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Breed-specific heterosis for growth and carcass traits in 18 U.S. cattle breeds

Bailey N. Engle,[1] Richard Mark Thallman, Warren M. Snelling, Tommy L. Wheeler, Steven D. Shackelford, David Andy King, and Larry A. Kuehn

USDA, ARS, U.S. Meat Animal Research Center, Clay Center, NE, USA

[1]Corresponding author: bailey.engle@usda.gov

Abstract

Heterosis, or hybrid vigor, is traditionally defined as the advantage of crossbred progeny relative to the average performance of their purebred parents. This advantage is due to increased heterozygosity in these crosses, which increases phenotypic expression in traits influenced by non-additive gene action. These heterosis effects may vary depending on the breed of animals in the original cross; however, breed-specific estimates are difficult to obtain because of a lack of contemporary comparisons among crossbred and purebred cattle. The Germplasm Evaluation Program at the U.S. Meat Animal Research Center was designed to evaluate 18 of the most highly utilized beef breeds in the United States and enable contemporary comparisons among purebreds and their crosses. Therefore, the primary objective of this study was to quantify the differences in breed-specific heterosis for growth and carcass traits in these 18 U.S. beef breeds. Specific traits analyzed were direct and maternal birth weight, direct and maternal 205d adjusted weaning weight, 365 d postweaning gain, marbling score, ribeye area, backfat thickness, and carcass weight. Specific heterosis effects were estimated using 2 different models: 1) a biological-group heterosis model where heterosis was estimated for crosses between British, Continental, and Brahman as breed groups, and 2) an average breed heterosis model where heterosis was estimated as the regression on average predicted breed heterozygosity arising from mating each of the 18 breeds to a randomly chosen animal in the population. Each model also included a random breed-specific cross-effect for each pair of breeds. Biological-group heterosis, or the expected deviations from a purebred mean between all crosses of British, Brahman, and Continental groups, was found for all traits ($P < 0.0001$), except marbling. The greatest increases in calf performance were estimated for crosses containing Brahman, especially for growth traits and maternal ability. Average breed-specific heterosis was also significant ($P < 0.05$) under the second model for all traits except marbling and maternal birth weight. Again, the greatest increase in calf performance across a majority of traits was found to be the result of crosses with Brahman. These estimates may be used by breeders to make more informed crossbreeding decisions and to tailor their choice of breeds to their specific production environment and breeding objectives.

Lay Summary

Heterosis, or hybrid vigor, is traditionally defined as the increase in the performance of crossbred progeny relative to the average performance of their purebred parents. These heterosis effects may vary depending on the breed of animals in the original cross; however, breed-specific estimates are difficult to obtain because of the resources required to estimate the effects. The Germplasm Evaluation Program at the U.S. Meat Animal Research Center is designed to evaluate crosses of 18 different prominent U.S. beef cattle breeds. This study estimated specific heterosis by breed group (British, Brahman, and Continental) as well as the average heterotic advantage of each of these 18 breeds. Results suggest strong hybrid vigor in Brahman crosses, as well as specific advantages of several other breeds. These results can be used by breeders to evaluate the relative advantages of different breeds in crossbreeding programs.

Key words: beef cattle, carcass, growth, heterosis

Abbreviations: AB, ancestral breed; ABH, average breed heterosis; AI, artificial insemination; AWWT, adjusted weaning weight; BGH, biological-group heterosis; BWT, birth weight; CWT, Carcass weight; ET, embryo transfer; FAT, fat thickness; GPE, Germplasm Evaluation program; MARB, marbling; PWG, postweaning gain; REA, rib eye area; USMARC, U.S. Meat Animal Research Center

Introduction

The benefits of heterosis on growth and carcass traits, particularly within crossbreeding systems, are well documented. Measured as the crossbred deviation from the expected purebred performance, heterosis is the consequence of non-additive gene action and has the potential to significantly affect phenotype within crossbred offspring. This has large implications within multibreed evaluations, where breed-specific differences need to be accurately considered, and in the development and implementation of crossbreeding systems, where differences in breed complementarity for a given trait are of interest. Understanding a breed's potential within a crossbreeding system, as well as any expected production gains from heterosis, is important for producers to be able to make informed decisions for their own herds.

The expression of heterosis is population-specific. Fundamentally, heterosis is the result of genomic heterozygosity and heterogeneity, resulting from divergent selection between parental lines or breeds (Legarra et al., 2023). This may be the result of natural selection and genetic drift in segregated populations, or the result of targeted selection in one population

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vs another for differing breeding objectives and environmental constraints. Genetic distance between species, lines, or breeds is predictive of the degree of expected heterosis in a cross (Legarra et al., 2023), as were differences in allele frequencies between parental populations (Wei et al., 1991). As genetic distance or differences in allele frequencies increase between parents, there is a greater expectation for heterosis in the crossbred offspring (Wei et al., 1991; Legarra et al., 2023). For example, domesticated cattle are represented by two divergent subspecies, *Bos taurus taurus* and *Bos taurus indicus*. Greater heterosis effects would therefore be expected between crosses of breeds representing each respective subspecies due to the high level of genetic divergence between them (Hiendleder et al., 2008). The degree of divergence or genetic differences between breeds will vary on a per-cross basis, so heterosis may only be observed among some breed-cross combinations (Peacock et al., 1982; Comerford et al., 1988b; DeRouen et al., 1992).

The expression of heterosis is also trait-specific, where traits and trait complexes will have variable degrees of influence from additive vs non-additive genetic variation, such as dominance (Bolormaa et al., 2015). Generally, heterosis is observed to have large effects on fitness traits such as health and reproduction (Merilä and Sheldon, 1999; Bunning et al., 2018), although in livestock, growth has also been found to be highly heterotic despite having a large additive component. Within beef cattle, heterosis has been previously found to significantly affect both growth and carcass phenotypes (Gregory et al., 1965, 1978; Koch et al., 1983; Williams et al., 2010; Elzo et al., 2012), 2 highly heritable trait complexes. Significant maternal heterotic effects have also been reported for a variety of growth traits, particularly prior to weaning (McDonald and Turner, 1972; Cundiff et al., 1974), but the effect of maternal heterosis on postweaning and carcass traits has consistently been found to be small or insignificant (Olson et al., 1978a, 1978b; Gregory et al., 1987; DeRouen et al., 1992). The majority of direct heterosis estimates in beef cattle are from the past (for example, Gregory et al., 1965, 1978; MacNeil et al., 1982; Frisch and O'Neill, 1998; Williams et al., 2010). Given that estimates of heterosis are specific to the precise population from which they were derived, there is still an ongoing need to investigate and report updated heterosis effects for economically relevant traits across multiple breeds and crosses.

The U.S. beef industry is typified by a diversity of production systems, and therefore a great diversity in the breeds and crosses utilized and available across the sector. The Germplasm Evaluation Program (GPE) herd at the U.S. Meat Animal Research Center (USMARC) was created to reflect the current breed composition of the national beef herd and is comprised of 18 of the most highly utilized beef breeds in the United States. Schiermiester et al. (2015) previously estimated heterosis among different breed groups (e.g., Continental breeds vs. British breeds) for birth, weaning, and yearling weights, and for breed-specific combinations between eight breeds in the GPE herd. However, due to an insufficient number of animals representing each breed cross and the general structure of the dataset at that time, heterosis effects for a majority of the breed-specific crosses were difficult to estimate. Subsequently, more purebred records have been added to the GPE dataset from animals comparably managed, alongside crossbred contemporaries. Additional years of crossbred data have also been included, increasing the representation of each breed cross in the dataset, and increasing power to estimate heterosis effects.

The objective of this study was to estimate breed-specific heterosis for a suite of growth and carcass traits for each of the 18 highly utilized breeds in the United States. We expect that dominance deviations change over time, reflecting the ongoing selection within these populations, and necessitating a contemporary update of heterosis expectations for each breed and trait.

Materials and Methods

Animals

Data for this study were obtained from the on-going USMARC GPE project. Animals were raised and managed following the USMARC standard operating procedures and Federation of Animal Science Societies guidelines (FASS, 2020), with ethics approval granted by the USMARC Animal Care and Use Committee.

Data included records from Cycles VII and VIII of the GPE project as well as more recent generations managed under a continuous evaluation protocol (Supplementary Figure 1). The majority of animals in Cycle VII-2 of the project were born between 1999 and 2000 (Figure 1). Sires from seven of the most influential breeds in the U.S. beef industry (Angus, Red Angus, Hereford, Charolais, Gelbvieh, Limousin, and Simmental) were bred via artificial insemination (AI) to USMARC base cows (Angus, Hereford, and MARC III composites [¼ Angus, ¼ Hereford, ¼ Pinzgauer, ¼ Red Poll]). F_1 bulls sired by the seven AI breeds and out of Angus and Hereford base cows were born in 2001 with a few additional F_1 bulls born in 2003 and 2005 to supplement underrepresented breed combinations. Additional Cycle VII-2 animals were produced from 2006 to 2007 to support genomics objectives while the overall design of GPE was being reevaluated (Figure 1). Animals in Cycle VII-3, collectively referred to as F_1^2, were produced by breeding Cycle VII-2 cows (mostly F_1s) to the VII-2 F_1 bulls, resulting in a mixture of 4-way cross, 3-way cross, F_2, and a few backcross progeny that were born between 2003 and2008 (Figure 1). Animals in Cycle VIII-2 of GPE were born in 2001 to 2002 (Figure 1) and sired by Angus, Hereford, Beefmaster, Brangus, Bonsmara, and Romsinuano AI bulls out of Angus and MARC III base cows. Animals descended from Bonsmara and Romosinuano bulls were removed from the data set because it would not have been feasible to estimate heterosis involving those breeds.

Since 2007, the GPE project has transitioned to a continuous evaluation approach (Figure 1). Currently, 18 of the most highly utilized breeds in the United States are evaluated via continuous sampling of the most influential sires of each breed and this new germplasm is introduced into the population via AI. For the recent GPE generations (since 2007), purebred AI sires were mated to purebred or crossbred dams to generate purebred and crossbred steers and heifers, and both purebred and F_1 bulls for use in natural-service matings to GPE cows (Figure 2). All parentage has been verified using SNP genotypes.

The foundation for continuous GPE was comprised of Cycle VII-2, VII-3, and VIII-2 cows supplemented with base cows of several breeds and composites. All AI-sired heifers and as many natural-service-sired heifers as necessary to achieve population size targets have been retained as replacement females. The remaining heifers have been finished for

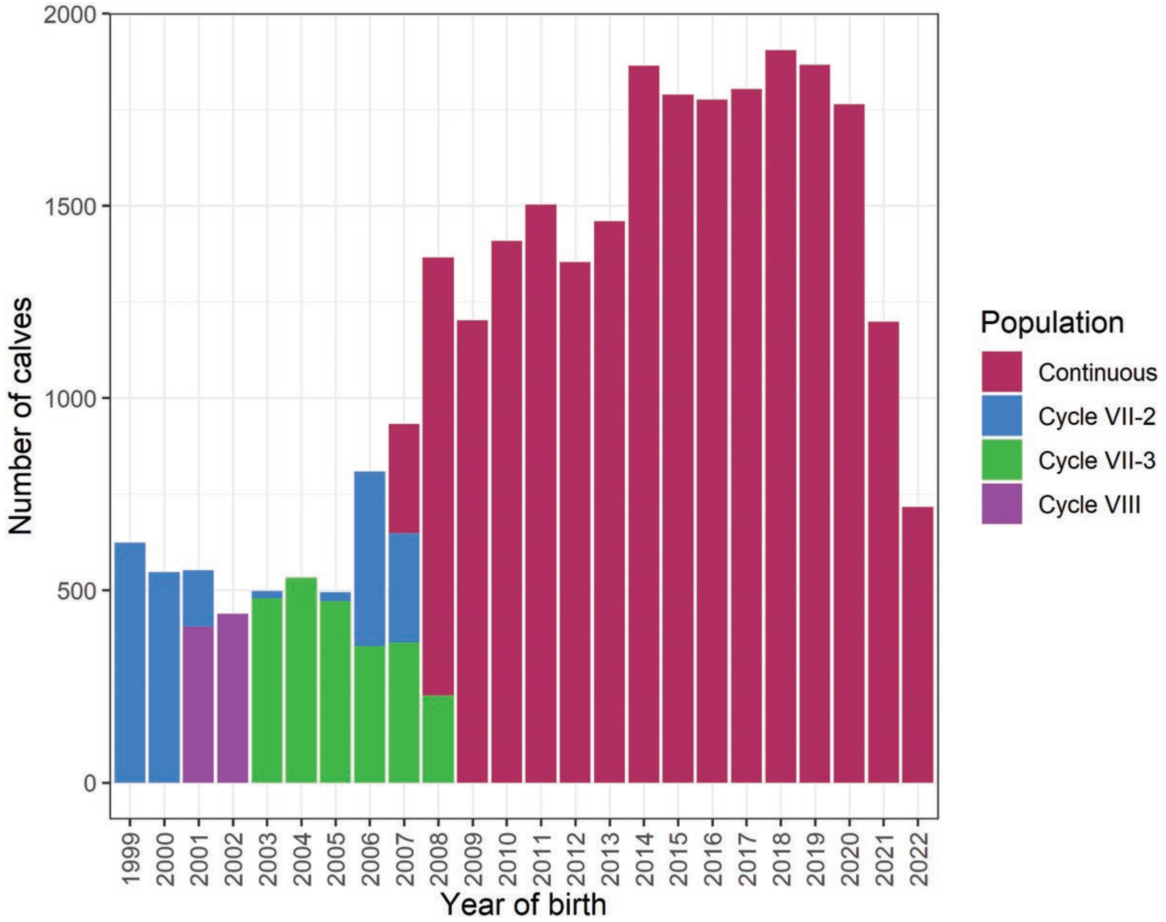

Figure 1. Distribution of the number of calves born to each population in the Germplasm Evaluation herd, by year.

harvest. Thus, the first few calf crops of GPE had approximately 50% contribution of base population genetics but the current population traces primarily to highly influential industry AI sires (Figure 3). The 18 breeds included the Cycle VII breeds and 11 others that conduct national cattle evaluations for beef production traits (South Devon, Shorthorn, Beefmaster, Brangus, Brahman, Santa Gertrudis, Braunvieh, ChiAngus, Maine-Anjou, Salers, and Tarentaise). Breeds more highly represented in the U.S. beef industry are more highly represented in GPE, although representation in GPE is more uniform than in industry (Figure 4). Although intentional crossbred matings were made alongside them, each of the 17 breeds (excluding Brahman) were graded up toward purebreds using AI (Supplementary Figure 2). Brahman was not graded up toward purebred because of concern that purebreds would not perform acceptably well in Nebraska winters. A group of multigeneration half-Brahman cattle is currently being bred instead of purebred Brahmans. The GPE program utilized a variety of breeding types, supporting the estimation of heterosis in a population of purebred and crossbred contemporaries.

Management

All cattle in Cycle VII and Cycle VIII of GPE were born in the spring calving season. Beginning in 2007, cattle in Continuous GPE were born in either spring or fall calving seasons (Figure 5). Although exact dates varied somewhat over the course of the project, spring calving generally occurred for about 60 d during March, April, and May and fall calving for about 45 d during August and September. The fall calving season was phased out beginning in 2019 and the last fall calves were born in 2021.

Most male calves were castrated at birth and managed to be finished for harvest in the USMARC feedlot. However, a small proportion were left uncastrated and developed for use as natural-service sires within the GPE project. Calves born as contemporaries remained together until weaning, at which time, bulls, steers, and heifers were separated into sex-specific management groups.

Traits

Heterosis was estimated for seven traits that are included in the national genetic evaluations of most or all of the 18 breeds included in GPE. Birth weight (BWT) was measured within 24 h of birth. Weaning weight was measured at an average age of 168 d. Adjusted weaning weight (AWWT) was the actual weaning weight adjusted to a constant 205 d of age according to the Beef Improvement Federation Guidelines (BIF, 2018). Cattle were typically weighed at least every 56 d during the period preceding and following 365 d of age. Weight at 365 d was predicted from a within-animal quadratic regression of weights collected at less than 500 d of age. Postweaning gain (PWG) was computed as the difference between predicted weight at 365 d and AWWT. A subset of the animals was finished for harvest and had the following traits collected during that process. Carcass weight (CWT)

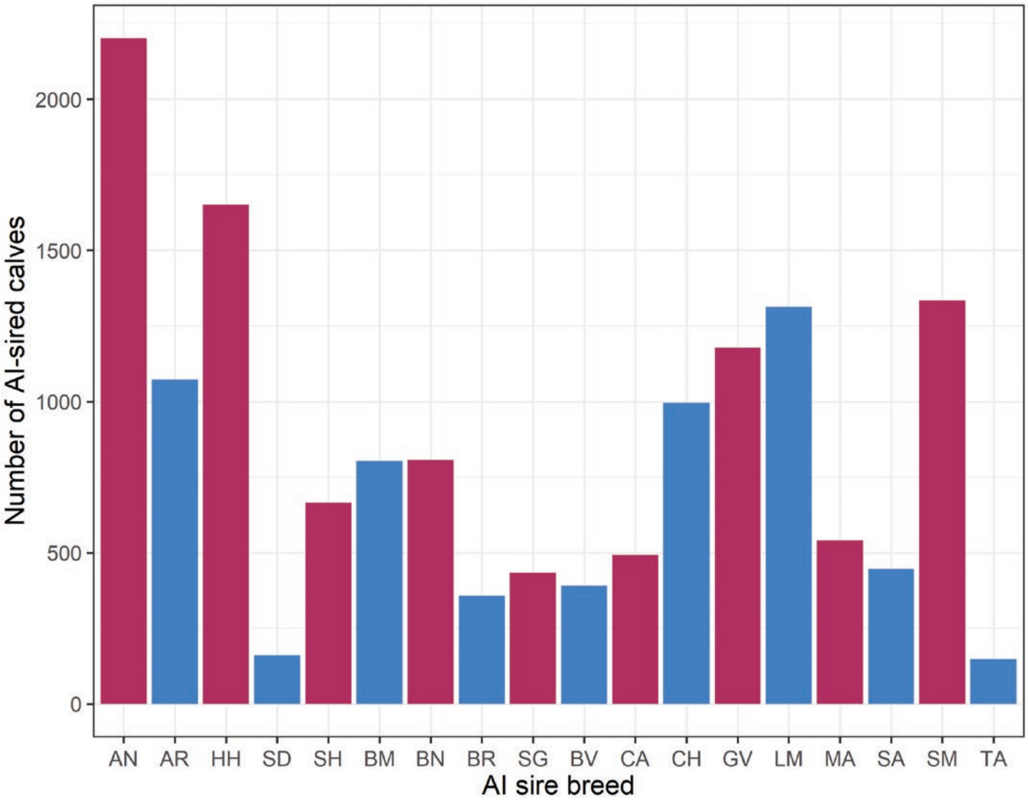

Figure 2. Number of artificial insemination-sired calves in the Germplasm Evaluation herd, by breed. AN, Angus; AR, Red Angus; HH, Hereford; SD, South Devon; SH, Shorthorn; BM, Beefmaster; BN, Brangus; BR, Brahman; SG, Santa Gertrudis; BV, Braunvieh; CA, ChiAngus; CH, Charolais; GV, Gelbvieh; LM, Limousin; MA, Maine-Anjou; SA, Salers; SM, Simmental; TA, Tarentaise.

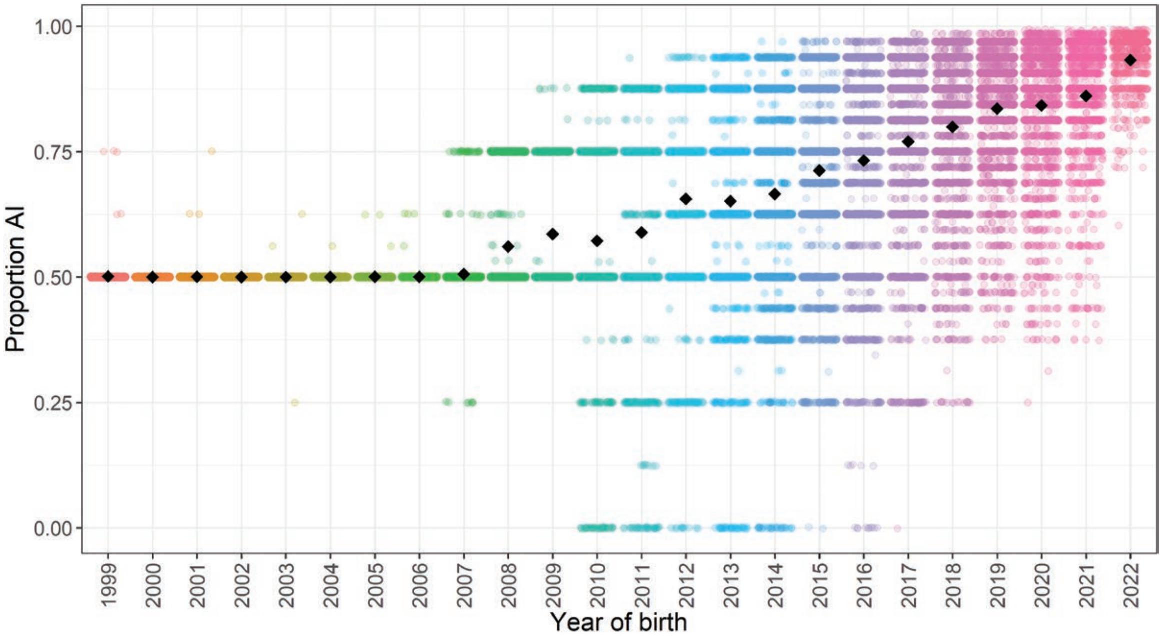

Figure 3. Distribution of the proportion of genetic contribution from artificial insemination (AI) sires in each animal of the Germplasm Evaluation herd, by year.

was collected automatically by the harvest facility. Marbling score (MARB), ribeye area (REA), and fat thickness (FAT) were collected by trained technicians in the earlier years and by the VBG 2000 camera grading system (Shackelford et al., 2003) in later years in harvest plants in which that system was used. Records from a total of 28,401 animals were used in the analysis. Table 1 provides the number of records and descriptive statistics for each trait.

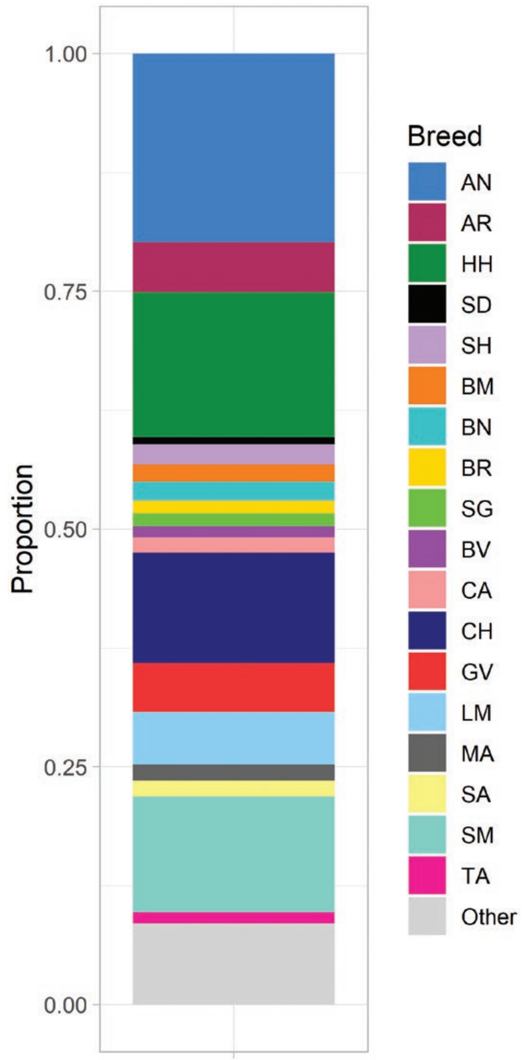

Figure 4. Distribution of breed representation in the Germplasm Evaluation herd. AN, Angus; AR, Red Angus; HH, Hereford; SD, South Devon; SH, Shorthorn; BM, Beefmaster; BN, Brangus; BR, Brahman; SG, Santa Gertrudis; BV, Braunvieh; CA, ChiAngus; CH, Charolais; GV, Gelbvieh; LM, Limousin; MA, Maine-Anjou; SA, Salers; SM, Simmental; TA, Tarentaise; Other, Red Poll, Pinzgauer, MARC II, MARC III.

Statistical analysis

All analyses were univariate and performed by ASREML-R version 4.2 (Butler et al., 2023). The significance of reported estimates was determined using a two-tailed *t*-test.

Non-genetic effects

The models for all traits included sex (bull, steer, or heifer) as a fixed effect. In the model for BWT, the levels of sex included only bulls and heifers. In the models for AWWT and PWG, steers were differentiated from bulls. Only steers and heifers had records for MARB, REA, FAT, and CWT. The models for BWT, AWWT, and PWG included a fixed contemporary group effect (same for all three traits) that was formed from the year and season of birth combined with age-of-dam class (2, 3, 4, 5 to 9, and 10+ years old; Table 1). A fixed linear regression on Julian birth date was fit in the models for BWT, AWWT, and PWG. The models for MARB, REA, FAT, and CWT included a fixed contemporary group effect comprised of slaughter date and a fixed linear regression on slaughter age. Some PWG, MARB, REA, FAT, and CWT contemporary groups were further divided based on treatments such as implants or feed additives that were evaluated in some years (Table 1).

Non-heterotic genetic effects

The models for all traits included 25 fixed covariates representing the contributions of each of the 25 genetic groups to estimate direct genetic group effects. The 25 genetic groups include AI sires of the 18 breeds listed above and seven groups of "base population" ancestors: Angus, Charolais, Hereford, Red Angus, Simmental, MARC II (25% Angus, 25% Hereford, 25% Simmental, and 25% Gelbvieh) and MARC III. The models for BWT and AWWT also included 25 similar genetic group covariates representing the genetic group contributions to the dam of the animal producing the data to estimate maternal genetic group effects.

The models for all traits included a random effect representing an individual's direct breeding value with a covariance structure determined by the numerator relationship matrix. The models for BWT and AWWT additionally included a random effect representing the (maternal) breeding value of the animal's dam, a random permanent environment uncorrelated residual effect of the dam, and the genetic covariance between direct and maternal breeding values.

Heterotic effects

Animals in this study are individually representative of numerous combinations of 25 "genetic groups" (Figure 6). For purposes of estimating heterosis, the 25 genetic groups were decomposed into the 16 ancestral breeds (AB) of which they are comprised (Figure 6). We define the term "ancestral breed" to represent a breed where mating members of two different AB results in progeny that express full heterosis (for that AB-pair) and mating two members of the same ancestral breed results in progeny that express zero heterosis. For example, Brangus cannot be an ancestral breed because a mating between two Brangus parents would result in Angus × Brahman heterosis.

AB were classified into three "biological groups" based on ancestral breed development and divergence (Magee et al., 2014): British, Continental, and Brahman (Figure 6). This approach and naming convention are in concordance with historical reporting of breed differences at USMARC (Smith et al., 1976; Wheeler et al., 1996; Schiermiester et al., 2015). Angus and Red Angus were treated as the same AB, so the British group was comprised of the Angus, Hereford, Red Poll, Shorthorn, and South Devon AB. The Brahman group was comprised only of the Brahman AB. The Continental group was comprised of the Braunvieh, Charolais, Chianina, Gelbvieh, Limousin, Maine Anjou, Pinzgauer, Salers, Simmental, and Tarentaise AB. The ChiAngus breed was assumed to be 1/5 Chianina and 4/5 Angus. The MARC II and MARC III composites were assumed to be comprised as described above. The Beefmaster breed was assumed to be ½ Brahman, ¼ Hereford, and ¼ Shorthorn. The Brangus and Santa Gertrudis breeds were each assumed to be 3/8 Brahman with the remaining 5/8 being Angus or Shorthorn, respectively. Recent genomic studies investigating the current breed composition of each of these American composite breeds suggest that over time the breeds have increasingly become more influenced by *B. taurus* haplotypes than their original compositions (Li et al., 2020, 2023; Paim et al., 2020b). However, in the current

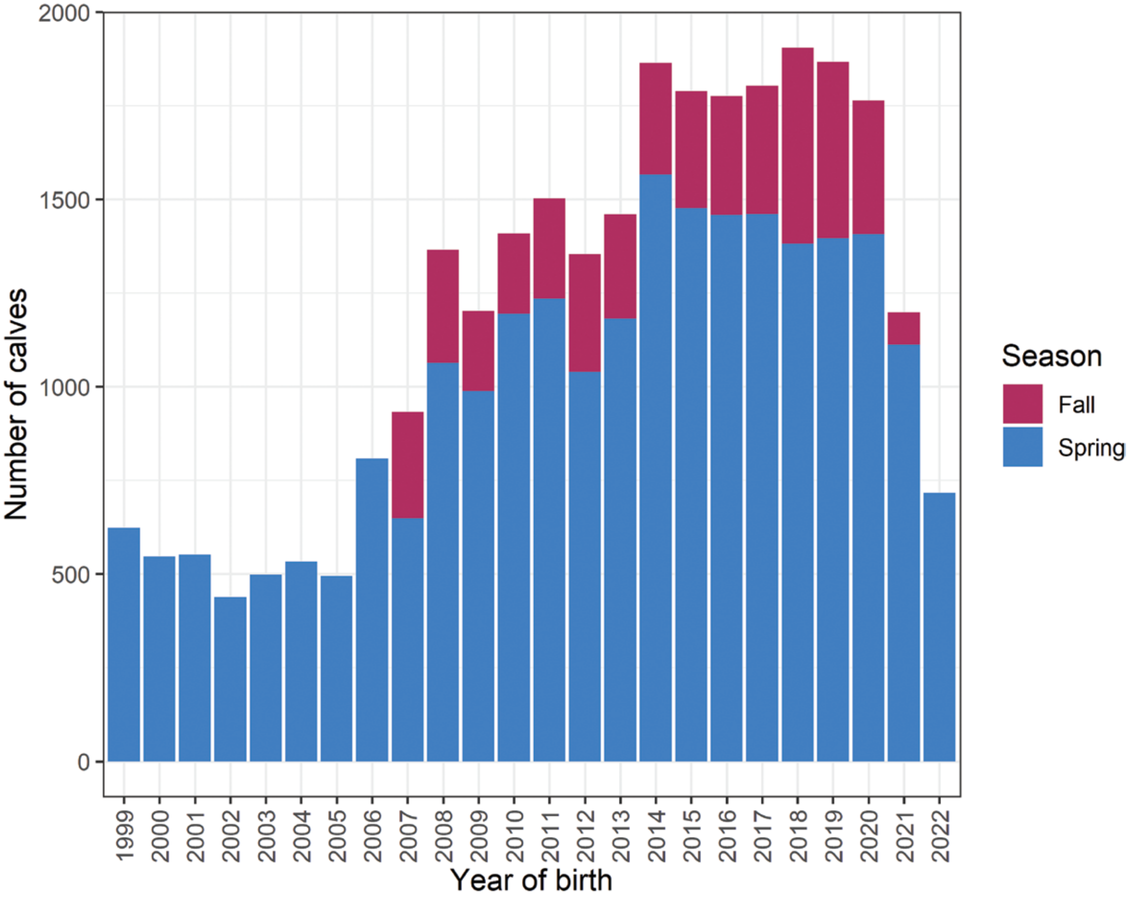

Figure 5. Distribution of spring and fall calving in the Germplasm Evaluation herd, by year.

Table 1. Descriptive statistics of each trait by sex

	Bulls		Heifers		Steers		
Trait[1]	*n*	mean	*n*	mean	*n*	mean	CG[2]
BWT, kg	14,523	42.8	13,878	39.6			159
AWWT, kg	602	266.6	13,116	240.6	12,867	256.9	159
PWG, kg	451	195.0	12,359	159.3	12,148	227.3	275
MARB[3]	0		3,506	5.240	11,268	5.124	159
REA, cm^2	0		3,512	85.74	11,282	86.31	159
FAT, mm	0		3,510	12.74	11,256	12.66	159
CWT, kg	0		3,515	345.3	11,296	384.1	159

[1] BWT, birth weight; AWWT, adjusted weaning weight; PWG, postweaning gain; MARB, marbling score; REA, rib eye area; FAT, fat thickness; CWT, carcass weight.

[2] Number of contemporary groups per trait.

[3] Marbling score units: 4.00 = Sl^{00}; 5.00 = Sm^{00}.

study, the original nominal breed compositions were assumed in each case for 2 reasons. First, the recent genomic reports were highly variable; for example, in Brangus, Crum et al. (2021) reported Angus content as high as 74.2%, whereas Li et al. (2023) removed Ultra Black animals from the analysis and reported genomic Angus content at 67.4%. Secondly, Crum et al. (2021) suggested that Brahman genome content has actually increased in advanced generations of these composite breeds, which is in contradiction to Paim et al. (2020a) who found that genomic regions under selection in Brangus were predominately of Angus origin and that the breed was becoming more taurine in its genomic composition. Sampling of these breeds in GPE has occurred over the past 24 yr, and in the absence of consensus in the literature about how these breeds have changed over time, a conservative approach using the original nominal breed proportions of each composite was preferred. The contribution of each composite for the biological-group assignments were based on the AB contributing to the composite, e.g., Beefmaster was assumed ½ Brahman and ½ British.

Two alternative approaches for fitting heterogeneous heterosis were applied in 2 separate analyses. The first was termed biological-group heterosis (BGH) and represents the expected heterosis for crosses between 2 different ABs, based on their biological group. In the BGH model, the heterosis due to different AB within each pair of the 3 biological groups was assumed different and estimated. The second was termed average breed heterosis (ABH) and was defined as the expected merit of a line or breed when randomly mated within the evaluated population at large, minus the weighted average of additive breed effects. In the ABH model, each of the 25 genetic groups was assumed to have a different level of heterosis across all other genetic groups and those were estimated. The details of each of these alternative models are described subsequently.

In both the BGH and ABH models, a random breed-specific heterosis effect was fit as follows: the AB composition of each parent was determined and, from that, a covariate representing the contribution of each parental pair of AB was formed, excluding those parental pairs comprised of the same AB (which would not contribute to heterosis).

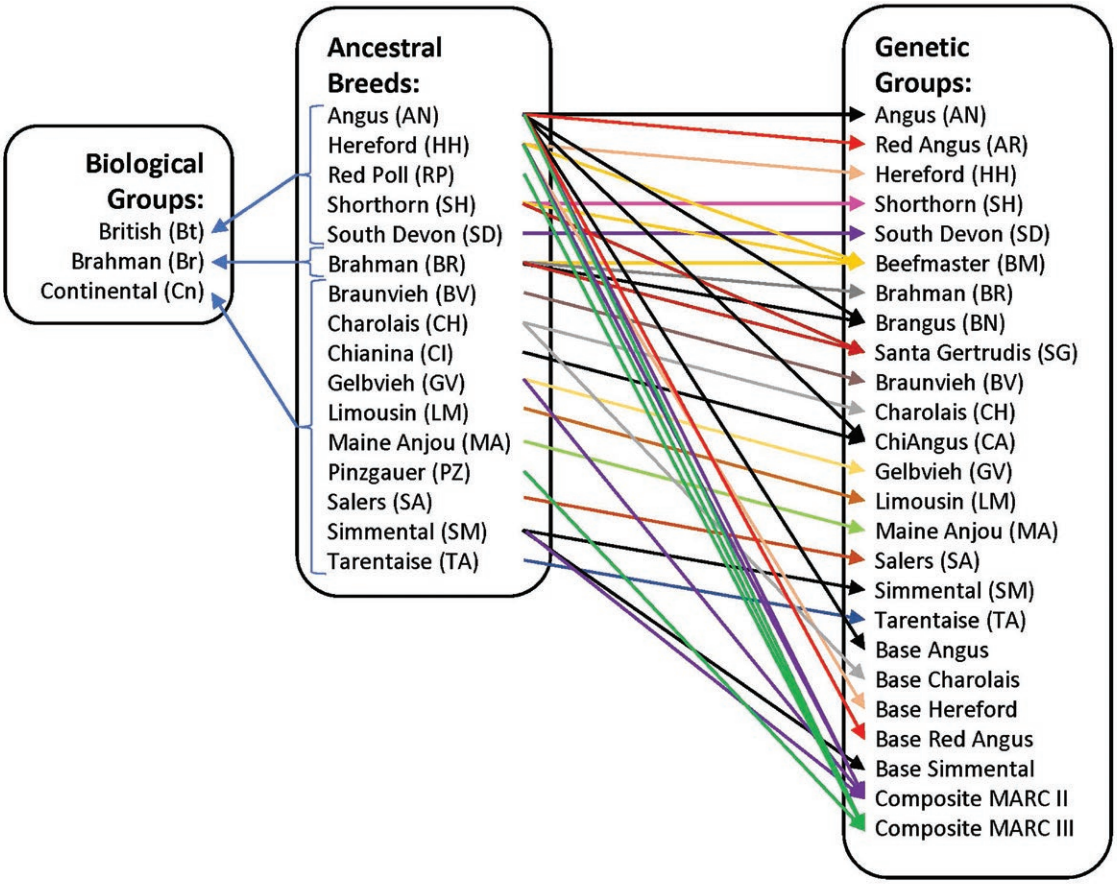

Figure 6. Relationship between genetic groups, decomposed ancestral breeds, and classification of biological groups.

Reciprocal cross pairs were combined into one covariate. Thus, $16 \times (16 - 1)/2 = 120$ pairs of AB were possible, and all were observed in the data.

Conceptually,

$$\mathbf{r}_{ij} = \mathbf{p}_i^{\mathrm{s}} \odot \mathbf{p}_j^{\mathrm{d}} + \mathbf{p}_j^{\mathrm{s}} \odot \mathbf{p}_i^{\mathrm{d}} \qquad \forall i < j$$

where i and $j > i$ are AB, $\mathbf{r}_{ij}$ is the random breed-specific heterosis covariate vector for AB-pair ij, $\mathbf{p}_i^{\mathrm{s}}$ is the vector of proportion of the sire of each animal that is comprised of AB i, $\mathbf{p}_j^{\mathrm{d}}$ is the vector of proportion of the dam of each animal that is comprised of AB j, and $\odot$ is the Hadamard (elementwise multiplication) operator.

For example, assume an animal's sire has AB composition 0.5 Angus, 0.5 Charolais, and its dam has AB composition 0.5 Angus, 0.25 Brahman, 0.25 Charolais. The resulting AB-pair covariates are: 0.25 Angus:Angus, 0.125 Angus:Brahman, 0.125 Angus:Charolais, 0.25 Charolais:Angus, 0.125 Charolais:Brahman, and 0.125 Charolais:Charolais. The AB-pair covariates sum to one before removing the same-AB pairs of 0.25 Angus:Angus and 0.125 Charolais:Charolais. The remaining AB-pairs sum to 0.625 (the overall breed heterozygosity value). AB-pair covariates are labeled with the ABs in alphabetical order: 0.125 is stored in the covariate labeled "Angus:Brahman", 0.375 = 0.125 + 0.25 is stored in the covariate labeled "Angus:Charolais", and 0.125 is stored in the covariate labeled "Brahman:Charolais". The other 117 = 120 − 3 covariates are zero for the row corresponding to this animal. These 120 covariates were fit as an independent and identically distributed random effect (with one common variance). The sum of the 120 covariates was equal to the AB heterozygosity covariate that is commonly used to estimate overall heterosis.

Biological-group heterosis effect

In the BGH model, the biological-group heterosis effects were fit as follows: the 120 pairs of AB were classified into British × British, British × Brahman, British × Continental, Brahman × Continental, and Continental × Continental biological-group pairs and summed within pair-to-form one covariate for each of the 5 biological-group pairs. The British × British and Continental × Continental pairs represented pairs of different British or Continental AB, respectively. Because the Brahman group comprised only the Brahman AB, there could be no heterosis to form a Brahman × Brahman group pair. This group of 5 covariates was fit as a fixed effect in the BGH model. Because there were no dependencies among the five covariates, their solutions directly estimated the heterosis of the corresponding biological-group pairs. The sum of the 5 covariates was equal to the AB heterozygosity covariate that is commonly used to estimate overall heterosis.

Conceptually,

$$\mathbf{b}_{kk} = \sum_{i \in \mathrm{B}_k} \sum_{j \in \mathrm{B}_k} \mathbf{r}_{ij} \delta_{i<j}$$

$$\mathbf{b}_{kl} = \sum_{i \in \mathrm{B}_k} \sum_{j \in \mathrm{B}_l} \mathbf{r}_{ij} \delta_{i<j} + \mathbf{r}_{ji} \delta_{i>j} \qquad \forall k < l$$

where k and $l > k$ are biological groups, $\mathbf{b}_{kl}$ is the biological-group heterosis covariate vector for biological-group pair kl, B_k is the set of AB in biological-group k, $\delta_x = 1$ if x is true or 0 if x is false, and $\mathbf{r}_{ij}$ is as previously defined.

ABH effect

In the ABH model, ABH was estimated as the regression on average predicted breed heterozygosity arising from mating each of the respective breeds to a randomly chosen animal in the population. The ABH effects of the 25 genetic groups were fitted as a group of 25 covariates designed to estimate the average breed-specific heterosis expressed by members of each of the genetic groups. The ABH covariates were computed as weighted sums of the 120 AB-pair covariates. For a given animal and genetic group, this weighted sum was computed as follows: the proportion of the animal's genome expected to have originated from this genetic group (genetic group covariate) is allocated among the ABs comprising the genetic group according to AB composition of the genetic group. For each AB, the sum of the AB-pair covariates that included 0AB as a member of the pair is multiplied by the proportion of the genome expected to have originated from the AB and have been inherited through the genetic group. These values were then summed over the ABs comprising the genetic group. The resulting group of 25 covariates was fit as a fixed effect in the ABH model. Because there were no dependencies among the 25 covariates, their solutions directly estimated the ABH of the corresponding genetic groups. The sum of the 25 covariates was equal to the AB heterozygosity covariate that is commonly used to estimate overall heterosis. Of the 25 genetic groups, seven correspond to USMARC "base" populations (Supplementary Figure 1, Figure 1). Only estimates from the remaining 18 genetic groups are reported.

Conceptually,

$$\mathbf{a}_k = 0.5 \times \left[\sum_{j \in \mathrm{A}} (\mathbf{g}_k^{\mathrm{s}} \odot \mathbf{p}_j^{\mathrm{d}} + \mathbf{g}_k^{\mathrm{d}} \odot \mathbf{p}_j^{\mathrm{s}})(1 - \mathrm{c}_{jk}) \right]$$

where A is the set of AB, $\mathbf{a}_k$ is the ABH covariate vector for the genetic group k, c_{jk} is the proportion of the genetic group k that is comprised of AB j, $\mathbf{g}_k^{\mathrm{s(d)}}$ is the proportion of each animal's sire(dam) comprised of the genetic group k, and $\mathbf{p}_j^{\mathrm{d(s)}}$ is as previously defined. For genetic groups comprised of only one AB, c_{jk} is 1 for that ancestral breed and 0 for all others. For genetic groups corresponding to composites, c_{jk} is nonzero for the constituent breeds and 0 for all others.

Results

The fixed effects of sex, Julian birth date, and age at slaughter were significant for each trait (Table 2). The larger effect for PWG in steers versus bulls reflects the differences in feeding and development protocols between type cohorts at USMARC. Variance components and genetic parameters are reported from the BGH Model (Table 3) as they were nearly identical to estimates from the ABH Model. Additive breed effects are not reported. In this model, additive effects of the breed were not adjusted for AI-sire EPDs, biasing these estimates in comparison to those reported in the most recent Across Breed EPD Adjustment Factor release (Kuehn and Thallman, 2023) where sampling was considered.

Breed-specific heterosis

Breed-specific heterosis effects were estimated in both the BGH and ABH Models (Supplementary File 1). No breed-specific heterosis was observed in the ABH Model. However, significant ($P < 0.05$) effects were estimated for REA between Angus and Limousin (−1.88 ± 0.81 cm^2) in the BGH Model.

Biological-group heterosis

Modeling heterosis as heterogenous with respect to 5 pairs of biological groups was a highly significant ($P < 0.001$, results not shown) model effect for all seven traits evaluated, except for MARB.

Significant biological-group heterosis effects were estimated for each of the 4 direct and maternal preweaning traits evaluated (Table 4). Calf BWT was found to increase due to direct heterosis for British × Brahman, British × Continental, and Brahman × Continental crossbred calves ($P < 0.05$). Heterosis effects were also estimated to increase calf BWT from British × Continental cross cows ($P < 0.05$) due to maternal heterosis. All biological-group combinations benefited from a significant increase in AWWT due to direct heterosis. In comparison to any of the taurine × taurine crosses, Brahman × British and Brahman × Continental cross calves were, estimated to have a 24.5 and 19.5 kg advantage for AWWT, respectively. Increases of 22.7, 5.0, and 15.7 kg in calf AWWT due to maternal heterosis ($P < 0.05$) were observed

Table 2. Estimates of non-genetic fixed effects[1]

	Sex				
Trait[2]	Bull	Heifer	Steer	Julian birth date	Age at slaughter
BWT, kg	0.0 ± 0.00	−3.16 ± 0.07		0.07 ± 0.00	
AWWT, kg	0.0 ± 0.0	−22.6 ± 1.3	−6.7 ± 1.3	−0.12 ± 0.0	
PWG, kg	0.0 ± 0.0	−30.4 ± 2.0	31.1 ± 2.1	0.07 ± 0.0	
MARB[3]		0.000 ± 0.000	−0.136 ± 0.028		0.007 ± 0.000
REA, cm^2		0.00 ± 0.00	2.97 ± 0.36		0.05 ± 0.00
FAT, mm		0.00 ± 0.00	−0.02 ± 0.17		0.05 ± 0.00
CWT, kg		0.0 ± 0.0	40.6 ± 1.4		0.58 ± 0.0

[1] Estimates from the Biological-Group Heterosis model.

[2] BWT, birth weight; AWWT, adjusted weaning weight; PWG, postweaning gain; MARB, marbling score; REA, rib eye area; FAT, fat thickness; CWT, carcass weight.

[3] Marbling score units: 4.00 = Sl^{00}; 5.00 = Sm^{00}.

Table 3. Variance components and genetic parameter estimates

Component[1]	BWT[2], kg	AWWT[2], kg	PWG[2], kg	MARB[2,3]	REA[2], cm^2	FAT[2], mm	CWT[2], kg
Direct genetic effect	12.89 ± 0.75	156.3 ± 12.8	298.1 ± 16.0	0.297 ± 0.016	34.67 ± 2.13	0.77 ± 0.05	669.9 ± 37.3
Direct × maternal covariance	0.24 ± 0.36	−11.8 ± 9.0					
Maternal effect	1.57 ± 0.34	89.7 ± 12.2					
Maternal permanent environment (PE)	0.60 ± 0.24	136.3 ± 9.2					
Residual variance	14.52 ± 0.45	315.2 ± 8.3	634.8 ± 12.5	0.194 ± 0.01	36.28 ± 1.57	0.84 ± 0.04	467.6 ± 26.3
Direct h^2	0.43 ± 0.02	0.23 ± 0.02	0.32 ± 0.02	0.60 ± 0.03	0.49 ± 0.03	0.48 ± 0.03	0.59 ± 0.03
Maternal h^2	0.05 ± 0.01	0.13 ± 0.02					
Direct × maternal correlation	0.05 ± 0.08	−0.10 ± 0.07					
PE variance ratio	0.02 ± 0.01	0.20 ± 0.01					
Breed × breed heterosis	<0.00001	<0.00001	18.0 ± 8.5	<0.00001	1.56 ± 0.84	0.006 ± 0.009	2.8 ± 6.6
Breed × breed maternal heterosis	0.0008 ± 0.05	<0.00001					
Breed × breed heterosis[4]	<0.00001	<0.00001	8.7 ± 6.1	<0.00001	0.57 ± 0.58	0.003 ± 0.007	1.48 ± 5.9
Breed × breed maternal heterosis[4]	0.0367 ± 0.06	2.10 ± 2.69					

[1] Effect estimates from the Biological-Group Heterosis model.

[2] BWT, birth weight; AWWT, adjusted weaning weight; PWG, postweaning gain; MARB, marbling score; REA, rib eye area; FAT, fat thickness; CWT, carcass weight.

[3] Marbling score units: 4.00 = Sl^{00}; 5.00 = Sm^{00}.

[4] Random effect estimates from the Average Breed Heterosis model.

from British × Brahman, British × Continental, and Brahman × Continental cows, respectively.

Significant biological-group heterosis effects were observed for 4 of the 5 postweaning traits evaluated (Table 4). Crossbred calves produced from any of the biological-group crosses should result in significant increases in PWG, ranging from 3.8 to 23.2 kg depending on the cross. Crossbred calves are also expected to express heterosis for multiple carcass characteristics, with significant heterosis estimates for REA (except in the case of Continental × Continental cross), FAT, and CWT. British × Brahman crosses had the largest increase in expected performance due to heterosis, with an increase in REA of 5.61 cm^2, 0.70 mm increase in FAT, and a 39.6 kg increase in CWT over estimates from any other cross not including Brahman. These estimates were similar to those of Brahman × Continental, although estimates for the latter were slightly reduced. No heterosis was observed for MARB between any of the biological-group combinations.

Average breed heterosis

Modeling heterosis as ABH of 25 genetic groups was a highly significant ($P < 0.001$, results not shown) model effect for all 7 traits evaluated, except for MARB and the maternal ABH effects on BWT, which were not significant. The maternal ABH effect on AWWT was significant ($P < 0.01$, results not shown).

Significant ABH was estimated using the ABH model for a variety of breeds and traits (Table 5). There were no significant ABH estimates for any breeds for maternal birthweight, but breed differences for heterosis were observed for each of the other traits. For BWT, increases due to heterosis were estimated for crossbred calves from Brahman, Charolais, or Maine-Anjou crosses ($P < 0.05$). Red Angus-cross cows were also estimated to increase BWT due to maternal heterosis ($P < 0.05$). Increased calf AWWT was also found for seven breeds ($P < 0.05$), with estimates ranging from an increase of 7.0 kg in Charolais crosses to 52.9 and 49.9 kg in Beefmaster and Brahman crosses, respectively. Maternal heterotic advantages were found for Brahman and Gelbvieh, with increases in calf AWWT due to maternal crossbreeding ($P < 0.05$).

Significant heterosis was also estimated for multiple carcass characteristics (Table 5). Beefmaster crossbred calves were found to have the largest increase in PWG ($P < 0.05$), with an estimated ABH that was 10.5 kg greater than Brahman crosses, and 27.7 kg greater than any other significant breed estimate. The only significant ABH estimate for MARB was for Angus. Significant ABH for REA were estimated for Shorthorn, Brahman, and Limousin, although the ABH for Limousin was estimated to be negative, whereas the other 2 breeds were positive. Three out of five of the British breeds had significant ABH estimates for FAT, along with Beefmaster, Braunvieh, Limousin, and Maine-Anjou. The majority of crosses using the evaluated breeds were estimated to increase CWT in their crossbred offspring. Among estimates for CWT ($P < 0.05$), Brahman ABH was the highest, followed by Beefmaster. Significant CWT ABH for Angus, Red Angus, Hereford, Shorthorn, Braunvieh, Charolais, Gelbvieh, Maine-Anjou, and Simmental were also found. The only breeds with no significant ABH, and therefore no significant heterosis effects expected from crossbreeding with any given breed in the population, were South Devon, Brangus, Santa Gertrudis, ChiAngus, and Salers.

Discussion

Heritability

Estimates of both direct and maternal heritabilities were as expected. Previous work has estimated variance components for growth and carcass traits from multibreed subsets of the GPE herd using both models fitting fixed specific biological-group heterosis with random breed-specific heterosis for a subset of the current breeds and data (Schiermiester et al., 2015) and

Table 4. Estimates of biological-group heterosis[1]

Type[2]	BWT[3] kg	BWT Mat[3] kg	AWWT[3] kg	AWWT Mat[3] kg	PWG[3] kg	MARB[3,4]	REA[3] cm²	FAT[3] mm	CWT[3] kg
Bt × Bt	0.45 ± 0.30	0.33 ± 0.32	6.0 ± 1.4[a]	2.1 ± 1.9	4.0 ± 2.9	−0.037 ± 0.055	2.77 ± 0.97[a]	1.68 ± 0.35[a]	22.6 ± 2.8[a]
Bt × Br	2.91 ± 0.76[a]	0.18 ± 0.88	30.5 ± 3.8[a]	22.7 ± 5.4[a]	23.2 ± 5.5[a]	−0.253 ± 0.145	8.38 ± 1.93[a]	2.38 ± 0.85[a]	62.2 ± 7.0[a]
Bt × Cn	0.38 ± 0.19[a]	0.48 ± 0.21[a]	5.5 ± 0.9[a]	5.0 ± 1.3[a]	6.7 ± 1.6[a]	−0.038 ± 0.034	1.47 ± 0.51[a]	1.15 ± 0.21[a]	22.2 ± 1.7[a]
Br × Cn	1.88 ± 0.68[a]	−1.02 ± 0.86	25.5 ± 3.4[a]	15.7 ± 5.3[a]	19.9 ± 4.7[a]	−0.064 ± 0.133	6.81 ± 1.70[a]	2.42 ± 0.78[a]	56.6 ± 6.4[a]
Cn × Cn	0.42 ± 0.25	0.21 ± 0.30	4.0 ± 1.2[a]	2.6 ± 1.8	3.8 ± 1.9[a]	0.019 ± 0.047	0.05 ± 0.66	1.13 ± 0.28[a]	14.7 ± 2.3[a]

[1] Estimates from the Biological-Group Heterosis model.
[2] Bt, British; Cn, Continental; Br, Brahman.
[3] BWT, birth weight; Mat, maternal; AWWT, adjusted weaning weight; PWG, postweaning gain; MARB, marbling score; REA, rib eye area; FAT, fat thickness; CWT, carcass weight.
[4] Marbling score units: 4.00 = Sl^{00}; 5.00 = Sm^{00}.
[a] Signifies $P < 0.05$.

Table 5. Average breed heterosis estimates[1]

Breed[2]	BWT[3], kg	BWT Mat[3], kg	AWWT[3], kg	AWWT Mat[3], kg	PWG[3], kg	MARB[3,4]	REA[3], cm²	FAT[3], mm	CWT[3], kg
AN	−0.16 ± 0.55	1.24 ± 0.70	2.5 ± 2.7	3.3 ± 4.3	2.3 ± 3.8	−0.32 ± 0.10[a]	2.13 ± 1.32	2.16 ± 0.60[a]	32.0 ± 4.9[a]
AR	0.61 ± 0.68	1.55 ± 0.76[a]	8.2 ± 3.2[a]	0.1 ± 4.6	13.8 ± 4.6[a]	−0.17 ± 0.13	−0.30 ± 1.70	1.94 ± 0.78[a]	26.2 ± 6.4[a]
HH	0.82 ± 0.64	1.16 ± 0.84	8.7 ± 3.1[a]	6.6 ± 5.2	12.9 ± 4.4[a]	0.12 ± 0.12	2.26 ± 1.52	2.41 ± 0.70[a]	29.8 ± 5.7[a]
SD	−0.31 ± 1.32	0.64 ± 1.65	5.9 ± 6.5	3.4 ± 10.2	−12.9 ± 8.5	−0.08 ± 0.30	4.90 ± 3.73	−2.05 ± 1.76	−11.2 ± 14.7
SH	1.28 ± 0.76	−0.24 ± 0.91	9.6 ± 3.7[a]	7.4 ± 5.7	9.8 ± 5.3	−0.16 ± 0.15	7.21 ± 1.93[a]	0.43 ± 0.89	31.4 ± 7.3[a]
BM	2.05 ± 2.60	−2.22 ± 3.23	52.9 ± 12.7[a]	0.2 ± 19.7	41.8 ± 16.6[a]	−0.23 ± 0.51	−6.83 ± 6.27	10.05 ± 3.0[a]	85.2 ± 24.5[a]
BR	3.73 ± 1.41[a]	−1.76 ± 1.80	49.9 ± 7.3[a]	39.1 ± 11.2[a]	31.3 ± 9.2[a]	−0.18 ± 0.28	16.46 ± 3.40[a]	2.47 ± 1.61	99.6 ± 13.3[a]
BN	2.03 ± 1.66	−0.43 ± 2.02	1.0 ± 8.1	−9.1 ± 12.2	16.7 ± 11.5	−0.01 ± 0.35	7.37 ± 4.37	1.18 ± 2.05	25.9 ± 16.9
SG	1.08 ± 1.74	3.11 ± 2.04	5.3 ± 8.4	20.2 ± 12.4	−9.4 ± 11.7	−0.03 ± 0.35	5.74 ± 4.37	2.41 ± 2.04	26.2 ± 16.8
BV	0.03 ± 1.06	−0.54 ± 1.28	4.5 ± 5.2	7.9 ± 7.9	9.2 ± 7.1	0.37 ± 0.23	0.94 ± 2.87	4.32 ± 1.36[a]	46.4 ± 11.2[a]
CA	−0.30 ± 1.29	0.49 ± 1.54	12.0 ± 6.2	−11.0 ± 9.7	−3.1 ± 8.8	−0.43 ± 0.25	−0.00 ± 3.12	−0.59 ± 1.46	3.7 ± 12.0
CH	1.67 ± 0.67[a]	0.51 ± 0.81	7.0 ± 3.2[a]	3.9 ± 5.1	1.0 ± 4.8	0.02 ± 0.13	2.11 ± 1.73	1.03 ± 0.79	*22.7 ± 6.5*
GV	−0.60 ± 0.56	0.39 ± 0.66	1.1 ± 2.7	10.3 ± 4.1[a]	10.4 ± 4.0[a]	0.05 ± 0.11	0.00 ± 1.40	0.39 ± 0.63	*11.3 ± 5.2*
LM	−0.65 ± 0.52	0.34 ± 0.63	−1.6 ± 2.5	1.0 ± 4.0	9.8 ± 3.9[a]	−0.08 ± 0.10	−4.27 ± 1.35[a]	1.64 ± 0.61[a]	6.6 ± 5.0
MA	2.34 ± 0.84[a]	−0.39 ± 0.99	14.4 ± 4.0[a]	6.2 ± 6.2	14.1 ± 5.8[a]	0.08 ± 0.17	2.31 ± 2.16	2.42 ± 0.99[a]	37.2 ± 8.2[a]
SA	−1.08 ± 0.91	0.24 ± 1.05	1.3 ± 4.3	5.6 ± 6.4	−3.2 ± 6.1	0.05 ± 0.18	−2.26 ± 2.16	1.66 ± 1.05	14.2 ± 8.7
SM	0.71 ± 0.61	0.99 ± 0.79	5.2 ± 2.9	1.9 ± 4.9	2.2 ± 4.3	−0.20 ± 0.11	2.01 ± 1.47	0.04 ± 0.66	16.8 ± 5.5[a]
TA	−2.45 ± 1.29	1.26 ± 1.61	−8.0 ± 6.2	0.3 ± 9.9	−19.5 ± 8.0[a]	0.40 ± 0.31	5.11 ± 3.78	−0.68 ± 1.78	8.5 ± 14.8

[1] Estimates from the Average Breed Heterosis model.
[2] AN, Angus; AR, Red Angus; HH, Hereford; SD, South Devon; SH, Shorthorn; BM, Beefmaster; BR, Brahman; BN, Brangus; SG, Santa Gertrudis; BV, Braunvieh; CA, ChiAngus; CH, Charolais; GV, Gelbvieh; LM, Limousin; MA, Maine-Anjou; SA, Salers; SM, Simmental; TA, Tarentaise.
[3] BWT, birth weight; Mat, maternal; AWWT, adjusted weaning weight; PWG, postweaning gain; MARB, marbling score; REA, rib eye area; FAT, fat thickness; CWT, carcass weight.
[4] Marbling score units: 4.00 = Sl^{00}; 5.00 = Sm^{00}.
[a] Signifies $P < 0.05$.

with only overall heterosis effect across breeds (Ahlberg et al., 2016; Kuehn and Thallman, 2017; Upperman et al., 2020; Russell et al., 2023). Heritability estimates for BWT were found to range between 0.34 and 0.54 (Schiermiester et al., 2015; Ahlberg et al., 2016; Kuehn and Thallman, 2017; Russell et al., 2023), and maternal heritability for BWT of 0.15 (Ahlberg et al., 2016) and 0.05 (Schiermiester et al., 2015). Heritability estimates for AWWT have been reported to range from 0.17 to 0.22 (Schiermiester et al., 2015; Kuehn and Thallman, 2017), with a maternal AWWT heritability of 0.17 (Schiermiester et al., 2015). Estimates in this study were also comparable to the PWG heritability reported by Russell et al. (2023) of 0.38. Furthermore, current heritability estimates were well within the range of previous estimates for MARB (0.34 to 0.55), REA (0.47 to 0.55), FAT (0.42 to 0.52), and CWT (0.34 to 0.51; Kuehn and Thallman, 2017; Upperman et al., 2020). While the additive genetic contribution to each trait was not the focus of this study, these heritability comparisons demonstrate that the modeling approaches employed here to estimate heterosis did not partition total genetic variance significantly different from previous evaluations of this population.

Breed-specific heterosis

In this study, heterosis in specific breed-crosses was not found to deviate from zero in nearly any combination or either model. No breed-specific heterosis was observed in the ABH model, but direct heterosis was observed for a single trait between a single cross in the BGH model. This was similar to findings from Schiermiester et al. (2015), who found no significant heterosis for any breed-specific crosses. While these estimates were not informative for any given breed or specific cross, the absence of significant differences between the crosses indicated that estimates of biological-group heterosis and ABH were robust to the unequal breed representation in the study population.

Biological-group heterosis

Biological-group heterosis estimates represent potential dominance effects when crossing any breed from one biological group (British, Brahman, or Continental) with any other. Regardless of the biological-group combination, there appeared to be a positive, heterotic advantage to crossbreeding for AWWT (Williams et al., 2010; Schiermiester et al., 2015). Similarly, Franke et al. (2001) found heterosis effects for AWWT in all cross combinations between Angus, Brahman, Charolais, and Hereford (except Angus-Charolais), representing each of the three biological-group classes evaluated here. A universal crossbreeding advantage between biological-group crosses was also observed for the postweaning growth trait of CWT. A majority of crosses were also estimated to increase PWG and REA due to heterosis. This was comparable to reports of direct heterosis between all combinations of Angus, Charolais, and Brahman, representative breeds of each biological group, for both carcass weight (Peacock et al., 1979; DeRouen et al., 1992) and rib eye area (Peacock et al., 1979). Prior evaluations of the influence of biological-group heterosis for PWG had mixed results. Retallick et al. (2013) reported heterosis between Angus and Simmental (British × Continental) for residual body weight gain, whereas Peacock et al. (1982) only found significant effects between Brahman crosses for postweaning average daily gain. Williams et al. (2010) reported heterosis for PWG in all biological-group combinations except Continental × Zebu, which is contrary to the majority of the literature. This has particular implications in the finishing stage of production, where regardless of breed composition, crossbred cattle were more likely to harvest a heavier carcass and measure a larger rib eye area, with greater PWGs than their purebred contemporaries.

Crossbreeding is also expected to increase FAT (Gregory et al., 1978; Koch et al., 1983), which has a negative relationship with carcass yield grade. Brahman crosses demonstrated the greatest potential increase in external fat deposition, similar to previous findings (Peacock et al., 1982; DeRouen et al., 1992; Williams et al., 2010). Interestingly, biological-group heterosis was not found to contribute to expected crossbred deviations for MARB, in any combination. Increases in marbling due to heterosis had previously been reported between all biological-group combinations except Continental × Continental (Williams et al., 2010). Increased marbling or improved USDA quality grade in crosses between Brahman and Continental breeds (Charolais, Simmental, and Limousin) have also been found in multiple populations (Peacock et al., 1979, 1982; Comerford et al., 1988b). Regardless, the absence of biological-group heterosis effects for marbling has been reported (Koch et al., 1983), including crosses with Brahman (DeRouen et al., 1992; Elzo et al., 2012).

Maternal heterosis is the phenomenon where the crossbred dam's increase in productivity due to their own heterosis is directly attributed to increases in the performance of their offspring (e.g., as a result of increased milk production by the dam). Two traits were assessed for maternal heterosis, BWT and AWWT. In this study, British × Continental cross cows were found to increase the BWT of their progeny due to heterosis (similar to Williams et al., 2010), which could increase rates of dystocia. Increased maternal heterosis could be further compounded by an expected increase in BWT for British × Continental calves due to direct heterosis (Franke et al., 2001; Williams et al., 2010; Schiermiester et al., 2015). Along with the crosses containing Brahman, British × Continental crossbred cows were also estimated to raise heavier calves at weaning due to maternal heterosis (Franke et al., 2001; Williams et al., 2010). Unexpectedly, no maternal heterosis for AWWT was observed for British × British crosses, which has been previously reported (Cundiff et al., 1974; Olson et al., 1978b; Dearborn et al., 1987; Williams et al., 2010).

Crosses including Brahman were estimated to benefit the most from heterosis, particularly for growth-related traits: AWWT, PWG, REA, and CWT. This was unsurprising given the degree of divergence between the *B. indicus* Brahman and British or Continental *B. taurus* cattle (Hiendleder et al., 2008). Previous work in other populations also found that breed combinations containing Brahman had greater heterosis estimates for weaning weight (Comerford et al., 1988a; Franke et al., 2001), postweaning gain (Peacock et al., 1982), carcass weight (Peacock et al., 1979; Comerford et al., 1988b; DeRouen et al., 1992), and rib eye area (Peacock et al., 1982; DeRouen et al., 1992) than those between other breeds. Additionally, crossbred cows from these biological-group combinations were estimated to express the greatest maternal advantage for calf weaning weight. Franke et al. (2001) found a similar maternal advantage between Brahman × Hereford crosses, but not in Brahman crosses with either Charolais or Angus.

Heterosis in crosses among Brahman and *B. taurus* is not as simple as commonly modeled or assumed, and this is due to the potential for large reciprocal cross effects and sexual dimorphism in these crosses. Dillon et al. (2015) reported that Brahman-sired embryo transfer (ET) calves out of Simmental donor cows were 12.2 ± 1.4 and 6.5 ± 1.2 kg heavier at birth than Simmental-sired ET calves out of Brahman donor cows for male and female calves, respectively. Within the Brahman-sired F_1s, male calves weighed 5.0 ± 1.4 kg more than the females whereas within the Simmental-sired F_1s, the male calves weighed 0.7 ± 0.5 kg less than the females (Dillon et al., 2015). Reciprocal cross effects of similar magnitude and sexual dimorphism have long been recognized in non-ET F_1 calves with a Brahman parent (Cartwright et al., 1964; Ellis et al., 1965; Frisch and O'Neill, 1998) and have generally been interpreted as classical maternal effects, typically attributed to prenatal differences in the uterine environment. It is likely that such differences exist. However, the reciprocal birth weight differences in ET calves cannot be attributed to classical maternal effects because they were gestated in randomly assigned recipients, suggesting an additional large, non-mendelian mode of inheritance.

In an analysis of all eight possible reciprocal back-crosses between Brahman and Angus produced by ET, Amen et al. (2007a) reported sex-specific reciprocal back-cross effects and reciprocal-specific sex differences for BWT that could not be predicted from the estimates of the reciprocal F_1's. Amen et al. (2007b) showed that similar, but proportionally smaller, departures from standard expectations also occur for postweaning traits. Together, Dillon et al. (2015) and Amen et al. (2007a, 2007b) represent a major departure from expectations under the traditional (direct + maternal + heterosis effects) model. While there is evidence that X-chromosome and parental imprinting effects (Thallman et al., 2014) may contribute to the observed departures from expectations under the traditional model, many questions remain. Consequently, for some uses of heterosis between Brahman and *B. taurus*, it may not be satisfactory to have a single estimate of heterosis, averaged over sexes and reciprocal crosses, especially for BWT, where heterosis of Brahman-sired progeny from *B. taurus* dams is typically much larger than heterosis among *B. taurus* breeds.

In the GPE herd, no purebred Brahman cows were maintained at USMARC and all purebred Brahman influence was of paternal origin, via AI. The GPE herd included cows graded up to high percentages of Beefmaster, Brangus, and Santa Gertrudis, although it should be noted that there was a greater contribution of these Brahman-influenced breeds to the paternal side of GPE pedigrees than to the maternal side. The GPE project was designed to address any departures from expectations using genomic models with additional terms to estimate the effects of putative mechanisms. However, those models are well beyond the scope of the present study.

Average breed heterosis

In this study, ABH was used to demonstrate the expected differences in progeny performance from crosses made between a breed and any other, due to heterosis effects. This approach was inspired by estimates of general combining ability, which is defined as the expected merit of a line or breed when randomly mated within the evaluated population at large (Henderson, 1952), or the general performance of a breed or line within crossbred or hybrid combinations (Sprague and Tatum, 1942). In plant breeding, general combining ability refers to the ability of parents to combine for desirable effects, and the value of the parental genotypes is determined by the performance of the offspring (Fasahat et al., 2016). This interpretation of general combining ability takes into consideration the effects of both additivity and dominance.

In beef cattle breeding, this approach has been widely employed in the past to describe variation between cattle breeds (Damon et al., 1961; Comerford et al., 1988b; Rohrer et al., 1988). While the concept of general combining ability is useful, in this study, the approach was to keep the heterosis term separate from the additive breed effect term in the model. These ABH results can be applied in mating strategies to determine which breed may provide the largest hybrid advantage, on average. These parameters could be applied to decision support programs to help with breeding decisions based on both direct breed effects and each breed's heterosis.

Similar to patterns observed in estimates of heterosis, greater dominance effects were expected for growth traits, such as AWWT, PWG, and CWT (Damon et al., 1961; Comerford et al., 1988a, 1988b). This was corroborated in this study where many breeds were found to transmit dominance effects for growth to their crossbred offspring, regardless of the breed they were crossed with. This pattern was also observed for FAT, where many breeds were estimated to increase their crossbred offspring's potential for fat deposition (Comerford et al., 1988b).

Maternal ABH represents the potential increase in progeny performance from using a given breed to produce a crossbred cow, due to that cow's own direct heterosis effects. Only one out of the 18 breeds were estimated to increase BWT due to maternal influence. This was advantageous as it suggested that there would be minimal risk of significantly increasing birth weights due to heterosis expression in the dam. Brahman or Gelbvieh crossbred cows were estimated to increase calf weaning weights due to maternal ability, regardless of the other breed in the cross. Gelbvieh is in the top 2 breeds for average maternal milk (Kuehn and Thallman, 2023) which may contribute to this maternal estimate. These findings suggest that a component of the cow performance for this trait in Gelbvieh may be due to dominance effects. The ABH for direct AWWT in Gelbvieh was not significant, indicating that increases in expected calf AWWT in these crosses would likely be the result of improved maternal milking ability due to heterosis effects, versus breed differences for growth or size.

Due to the degree of divergence between Brahman and European cattle breeds (Hiendleder et al., 2008), it is unsurprising that Brahman parents were found to transmit large heterosis effects for many traits to their crossbred offspring. In this study, Brahman was the only *B. indicus* breed represented in the dataset. Therefore, all potential crosses were with individuals from different subspecies, increasing the potential for and potential magnitude of any dominance effects. If assessed in crosses with other *B. indicus*, the ABH estimates would likely be reduced, as fewer dominance effects would be expected between crosses with Brahman and other indicus breeds. Estimates of increased growth were also observed for Beefmaster, but not the other indicus-influenced composites, Brangus and Santa Gertrudis. The nominal composition of founder breeds in Beefmaster included 50% Brahman influence, in comparison to the other composites, which were majority *B. taurus* origin. Differences in the degree of *B. indicus* haplotype introgression and influence in each breed may help to explain these between-breed differences for ABH. Additionally, Beefmaster was the only composite to include Hereford among its founding breeds, which may increase its divergence from other breeds as well. Beefmaster crosses were estimated to increase both AWWT and PWG above that of Brahman and to increase FAT where Brahman-crosses were not. Hereford-crosses, on the other hand, were also found to increase PWG and FAT. The influence of Hereford haplotypes in Beefmaster may also be contributing to these differences in ABH estimates.

Similar to heterosis, not all ABH are advantageous. Increased expectations for BWT and FAT in crossbred calves are 2 examples that may need to be addressed with increased or more careful management. Additionally, there may be instances were decreased productivity could result from heterosis, such as the case with Tarentaise for PWG. Tarentaise was one of the lightest weight breeds contributing to the population (Kuehn and Thallman, 2023), although this does not explain breed differences for heterosis. It is also one of the proportionally lowliest represented breeds in the population, which may be influencing the relatively large standard error of this estimate, despite it being significantly different from zero. The ABH for Limousin suggested that crossing would result in reduced REA in their crossbred offspring. However, Limousin measured the largest average REA among all evaluated breeds (Kuehn and Thallman, 2023), and therefore it is likely that despite the negative estimate, other breeds can still be crossed with Limousin without an expected reduction in REA due to additive genetics differences between breeds. This may also be the case for the negative ABH for MARB in Angus. On average, Angus is the highest marbling among all breeds evaluated in GPE (Kuehn and Thallman, 2023). Therefore, crosses with Angus should be unlikely to harvest lower marbling carcasses due to the additive genetic advantage of the trait. There may also be non-linearities in the heterosis effect for this high marbling breed, perhaps reflecting the enhanced selection intensity for this trait in Angus (Weaber, 2010).

This study aimed to produce useful estimates of heterosis that reflect the diversity of breeds most highly represented in the U.S. beef industry. The GPE Program was designed to estimate both additive genetic effects and heterosis and has a long history of estimating breed effects, including on a point-in-time basis and accounting for the random sampling differences in the AI sires chosen to represent each breed (Kuehn and Thallman, 2023). As the current iteration of the program has developed and matured, the contributions of influential and representative AI sires of each breed have also increased. These sires were carefully selected to capture the current genetic variation and averages of each breed, and therefore the national herd at large. In leveraging this population as it was designed, this study reports contemporary heterosis estimates that are expected to reflect each breed as it exists today. The results of this study reaffirmed the value of heterosis in crossbreeding systems and demonstrated the importance of considering biologically specific heterosis effects to predict the performance of crossbred animals. Furthermore, prediction of future performance within this and other crossbred populations should likely include the prediction of additive breed effects, biologically specific heterosis, as well as within-breed breeding values of potential parents.

Conclusions

In this study, ABH and biological-group heterosis were estimated for 18 highly influential breeds in the U.S. beef industry. Biological-group heterosis, or the expected deviations from a purebred mean between all crosses of British, Brahman, and Continental breed groupings, was found for all traits except for marbling. The greatest increases in calf performance were estimated for crosses containing Brahman, in particular for growth traits and maternal ability. ABH estimated breed-specific differences in crossbred progeny performance, regardless of the other breed in the cross. Significant ABH was estimated for all traits. Again, the greatest increase in calf performance across a majority of traits was estimated to be the result of crosses with Brahman. These estimates may be used by breeders to make more informed crossbreeding decisions and to tailor their choice of breeds to their specific production environment and breeding objectives.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

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Conflict of interest statement

The authors declare no conflicts of interest.

Author Contributions

Bailey Engle (Conceptualization, Methodology, Visualization, Writing—original draft, Writing—review & editing), Richard Mark Thallman (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing—original draft, Writing—review & editing), Warren Snelling (Conceptualization, Data curation, Methodology, Writing—review & editing), Tommy Wheeler (Data curation, Writing—review & editing), Steven D. Shackelford (Data curation, Writing—review & editing), David Andy King (Data curation, Writing—review & editing), and Larry Kuehn (Conceptualization, Data curation, Methodology, Project administration, Writing—review & editing)

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