo et al., 2012). The additional genetic variance accounted by VAGO from genomic-polygenic models resulted in heritability estimates that were between 30% and 76% higher than heritabilities from polygenic models (Table 4). These increments in heritability values due to higher VAGO estimates were larger for RFI (72%) and FCR (76%) than for DFI (45%) and PWG (30%; Table 4). Increments in heritability values with genomic-polygenic vs. polygenic models using the Illumina3k (Elzo et al., 2012) were substantially smaller for RFI (18%), DFI (11%), and PWG (13%) and comparable for FCR (40%). The larger VGTOT to VGPO ratios and the larger heritabilities from genomic-polygenic than polygenic models for all 4 traits (Table 4) suggested that the utilization of SNP markers from Illumina chips may have explained additional genetic variation beyond that accounted for by polygenic models. In addition, heritability ratios with the actual-imputed Illumina50k SNP set were higher for RFI (55%), DFI (19%), and FCR (21%), and lower for PWG (9%) than heritabilities obtained by Elzo et al. (2012) with the Illumina3k chip (Table 5). Thus, the additional SNP imputed from the Illumina50k chip explained a larger fraction of the genetic variation for RFI, DFI, and FCR, but not for PWG. This was due to

296 a proportionally much lower value of VAPO for PWG with the actual-imputed Illumina50k
297 SNP set (59.2 ± 20.3) than with the Illumina3k set (73.3 ± 21.9; Elzo et al., 2012) compared
298 to the other 3 traits. This resulted in a low VGTOT and a low heritability because PVAR
299 was similar in both studies. This likely occurred because of differences in the phenotypic
300 datasets used in these two studies (n = 807 here vs. n = 623 in Elzo et al., 2012).
301 The higher heritability ratios for RFI, DFI, FCR, and PWG estimated with genomic-
302 polygenic than with polygenic models using either the actual-imputed Illumina50k SNP set
303 or the Illumina3k SNP set (Elzo et al., 2012) suggested that higher selection responses for
304 these traits could be achieved with the utilization of SNP markers, phenotypes, and
305 pedigree information than with only phenotypic and pedigree data in this multibreed
306 population.
307 Estimates of VAGO to PVAR ratios with the 46,909 actual and imputed SNP here
308 were comparable to the value for RFI (0.12), higher than the value for DFI (0.03), and
309 lower than the value for postweaning average daily gain (0.90) obtained by Mujibi et al.
310 (2011) in a Canadian population of 721 crossbred steers (Goonewardene et al., 2003).
311 Mujibi et al. (2011) used random regression BLUP genomic-polygenic models and 37,959
312 SNP from the Illumina50k chip. Similarly, Peters et al. (2012) computed VAGO to PVAR
313 ratios for 6 preweaning and postweaning weight and average daily gain traits ranging from
314 0.04 for 205-d weight to 0.19 for 365-d weight and average daily gain from birth to 365 d
315 of age in a population of approximately 800 Brangus heifers in Texas. Peters et al. (2012)
316 utilized a Bayes-C genomic procedure (Kizilkaya et al., 2010; Habier et al., 2011) and a set
317 of 53,692 SNP from the Illumina50k chip. The similarity of values of VAGO to PVAR
318 ratios between Peters et al. (2012) and here may be an indication that imputation from
319 Illumina3k to 50k had little effect on these ratios in the Angus-Brahman multibreed

population. Contrary to results here and these two studies, Snelling et al. (2011) accounted for VAGO for RFI, DFI, and PWG completely using 44,163 SNP and REML procedures (WOMBAT; Meyer, 2007) in a population of *Bos taurus* crossbred cattle from the USMARC Cycle VII project. They estimated VAGO to PVAR ratios with genomic-polygenic models that were similar to or higher than heritability ratios with polygenic models (0.48 ± 0.07 vs. 0.56 ± 0.09 for RFI; 0.48 ± 0.07 vs. 0.40 ± 0.09 for DFI; 0.31 ± 0.1 vs. 0.25 ± 0.08 for PWG). Different estimation procedures and computer programs, small population sizes, differences in diet composition, different breeds involved in each population, dissimilar mating plans across populations likely generated different SNP marker frequencies and disequilibrium patterns which may have contributed to the diversity of estimates of VAGO, PVAR, and VAGO to PVAR ratios obtained in these cattle populations.

Genetic variances from GP models were higher (76% for RFI, 48% for DFI, 83% for FCR, and 32% for PWG) while phenotypic variances were only slightly higher (2% for RFI, DFI, and PWG, and 4% for FCR) than values from P models. This resulted in substantially higher heritability estimates for GP models than for P models (72% for RFI, 45% for DFI, 76% for FCR, and 30% for PWG). Because the same procedure (MCMC) and computer program (GS3) were used for the GP and P models, the higher heritability values may be an indication that the GP model explained additional genetic variation for these traits that was not accounted for by the P model.

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

Table 6 contains Spearman's rank correlations between calf EBV rankings from GP and G models, GP and P models, and G and P models for RFI, DFI, FCR, and PWG. Rank

344 correlations between calf EBV from the GP and P models had the highest values (0.93 to
345 0.98; $P < 0.0001$), those between calf EBV from GP and G models were somewhat lower
346 (0.89 to 0.93; $P < 0.0001$), and the lowest ones were between calf EBV from the G and P
347 models (0.69 to 0.81; $P < 0.0001$). Values of rank correlations between calf EBV from GP
348 and P models here were similar to rank correlations between calf EBV from these two
349 models using SNP from the Illumina3k chip (Elzo et al., 2012). In contrast, rank
350 correlations between calf EBV from GP and G models were 43% (RFI), 47% (DFI), 35%
351 (FCR), and 20% (PWG) higher and those between calf EBV from G and P models were
352 48% (RFI), 57% (DFI), 64% (FCR), and 25% (PWG) higher than corresponding rank
353 correlations between calf EBV using the Illumina3k (Elzo et al., 2012). The average
354 increment in rank correlation values was more than twice as large for RFI, DFI, and FCR
355 (56%) as for PWG (25%). The substantial increase in rank correlations between calf EBV
356 from GP and G and from G and P models for all traits suggested that the 44,261 imputed
357 SNP from the Illumina50k chip provided considerable information from QTL associated
358 with these markers, making calf EBV from G models more similar to their corresponding
359 values from GP and P models.

360 To evaluate the correspondence of calf EBV values computed with the actual-
361 imputed Illumina50k chip here and the Illumina3k chip in Elzo et al. (2012), rank
362 correlations between EBV for animals in common from the two studies ($n = 620$) for the
363 four traits were computed. As expected, rank correlations between calf EBV values with
364 actual-imputed Illumina50k SNP set here and the Illumina3k SNP set in Elzo et al. (2012)
365 were higher for GP models (from 0.93 for RFI and FCR to 0.95 for DFI) and P models
366 (from 0.93 for FCR and PWG to 0.97 for DFI) than for G models (from 0.71 for DFI to
367 0.83 for PWG; Table 7). Higher VAGO to PVAR fractions explained by the SNP from the

368 actual-imputed SNP set from the Illumina50k chip likely determined the higher rank
369 correlation values between calf EBV predicted with G and GP as well as between G and P
370 models here than those previously obtained with the Illumina3k chip.

371 Predictive abilities and accuracies (Legarra et al., 2008) of genomic-polygenic,
372 genomic, and polygenic values with the actual-imputed Illumina50k SNP set (Table 8)
373 were mostly lower than those obtained with the Illumina3k SNP set in Elzo et al. (2012) for
374 all traits. However, only 4 out of 12 predictive abilities were significant here with the
375 actual-imputed Illumina50k SNP set ($P < 0.0020$ to $P < 0.0118$). Contrarily, all predictive
376 abilities were significant with the Illumina3k SNP set (Elzo et al., 2012). Genomic models
377 had the lowest predictive abilities and accuracies for all traits, except for FCR. The number
378 of animals with phenotypes used in the training dataset with the actual-imputed
379 Illumina50k SNP set ($n = 618$) was somewhat larger than the one used with the Illumina3k
380 SNP set ($n = 455$; Elzo et al., 2012). These additional phenotypes likely contributed to
381 differences in predictive abilities and accuracies of genomic-polygenic and polygenic
382 models in these two studies. In addition, the amount of phenotypic information used to
383 predict each SNP in the actual-imputed Illumina50k set (0.013 records per SNP) was
384 substantially lower than for the Illumina3k set (0.08 records per SNP). This may have been
385 one of the factors that negatively affected the predictive ability of genomic and genomic-
386 polygenic models. Thus, the small size of the phenotypic datasets here and in Elzo et al.
387 (2012) did not allow a comparison of the potential increase in predictive ability and
388 accuracy of models that included genotypic information.

389 Rank correlations between calf EBV from the P and GP models for RFI, DFI, FCR,
390 and PWG suggested that a polygenic model would likely be sufficient to identify the best
391 animals for these 4 traits in this multibreed population. This was supported by the

predictive abilities computed for the P and GP models. Although the predictive abilities for the P and GP models were low for all traits, those for the P models tended to be higher than those for the GP models.

3.3. Predicted SNP values

Ranges of predicted SNP values with the set of actual-imputed Illumina50k markers went from -0.780 * 10^{-3} to 0.795 * 10^{-3} kg DM*d^{-1} for RFI, -0.912 * 10^{-3} to 0.813 * 10^{-3} kg DM*d^{-1} for DFI, -1.255 * 10^{-3} to 1.142 * 10^{-3} kg DM*d^{-1}/kg gain*d^{-1} for FCR and -6.364 * 10^{-3} to 6.776 * 10^{-3} kg for PWG. Ranges for all traits were smaller (24% for RFI, 60% for DFI, 78% for FCR, and 85% for PWG) than those previously computed with the Illumina3k in this multibreed herd (Elzo et al., 2012). Smaller ratios of additive SNP variances to residual variances used in the mixed model equations with the 46,909 actual-imputed Illumina50k markers (13.8% for RFI, 45.3 % for DFI, 83.8 % for FCR, and 88.7 % for PWG) than with the 2,899 Illumina3k markers were likely responsible for the lower range of predicted values for the four traits here.

Standardized predicted SNP values (i.e., predicted SNP values divided by their additive SNP standard deviations) were used to compare SNP values across traits. The SNP standard deviations (SDSNP) were 0.0056 kg DM*d^{-1} for RFI, 0.0057 kg DM*d^{-1} for DFI, 0.0068 kg DM*d^{-1}/kg gain*d^{-1} for FCR, and 0.0371 kg for PWG. The distribution of additive SNP values (Table 9) with the actual-imputed Illumina50k SNP set was slightly narrower (± 0.1 SDSNP) for RFI, DFI and FCR, and wider (± 0.5 SDSNP) for PWG than with the Illumina3k SNP set (Elzo et al., 2012). The SNP markers from the actual-imputed Illumina50k set within the top 30% based on their predicted additive SNP values were distributed across most chromosomes (184 SNP in 28 chromosomes for RFI, 95 SNP in 27

chromosomes for DFI, 150 SNP in 30 chromosomes for FCR, and 63 SNP in 26 chromosomes for PWG). Conversely, the SNP within the top 5% based on predicted additive SNP values were located in 4 chromosomes for RFI (6 SNP in chromosomes 1, 7, 10, and 28), 2 chromosomes for DFI (2 SNP in chromosomes 1 and 22), 1 chromosome for FCR (1 SNP in chromosome 15), and 1 chromosome for PWG (1 SNP in chromosome 3). However, over 99.7% of the predicted SNP values with the Illumina3k (Elzo et al., 2012) and the actual-imputed Illumina50k chips were within ± 0.3 SDSNP around the mean for all traits except for PWG with 83.2%. This indicated that approximately 17% of the QTL associated with SNP markers in the actual-imputed Illumina50k chip had predicted values that were larger than those associated with the SNP markers in the Illumina3k chip. Although the wider range of predicted SNP marker values for PWG was associated with higher VAGO with the actual-imputed Illumina50k set (23.2 ± 18.4 kg^2) than with the Illumina3k set (13.9 ± 11.4 kg^2), the heritability estimate was lower (0.33 ± 0.09 vs. 0.36 ± 0.10) due to lower values of VAPO (59.2 ± 20.3 kg^2 vs. 73.3 ± 21.9 kg^2) and VGTOT (80.8 ± 24.3 kg^2 vs. 87.2 ± 25.2 kg^2). Conversely, while similar ranges of values existed for RFI, DFI, and FCR, estimates of VAGO and VGTOT and heritabilities were higher with the actual-imputed Illumina50k than with the Illumina3k. This indicated that the vast majority of QTL associated with SNP markers in the actual-imputed Illumina50k set had small effects and were located throughout the genome as previously suggested by outcomes with the Illumina3k in this multibreed population (Elzo et al., 2012) and with the Illumina50k in cattle populations in Australia (Bolormaa et al., 2011), Canada (Mujibi et al., 2011), and the US (Snelling et al., 2011; Peters et al., 2012).

439 *3.4. Trends of genomic-polygenic, genomic, and polygenic predictions from Angus to*
440 *Brahman*

441 Regressions of EVB computed with the actual-imputed Illumina50k set of SNP
442 markers on Brahman fraction were negative with the G model for DFI ($P < 0.0344$) and
443 with all models for PWG ($P < 0.0171$ to $P < 0.0001$) and non-significant for all other model
444 by trait combinations (Table 10). This suggested that calves of similar EBV for RFI, DFI
445 and FCR existed in all breed compositions, but EBV for PWG tended to decrease as
446 Brahman fraction increased. In contrast, EBV computed with the set of SNP from the
447 Illumina3k chip (Elzo et al., 2012) showed negative trends for RFI (GP model, $P < 0.0311$;
448 G model, $P < 0.0001$), for DFI (GP model, $P < 0.0070$; G model, $P < 0.0001$), and for PWG
449 (GP model, $P < 0.0274$; P model, $P < 0.0122$). The imputed SNP marker effects from the
450 Illumina50k chip as well as the EBV of animals present here but not in the analysis with the
451 Illumina3k (Elzo et al., 2012) likely contributed to the changes in significance of the
452 negative trends from Angus to Brahman for the GP and G models.
453

454 **4. Conclusions**

455 Imputation from the Illumina3k to 50k with SNP genotypes from Brangus cattle
456 increased the explained fraction of additive SNP genomic variation for RFI, DFI, FCR, and
457 PWG relative to those obtained in a previous study with SNP genotypes from the
458 Illumina3k in this Angus-Brahman multibreed population. However, the explained fraction
459 of the total genetic variation increased only for postweaning RFI, DFI, and FCR. Rank
460 correlations between EBV predicted using genomic and genomic-polygenic as well as
461 between genomic and polygenic models also increased indicating increased correspondence
462 in the ranking of predicted values from the 3 models with the utilization of the actual-

463 imputed Illumina50k SNP set. The small size of the multibreed dataset prevented an
464 assessment of increases in predictive ability of genomic-polygenic and genomic models
465 with the actual-imputed Illumina50k SNP set over the Illumina3k SNP set.
466

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473

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581

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

		Trait[1]							
		RFI, kg DM*d^{-1}		DFI, kg DM*d^{-1}		FCR, kg DM*d^{-1}/ kg gain*d^{-1}		PWG, kg	
Breed group	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angus	123	-0.24	1.25	8.26	2.08	7.78	2.18	78.19	22.64
¾ A ¼ B	164	0.04	1.45	8.68	2.19	8.29	2.70	78.21	22.46
Brangus	141	0.10	1.48	8.57	2.08	8.23	2.60	77.57	20.67
½ A ½ B	190	0.10	1.50	8.60	2.21	8.41	2.89	73.41	22.10
¼ A ¾ B	86	0.15	1.13	8.80	1.81	8.65	2.41	75.14	18.22
Brahman	103	-0.25	1.17	7.74	2.04	9.36	3.04	62.18	17.85
All	807	0.00	1.38	8.47	2.12	8.41	2.70	74.59	21.68

583 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed conversion ratio;
584 PWG = postweaning gain.
585

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

Variance[2]	Trait[1]			
	RFI, (kg DM*d^{-1})^2	DFI, (kg DM*d^{-1})^2	FCR, (kg DM*d^{-1} /kg gain*d^{-1})^2	PWG, (kg)^2
VAGO	0.28 ± 0.19	0.32 ± 0.22	0.86 ± 0.51	23.2 ± 18.4
VAPO	0.27 ± 0.13	0.52 ± 0.18	0.83 ± 0.41	59.2 ± 20.3
VGTOT	0.55 ± 0.20	0.85 ± 0.25	1.68 ± 0.61	80.8 ± 24.3
PVAR	1.79 ± 0.10	2.28 ± 0.13	6.62 ± 0.49	245.6 ± 13.8
VGPO	0.31 ± 0.14	0.57 ± 0.19	0.92 ± 0.46	61.2 ± 20.4
PVARPO	1.75 ± 0.09	2.25 ± 0.12	6.36 ± 0.34	241.5 ± 13.1

588 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
589 conversion ratio; PWG = postweaning gain.
590 [2]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTOT =
591 total genetic variance = VAGO + VAPO; PVAR = phenotypic variance; VGPO = additive
592 genetic variance from a polygenic model; PVARPO = phenotypic variance from a
593 polygenic model.
594

595 Table 3. Posterior means and standard deviations for additive genetic and genomic
596 variance ratios

	Trait[1]			
Variance Ratios[2]	RFI	DFI	FCR	PWG
VAGO/VGTOT	0.48 ± 0.21	0.36 ± 0.19	0.50 ± 0.18	0.28 ± 0.18
VAGO/PVAR	0.15 ± 0.10	0.14 ± 0.09	0.13 ± 0.07	0.09 ± 0.07
Heritability	0.30 ± 0.10	0.37 ± 0.10	0.25 ± 0.08	0.33 ± 0.09
HeritabilityPO	0.18 ± 0.07	0.25 ± 0.08	0.14 ± 0.07	0.25 ± 0.08

597 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
598 conversion ratio; PWG = postweaning gain.
599 [2]VAGO = additive genomic variance; VGTOT = VAGO + VAPO; PVAR = phenotypic
600 variance; HeritabilityPO = heritability from a polygenic model.
601

602 Table 4. Ratios of posterior means of variances and variance ratios from genomic-
603 polygenic and polygenic models

	Trait[1]			
Ratio[2]	RFI	DFI	FCR	PWG
VAPO/VGPO	0.86	0.91	0.90	0.94
VGTOT/VGPO	1.76	1.48	1.83	1.32
PVAR/PVARPO	1.02	1.02	1.04	1.02
Heritability/HeritabilityPO	1.72	1.45	1.76	1.30

604 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
605 conversion ratio; PWG = postweaning gain.
606 [2] VAPO = additive polygenic variance; VGTOT = total genetic variance; PVAR =
607 phenotypic variance; VGPO = additive genetic variance from a polygenic model; PVARPO
608 = phenotypic variance from a polygenic model; HeritabilityPO = heritability from a
609 polygenic model.

610 Table 5. Ratios of posterior means of variances and variance ratios from actual-imputed
611 Illumina50k and Illumina3k[1] genomic-polygenic analyses

	Trait[2]			
Ratio 50k/3k	RFI	DFI	FCR	PWG
VAGO[3]	5.47	3.96	2.35	1.68
VAPO	0.90	0.81	0.82	0.78
VGTOT	1.58	1.16	1.23	0.93
PVAR	1.02	0.98	1.02	1.02
VAGO/VGTOT	3.18	3.21	1.97	1.83
VAGO/PVAR	5.33	4.02	2.30	1.64
Heritability	1.55	1.19	1.21	0.91

612 [1]Elzo et al. (2012).

613 [2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
614 conversion ratio; PWG = postweaning gain.

615 [3]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTOT =
616 VAGO + VAPO; PVAR = phenotypic variance.

617
618

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

	Trait[1]			
Correlation[2]	RFI	DFI	FCR	PWG
GP Model, G Model	0.93	0.91	0.89	0.89
GP Model, P Model	0.94	0.97	0.93	0.98
G Model, P Model	0.77	0.80	0.69	0.81

621 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
622 conversion ratio; PWG = postweaning gain.

623 [2]GP Model = genomic-polygenic model; G Model = genomic model; P Model = polygenic
624 model. All correlations were significant ($P < 0.0001$).
625

626 Table 7. Spearman rank correlations for animals evaluated using genomic-polygenic,
627 genomic, and polygenic models with actual-imputed Illumina50k and Illumina3k SNP
628 datasets[1]

	Trait[2]			
Correlation[3]	RFI	DFI	FCR	PWG
GPEBV50k, GPEBV3k	0.93	0.96	0.93	0.94
GEBV50k, GEBV3k	0.76	0.74	0.77	0.83
PEBV50k, PEBV3k	0.94	0.97	0.93	0.93

629 [1]Spearman rank correlations were computed using a subset of 620 animals in common
630 between this study and Elzo et al. (2012).

631 [2]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
632 conversion ratio; PWG = postweaning gain.

633 [3]GPEBV= genomic-polygenic EBV; GEBV = genomic EBV; PEBV= polygenic EBV. All
634 correlations were significant ($P < 0.0001$).
635

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

	Trait[1]			
Model	RFI	DFI	FCR	PWG
Heritabilities	0.30	0.37	0.25	0.33
Predictive abilities				
Genomic-Polygenic	0.05	0.14	0.05	0.22
	P < 0.5123	P < 0.0532	P < 0.4793	P < 0.0029
Genomic	-0.12	-0.18	0.08	-0.03
	P < 0.0914	P < 0.0118	P < 0.2763	P < 0.7311
Polygenic	0.12	0.21	0.04	0.22
	P < 0.0995	P < 0.0032	P < 0.5662	P < 0.0020
Accuracies				
Genomic-Polygenic	0.09	0.23	0.10	0.38
Genomic	-0.22	-0.29	0.16	-0.05
Polygenic	0.22	0.34	0.08	0.38

638 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
639 conversion ratio; PWG = postweaning gain.
640
641

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

	Trait[1]							
	RFI		DFI		FCR		PWG	
SDSNP Range[2]	N	%	N	%	N	%	N	%
-0.8 to -1.0	0	0	0	0	0	0	10	0.02
-0.7 to -0.8	0	0	0	0	0	0	36	0.08
-0.6 to -0.7	0	0	0	0	0	0	118	0.25
-0.5 to -0.6	0	0	0	0	0	0	310	0.66
-0.4 to -0.5	0	0	0	0	0	0	906	1.93
-0.3 to -0.4	0	0	0	0	0	0	2054	4.38
-0.2 to -0.3	0	0	0	0	0	0	4263	9.09
-0.1 to -0.2	66	0.14	129	0.28	387	0.83	7309	15.58
0 to -0.1	22148	47.21	22861	48.74	22339	47.62	9496	20.24
0 to 0.1	24587	52.41	23782	50.70	23715	50.56	9230	19.68
0.1 to 0.2	108	0.23	137	0.29	468	1.00	6678	14.24
0.2 to 0.3	0	0	0	0	0	0	3725	7.94
0.3 to 0.4	0	0	0	0	0	0	1780	3.80
0.4 to 0.5	0	0	0	0	0	0	702	1.50
0.5 to 0.6	0	0	0	0	0	0	221	0.47
0.6 to 0.7	0	0	0	0	0	0	60	0.13
0.7 to 1.0	0	0	0	0	0	0	10	0.02

644 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
645 conversion ratio; PWG = postweaning gain.
646 [2]SDSNP = additive SNP standard deviation.

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

	Trait[1]			
Prediction	RFI	DFI	FCR	PWG
Genomic-Polygenic	-0.0011	-0.0035	0.0010	-0.0748
	P < 0.5453	P < 0.1513	P < 0.7199	P < 0.0012
Genomic	-0.0013	-0.0025	-0.0004	-0.0203
	P < 0.1967	P < 0. 0344	P < 0.7761	P < 0.0171
Polygenic	0.0005	-0.0016	0.0025	-0.0769
	P < 0.6814	P < 0.4259	P < 0.1985	P < 0.0001

649 [1]RFI = residual feed intake; DFI = mean daily feed intake; FCR = mean daily feed
650 conversion ratio; PWG = postweaning gain.
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