Genomic-Polygenic and Polygenic Evaluation of Multibreed Angus-Brahman Cattle for Direct and Maternal Growth Traits Under Subtropical Conditions

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Synopsis
High rank correlations existed between estimated breeding value for birth weight direct, weaning weight direct, postweaning gain direct, birth weight maternal, and weaning weight maternal from a genomic-polygenic model that used all phenotypic, pedigree, and genotypic information and a polygenic model. Variance components and genetic parameters from these two models were similar for all traits. Incomplete pedigree or lack of it resulted in lower rank correlations and poor estimates of genetic parameters particularly for maternal traits. Thus, to maximize the benefits of genotyping, commercial producers would need to keep complete pedigree records as well as individual animal phenotypes.

Summary
The objectives of this research were to compare variance components, genetic parameters, and estimated breeding value (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. 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. Restricted maximum likelihood variance components and genetic parameters 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. 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 lack of calf-dam relationships. These results indicated that the polygenic model and GP1 should be preferred, although high genotyping costs still make the polygenic model preferable for commercial beef cattle operations.

Introduction
Utilization of genotype information for genetic evaluation of cattle has become widespread in beef and dairy cattle. Currently, genomic evaluations are routinely conducted in dairy cattle in the US and other countries. Conversely, the US beef industry has only recently begun to implement national genomic evaluations that combine phenotypic, pedigree, and genotypic information. 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

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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. 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 under subtropical conditions in Florida and 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; 2) to compare rankings of animals for birth weight direct and maternal, weaning weight direct and maternal, and postweaning gain direct; and 3) to evaluate EBV trends for each trait under four data scenarios (phenotypes, pedigree, and genotypes) as percentage Brahman increased from 0% to 100% in a multibreed Angus-Brahman population under subtropical environmental conditions.

Materials and Methods

Animals and Traits

Animals belonged to the long-term multibreed Angus-Brahman (MAB) project of the University of Florida, Gainesville. 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, lb; 2,689 bulls and 2,575 heifers), 5,262 calves with weaning weights adjusted to 205 d of age (WW, lb; 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, lb; 209 bulls, 1,784 heifers, and 1,853 steers). Number of calves per breed group, means, and SD for BW, WW, and PWG are shown in Table 1. 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).

Feeding and Management

Calves resided 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 on bahiagrass pastures supplemented with bermudagrass hay and cottonseed meal during winter (mid-December to mid-March) and had access to a complete mineral supplement. Postweaning, calves remained at the Pine Acres Research Station or the Beef Research Unit, except from 2006 to 2010 when they were transported to the University of Florida Feed Efficiency Facility (UFFEF). When calves remained at their birth locations (1987 to 2005 and 2011 to 2013), they were kept on bahiagrass pastures supplemented with bahiagrass hay, concentrate (3.5 lb to 7.9 lb per day; 14.0 % crude protein; 488 Pellet Medicated Weaning Ration, Lakeland Animal Nutrition, Lakeland, Florida; soy hull pellets), and free access to a mineral supplement. Calves that went to UFFEF (2006 to 2010) were randomly allocated to pens within sire group (BG1 to BG6) by sex category (bull, heifer, and steer) and 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 crude protein=12.9%, mean dry matter=98.2%, mean net energy for maintenance=0.7 mcal/lb DM, and mean net energy for gain=0.5 mcal/lb DM).

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. These samples included 161 parents (20 sires and 141 dams), and 1,071 progeny (109 bulls, 613 heifers, and 349 steers). Samples were processed and stored at -80 °C at New Mexico State University. Subsamples were sent to GeneSeek (Gene Seek, Inc., Lincoln, NE, USA) in 2010 for genotyping with the Illumina3k chip. Animals genotyped with Illumina3k were imputed to Illumina50k using software findhap2 (VanRaden, 2011) and a reference population of 828 Brangus heifers previously genotyped with version 1 of the Illumina50k chip (Fortes et

al., 2012). The output file "haplotypes" from findhap2 was subsequently utilized as input file for an in-house FORTRAN program used to construct phenotypic, genotypic, and pedigree files for the computation of variance components and genetic parameters with the BLUPF90 family of programs (Misztal et al., 2002). The genotype file contained 1,232 MAB animals, each with 46,768 SNP markers (2,639 actual Illumina3k SNP and 44,129 imputed Illumina50k SNP).

Variance Components and Genetic Parameters

Variance components, heritabilities, and genetic, environmental and phenotypic correlations for BW direct, BW maternal, WW direct, WW maternal, and PWG direct were computed using three multiple-trait genomic-polygenic models (Aguilar et al., 2010) for scenarios 1, 2, and 3, and a multiple-trait polygenic model for scenario 4. The four scenarios represented genetic evaluations using: 1) all available phenotypic, pedigree, and genotypic data (genomic-polygenic model 1; GP1); 2) all available phenotypic data, pedigree from non-genotyped animals only, and all available genotypic data (genomic-polygenic model 2; GP2); 3) all available phenotypic and genotypic data, but no pedigree information (genomic-polygenic model 3; GP3); 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. Variance components and genetic parameters from GP1, GP2, and GP3 were compared to those from the polygenic model. The fixed effects for the three genomic-polygenic and the polygenic models were: 1) contemporary group (location-year for BW and WW direct and maternal; location-year-pen for PWG); 2) age of dam (all traits); 3) sex of calf (males and females for BW, and bulls, heifers, and steers for WW and PWG; 4) direct heterosis for all traits as a function of calf heterozygosity; and 5) maternal heterosis for BW and WW as a function of dam heterozygosity. Random effects were direct additive genetic for BW, WW, and PWG, maternal additive genetic for BW and WW, and residual for all traits. Restricted maximum likelihood estimates of variance components, genetic parameters, and their standard errors were computed using the BLUPF90 family of programs (Misztal et al., 2002).

Genomic-Polygenic and Polygenic Predictions

Estimated breeding values (EBV) were computed for all traits (BW and WW direct and maternal, and PWG direct) for 5,190 animals (genotyped=1,232, non-genotyped=3,958) and genotyped animals using genomic-polygenic models 1, 2, and 3 and the polygenic model. Spearman rank correlations were used to compare rankings of animal EBV for each trait in the top 5%, 10%, 25%, and for all evaluated animals.

Results

Calves with Brahman fractions over 80% had higher BW and lower WW and PWG than calves with Brahman fractions 20% or lower (Table 1). Crossbred calves with Brahman fractions between 40% and 60% had the highest WW, whereas calves with Brahman fractions between 37.5% and 60% had the highest PWG.

Variance Components and Genetic Parameters

Estimates of additive genetic variances and covariances from genomic-polygenic model 1 were, on the average, slightly larger than those from the polygenic model (mean difference=15.8 lb^2), thus the inclusion of genotypic information had little effect on estimates of variance components for growth traits in this multibreed population. Contrarily, exclusion of pedigree information from genotyped animals (genomic-polygenic model 2) or from all animals (genomic-polygenic model 3) underestimated additive genetic variance and covariance components compared to those from the polygenic model (mean difference=-44.5 lb^2 for model 2 and -132,5 lb^2 for model 3). Estimates of environmental variances and covariances for BW, WW, and PWG were, on the average, slightly lower for genomic-polygenic model 1 (mean difference=-11.3 lb^2), and higher for genomic-polygenic models 2 (mean difference=61.0 lb^2) and 3 (mean difference=225.2 lb^2) than estimates from the polygenic model. Estimates of phenotypic

variances and covariances followed the same pattern across models as additive genetic variance components. Estimates of phenotypic variances and covariances for BW, WW, and GW from genomic-polygenic model 1 were slightly higher (mean difference=20.7 lb^2), whereas those from genomic-polygenic models 2 (mean difference=-57.9 lb^2) and 3 (mean difference=-96.8 lb^2) were lower than those from the polygenic model.

The pattern for estimates of variance ratios across models mimicked the one for estimates of additive variance components. Estimates of heritabilities and genetic correlations (Table 2) from GP1 and the polygenic model were very similar (mean difference=0.01), while mostly lower estimates were obtained with GP2 (mean difference=-0.04) and GP3 (mean difference=-0.06). Environmental correlations (Table 3) from genomic-polygenic model 1 were nearly identical to those of the polygenic model (mean difference=-0.003), whereas those from genomic-polygenic models 2 (mean difference=0.05) and 3 (mean difference = 0.18) tended to be somewhat higher than estimates from the polygenic model. Nearly identical phenotypic correlations (Table 4) were obtained with GP1and the polygenic model (mean difference=0.003), but slightly lower estimates were computed with GP2 (mean difference=-0.013) and GP3 (mean difference=-0.020) than with the polygenic model.

Rankings of Animals Evaluated with Genomic-Polygenic and Polygenic Models

Rank correlations between EBV from the three genomic-polygenic and the polygenic models increased as the fraction of the population included in the computations increased from 5% to 10% to 25% to 100%. The highest rank correlations were between EBV from GP1 and the polygenic model (top 5% mean = 0.89; complete population mean=0.98). The second highest rank correlations were between EBV from GP1 and GP2 (top 5% mean=0.52; complete population mean=0.87), and between GP2 and the polygenic model (top 5% mean=0.53; complete population mean=0.87). The lowest rank correlations were between EBV from GP3 and EBV from any of the other models. Considering the cost of genotyping and the short time required for collecting phenotypes for growth traits, the close agreement between the polygenic model and GP1 would favor the use of the polygenic model for growth traits. However, genotypes here were a mixture of actual SNP from Illumina3k and imputed genotypes from Illumina50k. Imputation accuracy from Illumina3k to Illumina50k has ranged from 81% and 93% depending on the imputation procedure (Dassonneville et al., 2011; Huang et al., 2012). Thus, if animals had been genotyped with the Illumina50k, then perhaps larger differences between variance components, genetic parameters, and EBV from GP1 and the polygenic model could have been obtained. However, the issue of genotyping costs would have remained. High genotyping cost is still likely to be the main constraint to widespread use of genotyping for genomic-polygenic evaluation by purebred and commercial cattle producers.

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

	Trait[1]								
	BW, lb			WW, lb			PWG, lb		
Breed group[2]	N	Mean	SD	N	Mean	SD	N	Mean	SD
BG1	764	69.7	12.3	764	464.1	71.7	576	165.8	138.2
BG2	792	70.3	12.1	792	487.4	67.5	625	183.2	134.9
BG3	730	74.3	13.4	728	478.8	73.4	531	183.2	137.8
BG4	1,338	74.5	14.1	1,338	493.4	64.2	944	176.1	129.9
BG5	722	76.3	14.1	722	487.9	69.4	574	157.4	119.5
BG6	918	74.3	13.4	918	457.7	67.2	596	159.4	116.8
Total	5,264	73.4	13.4	5,262	479.3	69.7	3,846	171.3	130.1

[1]BW = Birth weight; WW = Weaning weight adjusted to 205 d of age; PWG = Postweaning gain from 205 d to 365 d of age.

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

Table 2. REML[1] 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[2]	GP1	SD	GP2	SD	GP3	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

[1]Restricted maximum likelihood.

[2]BWD = birth weight direct, WWD = weaning weight direct, PWGD = postweaning gain direct, BWM = birth weight maternal, WWM = weaning weight maternal; GP1, GP2, GP3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.

Table 3. REML[1] estimates of environmental correlations for growth traits using genomic-polygenic and polygenic models

	Environmental correlations							
Trait pair[2]	GP1	SD	GP2	SD	GP3	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

[1]Restricted maximum likelihood.
[2]BWE = birth weight environmental, WWE = weaning weight environmental, PWGE = postweaning gain environmental; GP1, GP2, GP3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.

Table 4. REML[1] estimates of phenotypic correlations for growth traits using genomic-polygenic and polygenic models

	Phenotypic correlations							
Trait pair[2]	GP1	SD	GP2	SD	GP3	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

[1]Restricted maximum likelihood.
[2]BWP = birth weight phenotypic, WWP = weaning weight phenotypic, PWGP = postweaning gain phenotypic; GP1, GP2, GP3 = genomic-polygenic models 1, 2, and 3; PM = polygenic model; SD = standard deviation of 5,000 samples.