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Estimation of Breed-Specific Heterosis Effects for Birth, Weaning and Yearling Weight in Cattle

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ESTIMATION OF BREED-SPECIFIC HETEROSIS EFFECTS FOR BIRTH,
WEANING AND YEARLING WEIGHT IN CATTLE.

By

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A THESIS

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ESTIMATION OF BREED-SPECIFIC HETEROSIS EFFECTS FOR BIRTH,
WEANING AND YEARLING WEIGHT IN CATTLE.

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University of Nebraska, 2014

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Genetic selection decisions are important components of improved beef production efficiency. Exploiting heterosis and breed complementarity can improve economically relevant traits and system efficiency. The objective of the current study was to estimate breed-specific heterosis for the seven largest beef breeds (according to registrations) for birth, weaning and yearling weight.

Birth, weaning and yearling weights were recorded for steers, heifers and bulls (n= 6,834) from Cycle VII and advanced generations of the Germ Plasm Evaluation project of the U.S. Meat Animal Research Center. Breeds represented in these data included: Angus, Hereford, Red Angus, Charolais, Gelbvieh, Simmental, Limousin and composite MARC III. Model 1 estimated heterosis assuming different levels within and between biological types (British or Continental). Model 2 estimated breed-specific heterosis (a different level of heterosis for each pair of breeds). Heterosis was assumed proportional to expected breed heterozygosity.

Direct heritability estimates (SE) for birth, weaning and yearling weight for Model 1 were 0.42 (0.04), 0.22 (0.03) and 0.39 (0.05), respectively. The direct heritability estimates (SE) for Model 2 were the same as Model 1 except yearling weight heritability was 0.38 (0.05). There were differences in levels of heterosis based on

biological type (Model 1) and breed (Model 2). Model 1 results for the British x British (BxB), British x Continental (BxC) and Continental x Continental (CxC) heterosis estimates for birth weight were 0.47 (0.37), 0.75 (0.32) and 0.73 (0.54) kg, respectively. The BxB, BxC and CxC heterosis estimates for weaning weight were 6.43 (1.80), 8.65 (1.54) and 5.86 (2.57) kg, respectively. Yearling weight estimates for BxB, BxC and CxC heterosis were 17.59(3.06), 13.88 (2.63) and 9.12 (4.34) kg, respectively.

Breed differences exist and can lead to varying levels of heterosis. Specific estimates of heterosis could be useful when selecting breeds for a crossbreeding system and developing composite populations for various production environments and could be useful in multibreed evaluations as heterosis and breed differences are needed to accurately adjust records to produce genetic predictions.

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Introduction

Maximum profitability, in a sustainable manner, should be the single goal of beef cattle enterprises. To achieve this goal, all available resources should be utilized to optimize beef cattle breeding systems. Maximizing efficiency of beef production is of critical importance to the Beef Industry. The world population is expected to grow to nine billion people by 2050 (UN Dept. of Economic and Social Affairs, 2008). By 2020, not only will the global population be increasing rapidly, population shifts will add 1.8 billion people to the middle class (Kharas, 2010). Due to the increase in social rank and income, demand for higher quality food and protein will increase. Globally, meat consumption is expected to double by 2020 due to the increase in the middle class (FAO, 2002). However, the USDA cattle inventory report (2014) reported that all cattle and calves in the United States as of January 1, 2014 totaled 87.7 million head, the lowest January 1 inventory of all cattle and calves since 1951 (82.1 million). Much of the decreasing cowherd can be attributed to the drought and decrease in pasture availability. Meeting the demands of a growing population and a protein hungry middle class will require the use of technologies and strategies to increase the production of beef. Genetic improvements will provide a way for beef producers to realize increased efficiency. Heterosis and breed complementary offer a means to achieve greater system efficiency, when utilized correctly, when considering the suite of traits (e.g., reproduction and growth) that could impact overall system efficiency the most within the cowherd. Heterosis is defined as the genetic superiority of the crossbred individual relative to the average of the purebred parental breeds involved in the cross and has

been demonstrated to increase production efficiency in the cowherd and feed yard.

Individual and maternal heterosis are of particular interest to breeders as they both contribute to system efficiency. Research has shown through time that heterosis, when employed correctly, can increase the overall profitability of commercial cow/calf enterprises. Heterosis achieved through crossbreeding can be used to increase calf weaning weight per cow exposed by upwards of 20% (Gregory and Cundiff, 1980). The advantages of individual and maternal heterosis are summarized in Tables 1 and 2, respectively.

Crossing breeds that are more divergent generates increased levels of heterosis as compared to crossing breeds that are more closely related. Thus, *Bos taurus* X *Bos indicus* crosses offer a greater amount of heterosis as compared to *Bos taurus* X *Bos taurus* crosses. To take advantage of breed complementarity, breeds that excel in different areas that lead to profitability should be matched to attain production goals and to match genetic potential with markets, feed resources and climates (Cundiff et al., 1998). The primary benefits of heterosis are found within the cowherd based upon traits that lead to improved fertility, longevity and survivability. Heterosis also benefits weight traits.

Despite these advantages, only 45% of commercial producers classify their cowherd as “crossbred” according to the USDA’s 2008 National Animal Health Monitoring System (NAHMS). Questions remain and debate persists within the industry over the issue of crossbreeding and utilizing breed differences (Speer, 2011). No single breed excels in all traits that lead to profitability, so breed differences and

complementarity hold value in matching breeds to achieve specific production goals.

The objective of crossbreeding is to optimize simultaneously the use of nonadditive (heterosis) and additive (breed differences) effects of genes (Gregory and Cundiff, 1980).

Specific crossbreeding systems allow producers the capability to optimize production goals, environmental fitness, and resources to develop a sustainable and economically feasible system for their operation. Breed specific estimates of heterosis are not widely available in the literature and would be useful to refine breeding schemes to maximize the benefits of heterosis and breed complementarity.

The objective of the current study was to evaluate breed-specific heterosis and breed effects on growth traits. This has the potential to enable producers to evaluate and select different breeds to utilize in a crossbreeding system to achieve specific production goals. Additionally, these estimates could provide more precise estimates of heterosis for multibreed genetic evaluations.

Literature Review

Genetic Basis of Heterosis

Breed differences present the opportunity for utilization of a combination of different genetic resources to achieve greater efficiency. Comprehensive programs of breed characterization have revealed large differences among breeds for most bio-economic traits (Gregory et al., 1982; Cundiff et al., 1986). Using breeds with similar performance characteristics restricts the gains that can be achieved by exploiting breed differences in genetic merit to meet market and production requirements (Gregory and Cundiff, 1980). Diversity among different breeds provides a basis for achieving and maintaining optimum additive genetic composition (Gregory et al., 1991a,b,c).

The genetic basis of heterosis is centered on dominance and epistatic effects resulting in increased performance. Gregory et al. (1991a,b,c) concluded that heterosis is primarily due to dominance effects, which models the retention of heterosis proportionate to breed heterozygosity. Retention of initial F_1 heterozygosity after crossing and subsequent random (*inter se*) mating within the F_1 population is proportional to $(n-1)/n$ when n breeds contribute equally to the foundation (Wright, 1922; Dickerson, 1969, 1973). When the breeds used do not contribute equally to the population, retained heterosis is proportional to $1 - \sum_i^n P_i^2$, where P_i is the fraction of each contributing breed to the composite (Dickerson, 1973). Loss of heterozygosity occurs between the F_1 and F_2 generations. If inbreeding is avoided, further loss of heterozygosity does not occur in subsequent generations (Wright, 1922; Dickerson,

1969, 1973). Studies performed at the U.S. Meat Animal Research Center (USMARC) have detailed the results of heterosis effects and the resulting retained heterosis. Heterosis retained in combined F₃ and F₄ generations was significantly greater than genetic expectation based on retained heterozygosity for birth weight and for 368-d weight, but did not differ ($P > 0.05$) from genetic expectation for other traits (Gregory et al., 1991c). The proportion of retained heterosis was not less than the proportion of retained heterozygosity in rotational crossbreeding (Gregory and Cundiff, 1980). Koch et al. (1985) compared *inter se* mated F₃ versus F₁ populations of Hereford X Angus crosses and found that retained heterosis was greater than expected based on expected heterozygosity for growth related traits (postweaning gain, final weight, carcass weight, and ribeye area). Retained heterosis was equal to expectations for day born, birth weight, calving ease, preweaning gain, weaning weight and fat thickness but less than expected for survival rate, pregnancy rate and marbling (Koch et al., 1985).

Competing Models of Heterosis

The previously described model omits the contributions of epistasis to heterosis. Arthur et al. (1999) and Fries et al. (2000) suggested that epistatic loss could be added to the additive-dominance model to provide a better explanation relative to the genetic differences between animals of varying breed compositions. Sheridan (1981) also indicated that the dominance and epistatic effect theories are not mutually exclusive and could be due to a combination of those effects in any proportion. Epistatic loss in crossbred animals is the breakdown of favorable inter-loci allelic interactions in purebred animals (Roso et al., 2004). Roso et al. (2004) suggested that epistatic effects

can be either favorable or unfavorable depending on the genetic selection of the breed and the correlations among traits. Sheridan (1981) noted two forms of epistasis as contributing to lower or greater levels of retained heterosis past the first cross. The two forms of epistatic heterosis are defined as: F_1 epistasis attributed to complementary genes, and parental epistasis, which can be due to complementary and duplicate genes (Sheridan, 1981). F_1 epistasis occurs from different genes from the two parent lines interacting together in the crossbred while parental epistasis is attributed to different homozygous epistatic gene combinations present in the parental lines being passed to the crossbred animal (Sheridan, 1981). By incorporating these two forms of epistasis into the modeling of retained heterosis the expected levels due to parental epistasis vary greatly due to duplicate genes, which leads to greater than expected heterosis, or the reverse with complementary genes (Sheridan, 1981). Koch et al. (1985) noted that Sheridan's 1981 review of parental epistasis emphasized differences among traits and species as well as a need for more adequate experimental evidence. The loss of heterosis in progeny from crossbred parents could be extreme relative to the corresponding reduction in heterozygosity (Koch et al., 1985). Koch et al. (1985) reported that adding epistatic parameters did not increase the accuracy in predicting observed variation among mating types for the dominance model.

The theory of recombination loss is defined by the breakup of epistatic effects during meiosis to form non-parental inter-loci combinations of alleles in gametes of crossbred parents (Dickerson, 1973). The term "recombination loss" was introduced by Dickerson (1973) to measure deviations from linear association of heterosis with the

degree of heterozygosity. It describes the average fraction of independently segregating pairs of loci in gametes from both parents, which are expected to be non-parental combinations. Recombination loss is defined as including additive x additive effects only (Dickerson, 1973). If recombination loss is important, then composites would have less advantage in performance over the parent breeds and the justification of composites would be upon the need for rapid change in combinations of traits (Koch et al., 1985). Dickerson (1973) noted that the recombination parameters measure deviations from linear association of heterosis with degree of heterozygosity. The coefficient of r^l describes the average fraction of independently segregating pairs of loci in gametes from both parents which are expected to be non-parental combinations. The recombination coefficients consider loss relative to the total loss of parental epistatic superiority. Koch et al. (1985) indicated that the recombination coefficient is zero for the F_1 's and then increases to $\frac{1}{2}$ for a backcross and 1 for F_2 and F_3 . Koch et al. (1985) also reported that epistatic effects might be important for some traits in beef cattle causing heterosis retention in the F_3 population to differ significantly from the expected retention of $\frac{1}{2}$ for purely dominant action. Dickerson (1973) discussed the various crossbreeding systems fitting with recombination loss and noted that rotational crossbreeding requires only male replacements from purebred matings and utilizes a high proportion of potential heterozygosity with low recombination effects because only the female parents produce recombinant gametes and that the disadvantage of this is that there is less uniformity between generations and less opportunity for adaptation to particular environments. If using males from a superior sire breed on

rotational females selected for maternal type traits, all of individual and most of the maternal heterosis can be utilized with little effect from recombination (Dickerson, 1973). Dickerson (1973) reported that composites are subject to maximum recombination effects and do not allow for different genotypes for male and female parents. Thus, crossbreeding would have the advantage over composites if epistatic superiority is significant.

Heterosis in Various Crossbreeding Systems

Gregory and Cundiff (1980) described crossbreeding systems and evaluated the retention of heterosis resulting from the particular system utilized. Rotational crossbreeding takes advantage of using heterosis in all females and progeny in a self-contained commercial herd (Gregory and Cundiff, 1980). The fluctuation that results between generations in rotational crossbreeding requires the use of breeds that are similar in type restricting the ability to optimize breed complementarity (Gregory and Cundiff, 1980). The rotational system allows for maternal and individual heterosis to be utilized while the terminal cross exploits breed differences and maximizes individual heterosis (Gregory and Cundiff, 1980). The static terminal system does not use heterosis in all animals and rotational terminal systems do not use all maternal heterosis in either component (Gregory and Cundiff, 1980). Ritchie and others (1999) summarized the benefits of multiple crossbreeding systems and the amount of retained heterosis achieved under each system (Table 3). In a two-breed terminal system the F_1 offspring benefit from 100% of the individual heterosis. In a three-breed terminal

system F_1 females are mated to a purebred bull for the production of terminal offspring. Both Individual heterosis and maternal heterosis are maximized in this system (Gregory and Cundiff, 1980). In a two-breed rotation, each succeeding generation of replacement heifers is mated to the opposite breed of their sire. The three-breed rotational system realizes a higher level of retained heterosis than the two-breed rotational system does (Ritchie et al., 1999), but can be far more cumbersome in practice. In this system, cow groups are mated to bulls of the breed that represents the smallest fraction of the cow's breed makeup (Ritchie et al., 1999).

The utilization of composite seedstock animals based on multibreed evaluations is an appealing alternative to producers with small herd sizes wanting to utilize heterosis. Farms with fewer than 100 beef cows accounted for 90.4 percent of all U.S. farms with beef cows and 45.9 percent of all U.S. beef cows (NASS Census of Agriculture, 2008). Composite breeds have been proposed as an alternative for crossbreeding to achieve more optimum additive genetic composition (Dickerson, 1969,1973). The management problems associated with small herd sizes and fluctuations between generations in additive genetic composition in rotational crossbreeding systems can be avoided (Gregory and Cundiff, 1980). The resulting retained heterosis after subsequent *inter se* mating in composite populations is because expected heterosis is proportional to the retention of heterozygosity (Gregory and Cundiff, 1980). Composite breed formation offers similar opportunities as rotational crossbreeding (Gregory and Cundiff, 1980). Composites maybe advantageous to some producers as they have greater response to selection than parental breeds because of increased genetic variation expected as a

result of differences in gene frequencies in the parent breeds and greater selection intensity possible because of a high reproduction rate as a result of heterosis (Dickerson, 1973; Cundiff, 1977). Gregory et al. (1999) summarized work done at USMARC showing that there was not a significant difference in the coefficients of variation for reproduction, production, or carcass traits between the composite USMARC populations and their parental breeds (Table 4), thus alleviating the concern that crossbred animals will be more variable and thus discounted in the marketplace.

Sex Differences

Several heterosis studies have indicated that there are sex specific differences that affect how much heterosis is exhibited by an individual. The sex of calf was evaluated relative to the efficiency of the cow-calf unit. Greater sire differences for heifers were observed as compared to steers in average daily gain and weaning weight, consistent with the higher heritability estimates reported for weaning weight of heifers than for steers (Pahnish et al., 1961). Somewhat in contrast to Pahnish et al. (1961), Stonaker (1963) reported greater heterosis effects for weaning weight in heifers than in steers. Brinks et al. (1963) reported that inbreeding depression had a greater impact on weaning weight of heifers than male calves and inbreeding of dams manifested in a greater effect on weaning weight of male than female calves.

Reproductive Traits

The ability of a cow to have a long productive life is important for commercial beef producers; a long reproductive life is related to a decrease in costs associated with

developing replacement heifers, and the potential for increased revenue due to fewer young cows and thus a larger calf crop and proportion of calves available for sale (Nunez-Dominguez et al., 1991). Results from crossing studies of *Bos taurus* breeds have shown that heterosis for maternal traits were twice that of individual heterosis in contributing to calf weight weaned per cow exposed (Cundiff et al., 1974a,b). Green et al. (1991) utilized data from GPE Cycle III to study input/output differences among nonpregnant, lactating *Bos indicus* X *Bos taurus* and *Bos taurus* X *Bos taurus* F₁ cows and reported substantial advantages in *Bos indicus* X *Bos taurus* over *Bos taurus* crossbred cows for efficiency. Maternal traits such as fertility, maternal instinct, milking ability and reproductive longevity are important to consider when evaluating heterosis and its effects on production. While longevity takes several components of production into account, it is of considerable value to investigate the direct and maternal genetic values of longevity to improve efficiency to commercial producers.

Analyses over all breeds, ages and systems of management revealed that the effects of heterosis reduced the interval from parturition to first estrus and the average date of conception ($P < 0.05$) (Cundiff et al., 1974b). Calf crop weaned was 6.4% greater for crossbred compared to straightbred cows ($P < 0.01$). This difference was due to higher pregnancy rates ($P < 0.01$; 5.6% greater) and first service conception rate (6.6% greater) ($P < 0.01$) in the crossbreds (Cundiff et al., 1974b). Significant effects of breed group on calving difficulty and survival at birth, 72 h, and weaning revealed differences among breeds for these traits (Gregory et al., 1991a). Gregory et al. (1991a) presented results that showed large differences among breeds in calving difficulty, especially in

calves with 2-yr-old dams. The results showed a significant effect of heterosis on birth weight in progeny of cows of all ages; effects of heterosis on birth weight are not shown in increased calving difficulty as traits of the dam, heterotic effects on cow size are sufficient to accommodate increased birth weight resulting from heterosis without increasing dystocia (Gregory et al., 1991c).

Cow Longevity

Correct breed utilization and crossbreeding for longevity and components of lifetime productivity are critical for the development of sound beef production systems (Nunez-Dominguez et al., 1991). At any age, cumulative survival of crossbreds was greater than that of straightbreds, illustrating that crossbreds had lower probabilities of being culled than straightbreds (Nunez-Dominguez et al., 1991). The magnitude of heterosis for cow survival among three crosses (Hereford X Angus, Hereford X Shorthorn and Angus X Shorthorn) was similar (15 to 19%) but tended to be higher for Hereford X Angus than for the other crosses (Nunez-Dominguez et al., 1991). Differences in longevity and survivability between crossbred and purebred cows may be due to various reasons. Nunez-Dominguez et al. (1991) found that the proportion of cows culled for various reasons differed ($P < 0.005$) for straightbred and crossbred cows. The authors found that more straightbred (7.1%) than crossbred (1.7%) cows were culled for emaciation because straightbreds had shorter teeth and more missing teeth than did the crossbreds (Nunez-Dominguez et al., 1991). While investigating emaciation due to teeth and mouth scores, breed group was found to be significant for every pair of teeth and the whole mouth, indicating that differences in breed effects exist for tooth size

(Nunez-Dominguez et al., 1991). Heterosis for teeth size scores was important averaging 37%. The authors concluded that cows with unsound mouths may require more eating time, especially on range conditions, and may not meet their nutritional requirements for optimum body condition. Nunez-Dominguez et al. (1991) found that more replacements were needed for straightbreds (13.5%) than for crossbreds (11.9%). Utilizing breed differences and heterosis to improve cow longevity should result in decreasing costs and increasing the number of calves available to market each year.

Beef Cow/Calf Efficiency

If the utilization of crossbreeding is to achieve greater weights, consideration of how growth affects the efficiency of cows and calves as a unit is important in order to develop a sustainable and profitable breeding system. The average advantage of all crosses over the straightbred parents for the conversion of total feed consumed by a cow-calf pair to calf weight at weaning has been estimated to be 2% (Urlick et al., 1984). This study also found that there was a slight advantage in cow-calf efficiency exhibited by the Angus X Hereford cross; while the breed of a cow was a significant source of variation for all body weights and measurements taken for feed consumed, heterosis did not influence cow weights and feed consumption significantly except for Angus x Charolais (Urlick et al., 1984). Consequently, the crossbred cows were not significantly different from midparents for energy intake (Urlick et al., 1984). Differences in efficiency based upon differences in biological type has been well demonstrated at USMARC evaluating the *Bos indicus* X *Bos taurus* and *Bos taurus* X *Bos taurus* cross cows using the Hereford-Angus reciprocal cross and Brahman cross cows produced in GPE Cycle III.

Brahman cross cows were found to be 10% more efficient (calf gain divided by Mcal metabolizable energy intake by cow and calf) than the Hereford-Angus crosses (Green et al., 1991). Further studies conducted at USMARC evaluated the reproduction and maternal performance of *Bos indicus* X *Bos taurus* F₁ and *Bos taurus* X *Bos taurus* F₁ cross females. While it was shown that Brahman sired calves out of Hereford and Angus dams were significantly heavier at birth than Hereford-Angus reciprocal crosses, *Bos indicus* X *Bos taurus* cross females have the ability to limit prenatal growth of their offspring and tend to excel in terms of calving ease (Green et al., 1991).

Growth Traits

Several studies have evaluated traits from birth to weaning and describe breed and heterosis effects. The Germplasm Evaluation (GPE) studies, conducted at USMARC, were designed to characterize new germplasm (breeds) entering the US to allow for informed breed utilization. In GPE Cycle IV, significant effects of breed of sire and sire within breed indicated that genetic variation is important between and within breeds for gestation length, calving difficulty, birth weight and 200-d weight (Cundiff et al., 1998). These results suggest that genetic variation between breeds is comparable in magnitude to additive genetic variation within breeds for these traits (Cundiff et al., 1998). Gregory et al. (1965) considered preweaning traits in an early analysis of heterosis. Interactions between breed of sire and breed of dam were significant for all traits in both sexes except for weaning conformation score; these interactions reflect the importance of heterosis on traits such as birth weight, daily gain, and 200-d weight (Gregory et al., 1965).

Weaning weight is of particular interest to most producers as it directly influences potential profit. Heterosis achieved through continuous crossbreeding can be used to increase calf weaning weight per cow exposed to breeding by 20% (Gregory and Cundiff, 1980). In a previous study, weaning weight per cow exposed was 10.4 kg or 14.8% greater ($P < 0.01$) for crossbred cows than straightbred cows (Cundiff et al., 1974b). The effects of heterosis on 200-d weaning weight per cow exposed reflect the combined effects of reproduction, survival and maternal ability (Cundiff et al., 1974b). These findings provide evidence that the impact of heterosis can have a measureable impact on economically relevant traits.

Carcass Traits

Crossbreeding, and resulting heterosis, has led to increases in not only weaning weights but also carcass weights and weight at the time of slaughter. Heterosis effects were significant for most carcass traits related to weight when data were analyzed on an age-constant basis (Gregory et al., 1978). Heterosis effects were significant for slaughter weight (13.7 kg), hot carcass weight (9.0 kg), adjusted fat thickness (0.10 cm), estimated retail product (4.0 kg), estimated fat trim (2.3 kg) and estimated bone (1.0 kg) (Gregory et al., 1978). The authors found similar results in a later study evaluating the effects of retained heterosis on carcass traits using the USMARC composite populations relative to the purebred groups utilized in the composites. The mean of the composites showed 6.2 kg greater retail product, 7.5 kg more fat trim and 1.2 kg more bone ($P < 0.01$) when trimmed to 8 mm of subcutaneous fat (Gregory et al., 1994). Retained heterosis generally was significant for each composite population for weight of retail

product, fat trim, bone, and carcass lean, fat, and bone (Gregory et al., 1994). Gregory and others (1994) reported that these results indicate that composite populations or breed differences provide an opportunity to achieve and maintain optimum additive genetic (breed) composition for carcass composition traits and to use heterosis to increase lean tissue growth rate and to increase rate of fat deposition.

Utilizing different breeds in crosses has also lead to variability in the effects of heterosis. Gregory et al. (1978) found that the heterosis and reciprocal effects observed on an age-constant basis were related to growth rate. Breed effects were important for the traits associated with carcass composition after adjustments were made for the effects of weight; these results demonstrate important breed differences in additive effects of genes on carcass traits independent of carcass weight (Gregory et al., 1978). Results from Gregory et al. (1978), showed that increased weight gains associated with maternal effects during the prenatal and postnatal preweaning periods reflected at slaughter do not have the same effect on composition of the increased weight gain as does a higher nutritive environment provided during the growing-finishing period through increased dietary energy density. A higher nutritive environment provided during the growing-finishing stage through increased dietary energy density influenced composition of weight gain. Ranking of breed groups varies for several carcass traits depending on the slaughter end point (age, carcass weight, fat thickness, fat trim percentage or marbling score) (Koch et al., 1979; Wheeler et al., 1996). Rios-Utera et al. (2006) suggested that if growth and/or fattening rates differ among breed groups evaluated, comparison of breeds at different levels of a physiological end point could

result in re-ranking of breeds or changes in the magnitude of differences.

Argument Against Crossbreeding

Branded beef programs have created a demand that prompts producers to focus on carcass traits and single breed use. Busby and others (2008) reported that higher percentage Angus cattle had higher rates of low choice and better quality grades ($P < 0.0001$) and that for every one percent increase in Angus inheritance, the low Choice and better rate of a lot of cattle would be expected to increase by 0.264% (Busby et al., 2008). The same study evaluated Certified Angus Beef acceptance rate and reported similar results: cattle with a higher percentage of Angus breed composition had higher premium choice acceptance rates ($P < 0.0064$). In addition, for every one percent increase in Angus, lot premium choice acceptance rate would be expected to rise by 0.093%. Corah et al. (2010) investigated the effect of hide color and percentage Angus on feedlot performance and carcass traits. The conclusion drawn from the study suggests that feedlot performance, health and carcass quality were positively influenced by the black hided and higher percentage Angus calves, while average yield grade was negatively affected. The current push towards single breed use is asking commercial beef producers to decide if quality or branded beef premiums are more important than production efficiency contributed by crossbreeding and heterosis effects such as fertility, longevity and weight traits. Substantial data suggest that heterosis is beneficial in both the feedlot and the cowherd.

Breed Complementarity

Although all carcass traits do not benefit greatly from heterosis, breed complementarity can be beneficial for optimizing quality and yield characteristics. The USMARC GPE has well documented breed differences and comparisons through eight cycles. Complementarity occurs when breeds are matched based upon differences in strengths of particular traits between the breeds being crossed. As breeds become more similar the opportunities to achieve complementarity begin to erode. The GPE project has evaluated progeny from *Bos taurus* and *Bos indicus* breeds and reciprocal crosses. The *Bos indicus* breeds have higher yields than *Bos taurus*, but *Bos taurus*, specifically the British breeds, have excelled in marbling. Although gains in heterosis and yields can be achieved by utilizing *Bos indicus* germplasm, sacrifices might exist. For each 25% increase in *Bos indicus* inheritance the shear force required to slice through 1.27 cm cores of cooked rib steaks increased 0.73 kg (Crouse et al., 1989). However, given the heritability of Warner-Bratzler shear force tenderness of 0.40 (Dikeman et al., 2005), using within breed selection for tenderness gains can be made to make the product more tender relatively quickly. These trade offs are a perfect example for the need to utilize multiple breeds to optimize production efficiency. Combining breeds that excel in maternal and terminal traits to achieve production goals ultimately improves the efficiency of beef production and crossbreeding systems.

Application of Heterosis and Breed Estimates

Practical applications of continuing to evaluate heterosis are the use and need for such data in multibreed genetic evaluations. Because some breed associations

register and/or record composites, heterosis and breed effects are required to make accurate genetic predictions for composite seedstock. Multibreed genetic evaluations assume a common base among breeds, enabling producers to compare cattle of different breed makeups (Williams et al., 2010). For those operations that desire to evaluate cattle with different breed makeups, a multibreed evaluation would prove useful. Breed and heterosis effects are needed in a multibreed evaluation because databases maintained by breed associations include few crossbred animals, which may not be enough to accurately estimate these effects (Williams et al., 2010). Using field data to estimate heterosis effects can be problematic for two primary reasons. Although breed associations may contain crossbred animals and animals from one of the purebred parental breeds, data can be sparse or non-existent for the other purebred parental breed. Although some seedstock producers may produce and record multiple breeds and crossbred animals, they do not always manage them in a similar fashion and thus true contemporary group can become confounded with breed. The maternal and direct heterosis effects can be estimated directly from the breed association data or combined with estimates using results from crossbreeding studies found in the literature (Klei et al., 1996). Breed association data is structurally limited as it is not designed to estimate breed effects and heterosis, thus utilizing data from literature will provide valuable estimates. In a study conducted by Williams et al. (2010) least-squares means reported in the literature from 1976 to 1996 for birth weight, weaning weight, post weaning gain, carcass weight, fat thickness, ribeye area and marbling score were used to develop a database for the investigation of direct and

maternal breed and heterosis effects. The objective of the study was to infer breed effects, maternal effects, direct heterosis effects, and maternal heterosis effects using least square means estimates from previous crossbreeding studies. This approach assumes that the animals in the experiments were a representative sample of the same founder populations that contributed to the animals in the multibreed evaluation (Klei et al., 1996). As multibreed evaluations become more prevalent driven by commercial producer demand, the need for breed comparisons and heterosis effects will be critical to accurately compute EPD for composite seedstock.

Future Direction

Historical data on breed differences and heterosis indicate that utilizing crossbreeding leads to greater efficiencies in growth, performance and maternal traits. Re-evaluation of these traits investigating maternal and individual heterosis will prove useful, as breeds have changed over time decreasing complementarity between some breeds but most likely not affecting heterosis. Uncovering the specific loci that lead to heterosis could prove useful as genomic technologies advance. Currently the industry has mature data sets to evaluate changes and further investigate heterosis and its effects. In the near future, the investigation of breed-specific heterosis to determine how breeds contribute differently to heterosis will be available to aid in developing crossbreeding programs.

Summary

Various models have been evaluated to understand the effects that contribute to heterosis. While the theoretical models may not be fully understood, the effects of crossbreeding and the resulting heterosis encompass a wide variety of traits that are of economic importance to beef producers. The efficiencies gained by utilizing crossbreeding are primarily realized in the cowherd. One of the greatest reasons for utilizing crossbreeding is that reproductive traits are lowly heritable and the fact that heritability and heterosis are usually inversely related. Thus, selecting within breed for reproductive and maternal traits proves challenging and crossbreeding exploits the opportunity to improve reproductive efficiency quickly. Heterosis effects are measurable and have been found to be significant for weight related traits in carcass measurements and growth. Unfortunately, growth traits, including weaning weight, are thought of as the primary benefits of heterosis although the impact of maternal heterosis is critical. By utilizing breed complementarity, combining and matching breeds that excel in different areas of production, meeting profitability and production goals are realized more fully. The breeds that are utilized in a crossbreeding system should be chosen based on the current competencies of the particular breeds and matching breeds based upon those differences. Still, questions and debate remain as to whether or not crossbreeding should be utilized as branded beef programs may indicate that the economics favor the premiums received from single breed use. Utilizing a single breed has not been shown to maximize all traits that lead to profitability and efficiency in the cowherd. To address carcass merit, breed complementarity and breed differences are

suited to match breeds to optimize carcass quality and yield. The beef market is variable; production environments are vastly different in modern beef production and operational goals change with time and availability of resources. Producers must consider these variables to decide what type of crossbreeding system and production type fits best with their resources. It is with those different variables that producers can decide how they want to utilize breed differences and achieve heterosis to benefit system efficiency in their cowherd.

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Table 1. Individual heterosis: Advantage of the crossbred calf¹

Trait	Units	% Heterosis
Calving rate, %	3.2	4.4
Survival to weaning, %	1.4	1.9
Birth weight, kg	0.8	2.4
Weaning weight, kg	7.4	3.9
ADG, kg/d	0.04	2.6
Yearling weight, kg	13.2	3.8

¹Cundiff and Gregory, 1999.

Table 2. Maternal heterosis: Advantage of the crossbred cow¹

Trait	Units	% Heterosis
Calving rate, %	3.5	3.7
Survival to weaning, %	1.4	1.5
Birth weight, kg	0.8	1.8
Weaning weight, kg	7.4	3.9
Longevity, years	1.4	16.2
Cow Lifetime Production:		
Number of calves	0.97	17.0
Cumulative Wean. Wt., kg.	272.1	25.3

¹Cundiff and Gregory, 1999.

Table 3. Summary of crossbreeding systems by retained heterosis¹

Crossbreeding system		Retained Heterosis ²
2-breed rotation	A*B rotation	67%
3-breed rotation	A*B*C rotation	86%
Terminal cross with straightbred females ³	T*A	0.0% ⁴
Terminal cross with F1 females	T*(A*B)	100%
Rotating	A*B x A*B	50%
Unrelated	A*B x A*C	67%
F1 bulls	A*B x C*D	83%

¹Ritchie et al., 1999.

²Relative to F1 with 100% heterosis.

³Gregory and Cundiff, 1980.

⁴Straightbred cows are used in this system, which by definition have zero percent maternal heterosis; calves produced in this system exhibit heterosis, which is responsible for the expected improvement in weaning weight per cow exposed.

Table 4. Coefficients of variation for purebred vs. composite steers¹

Trait	Purebreds	Composites
Birth weight	0.12	0.13
Wean weight	0.10	0.11
Carcass weight	0.08	0.09
Retail product %	0.04	0.06
Marbling	0.27	0.29
Shear Force	0.22	0.21

¹Gregory et al., 1999.

**Estimation of breed-specific heterosis effects
for birth, weaning and yearling weight in cattle.**

Abstract

Heterosis, assumed proportional to expected breed heterozygosity, was calculated for 6,834 individuals with birth, weaning and yearling weight records from Cycle VII and the advanced generations of the U.S. Meat Animal Research (USMARC) Center Germplasm Evaluation project (GPE). Breeds represented in these data included: Angus, Hereford, Red Angus, Charolais, Gelbvieh, Simmental, Limousin and the MARCIII population. Heterosis was further estimated by proportions of British x British (BxB), British x Continental (BxC) and Continental x Continental (CxC) crosses and by breed-specific combinations. Angus and Red Angus were considered a single breed for combination of biological types (British and Continental) and were considered different breeds for the breed-specific proportions. Direct heritability estimates (SE) for birth, weaning and yearling weight for Model 1 were 0.42 (0.04), 0.22 (0.03) and 0.39 (0.05), respectively. The direct heritability estimates (SE) of birth, weaning and yearling weight for Model 2 were the same as Model 1 except yearling weight heritability was 0.38 (0.05). Model 1 fitted fixed covariates for heterosis among biological types. The BxB, BxC and CxC heterosis estimates for birth weight were 0.47 (0.37), 0.75 (0.32) and 0.73 (0.54) kg, respectively. The BxB, BxC and CxC heterosis estimates for weaning weight were 6.43 (1.80), 8.65 (1.54) and 5.86 (2.57) kg, respectively. Yearling weight estimates for BxB, BxC and CxC heterosis were 17.59(3.06), 13.88 (2.63) and 9.12 (4.34) kg, respectively. Estimates for heterosis based of breed-specific combinations fitted as

random effects nested within the fixed covariates of biological type (Model 2) were also estimated. Differences did exist among breed-specific combinations relative to heterosis for weaning and yearling weight, although the variance component associated with breed-specific heterosis was not significant. These results illustrate that there are differences in breed-specific heterosis and exploiting these differences can lead to varying levels of heterosis among mating plans.

Introduction

The benefits of crossbreeding and the effects of heterosis on growth traits have been well documented. The cumulative effects of heterosis on individual and maternal traits obtained from breed crosses have been shown to be economically important (Gregory and Cundiff, 1980; Long, 1980). However, these estimates were derived from comparisons of Hereford, Angus and Shorthorn crosses. There are examples where extreme breed differences, represented by *Bos taurus* x *Bos indicus*, were estimated to exhibit greater levels of heterosis. Cartwright et al. (1964) and Koger et al. (1975) presented results that suggested the cumulative effects of heterosis contributing to calf weaning weight per cow exposed may be more than twice as great for crosses between *Bos indicus* breeds and *Bos taurus* breeds than among *Bos taurus* breeds.

Current estimates for commonly used combinations of beef breeds could provide more descriptive results as to how popular beef breeds involved in crossbreeding systems can impact the level of heterosis. Specific estimates of heterosis for various crosses of breeds could be useful when selecting breeds for a crossbreeding system and developing composite populations for various production environments.

Differences in estimates of heterosis based on breed combinations could also be useful in multibreed evaluations as heterosis and breed differences are needed to appropriately adjust phenotypes used in genetic evaluations. The objectives of the current study were to estimate heterosis effects by biological type and for breed-specific combinations for birth, weaning and yearling weight.

Materials and Methods

Animal Populations and Management

In Cycle VII of the U.S. Meat Animal Research Center (USMARC) Germplasm Evaluation (GPE) project, purebred Angus (AN), Hereford (HH), Red Angus (AR), Charolais (CH), Gelbvieh (GV), Simmental (SM) and Limousin (LM), sires were mated by artificial insemination (AI) to AN, HH, and composite MARC III [1/4 AN, 1/4 HH, 1/4 Pinzgauer (PZ), 1/4 Red Poll (RP)], AN and HH cows to produce progeny designated as F_1 , born in 1999, 2000, and 2001. The 1999- and 2000-born male calves were castrated and fed for slaughter. Female F_1 and the 2001-born F_1 males were kept for breeding, and mated in multiple-sire pastures to produce 2-, 3-, and 4-breed cross progeny designated F_1^2 . The F_1^2 calves were born from 2003 to 2007 from 3-yr-old and older dams (Snelling et al., 2010). More recent GPE records were included from individuals produced through continuous sampling that were of varying proportions of the seven breeds used in Cycle VII. For the more recent GPE generations, purebred AI sires were mated to purebred or crossbred dams to generate purebred and crossbred steers and heifers and purebred and F_1 bulls. The F_1 bulls were mated to the purebred and halfblood females to produce purebred, halfblood and F_1^2 steers and heifers. All germplasm introduced into the

population entered through AI. Selected sires had high accuracy (BIF scale) EBV and represented heavily used sires in the US industry. Cycle VII animals included only spring-born records while the advanced generations of GPE included spring and fall calving records.

Male calves were castrated within 24 h after birth. Calves were weaned in September at approximately 165 d of age for Cycle VII of the GPE project. Advanced generations of the GPE were weaned at approximately 150 d of age. Age at weaning varied between years depending on environmental conditions. After weaning, steers were managed and fed for slaughter and heifers were developed for breeding starting the following May.

Data

Birth, weaning and yearling weights adjusted to a common age and for age of dam were recorded for 6,834 animals. Outliers were removed if the record was greater than three standard deviations from the mean after correcting for systematic effects of sex, age of dam and year and season of birth. After outliers were removed, there were 6,804 birth weight records, 6,451 weaning weight records and 6,293 yearling weight records. Contemporary groups were formed based on year and season of birth, location of birth and age of dam. All AI sires were assigned a genetic group according to their breed of origin. Dams mated to AI sires and natural service sires mated to F₁ females were assigned to different genetic groups (i.e., Hereford dams were assigned to different genetic groups than Hereford AI sires). A four-generation pedigree containing 9,211 animals was used including founder animals representing the 13 genetic groups

including the seven AI sire groups (AN, AR, HH, CH, GV, LM, and SM), commercial AN, commercial HH, commercial SM, commercial CH, commercial ARxSM and the MARC III population.

Statistical analysis

Breed fractions were assigned for each individual based on pedigree information. Expected breed heterozygosity for each individual was calculated as one minus the proportion of the same breed from the sire and dam. Proportions of heterozygosity were then assigned as either British (AN, AR, or HH) or Continental (CH, GV, LM, or SM) to form the fixed linear covariates of British x British (BxB), Continental x Continental (CxC) or British x Continental (BxC). The proportion of Angus x Red Angus represented in these data was 0.15 averaged over all three traits. Angus and Red Angus were considered a single breed in developing the covariates above. The breed proportions for the MARC III composites, which are 3/4 British and 1/4 Continental, were partitioned based on expected breed contribution to all three biological type classifications (BxB, CxC and BxC). Expected breed-heterozygosity was also evaluated through breed x breed random covariates, treating AN and AR as disjointed breeds and including MARC III as a unique breed.

All traits were analyzed using ASReml Version 3.0 (Gilmour et al., 2009). Two models were fitted: Model 1 - including the fixed covariates of BxB, BxC, and CxC and Model 2 - including breed x breed random covariates nested within the fixed covariates of BxB, BxC, and CxC. In both models, sex (heifer, bull, steer), breed (fitted as genetic groups), maternal heterosis (non-specific), contemporary group (birth year and season,

birth location and age of dam) were fitted as fixed effects. Random effects included direct and maternal additive genetic effects, maternal permanent environmental effect, and a residual.

Overall direct heterosis was not included in either model as the sum of the covariates accounting for heterozygosity are equivalent to the overall direct heterosis. Contrasts among heterosis of breed groups were obtained after adding overall direct heterosis as a fixed effect to the model. Contrasts were estimated as the difference between crosses of British breeds and those of Continental breeds ($B \times B - C \times C$) and between crosses including both British and Continental breeds and the average of British only and Continental only crosses $\{B \times C - [(B \times B + C \times C)/2]\}$.

Results and Discussion

Genetic parameters

Summary statistics of all growth traits are outlined in Table 1. As expected, genetic parameters and variance component estimates were similar for both models (Table 2). The breed-specific analysis (Model 2) included an additional variance component for the random breed-specific covariates nested within the fixed biological type covariates. A likelihood ratio test indicated that the variance component associated with the breed x breed random covariate was not significant ($P > 0.05$). The direct heritability estimates (SE) of birth, weaning and yearling weight for Model 2 were 0.42 (0.04), 0.22 (0.03) and 0.39 (0.05), respectively. The direct heritability estimates (SE) of birth, weaning and yearling weight for Model 1 were the same as Model 2 except yearling weight heritability was 0.38 (0.05). The estimates of heritability reported here

are slightly higher than previously reported estimates for birth, weaning and yearling weight of 0.47, 0.28 and 0.44, respectively, from the USMARC purebred populations (Bennett and Gregory, 1996). Maternal heritability estimates were 0.04 (0.03), 0.17 (0.05) and 0.05 (0.04) for birth, weaning and yearling weight, respectively. These estimates correspond closely to the estimates of maternal heritability for birth, weaning and yearling weight from Koch et al. (1994). Sex had a significant effect on all traits ($P < 0.001$). Heifers were lighter at birth, weaning, and yearling ages and steers were intermediate to bulls and heifers at weaning. The steers were heavier than the bulls as yearlings because the steers were being fed for harvest, while the bulls were being developed for breeding.

Biological Type Heterosis Effects

Estimates of heterosis for the BxB, BxC and CxC covariates are presented in Table 3. The heterosis estimates for BxB and CxC proportions were 0.47 (0.37) and 0.73 (0.54) kg, respectively, but were not significant. The BxC estimate for birth weight was 0.75 (0.32) kg ($P = 0.02$), which is similar to the BxC heterosis estimate reported by Williams et al. (2010) of 0.70 (0.05) kg for birth weight. Williams et al. (2010) reported a larger BxB estimate of 0.90 (0.06) and a smaller CxC estimate of 0.63 (0.23) kg for birth weight. The BxB, BxC and CxC estimates of heterosis for weaning weight were 6.43 (1.80), 8.65 (1.54) and 5.86 (2.57) kg, respectively, and were all significantly different from zero. Williams et al. (2010) reported estimates of heterosis for BxB, BxC and CxC crosses for weaning weight of 8.22 (0.25), 5.79 (0.25) and 3.47 (1.28) kg, respectively. Both the results from the current study and those from Williams et al. (2010) suggest that the CxC

heterosis estimates are the smallest among the three biological type combinations for birth and weaning weights. Biological type heterosis estimates for yearling weight were 17.59 (3.06), 13.88 (2.63) and 9.12 (4.34) kg for BxB, BxC and CxC, respectively, and were all significantly different from zero. The estimates of biological type heterosis for birth and weaning weight from Williams et al. (2010) were obtained from least-squares means reported in the literature from 1976 to 1996, which could indicate differences across studies as breed averages, and trends have changed over time. Although the Continental breeds used herein and by Williams et al. (2010) were the same, the British breeds represented in the literature used by Williams et al (2010) included Angus, Hereford and Shorthorn, which could indicate why there were differences in estimates from the current study.

Contrasts between the estimates of BxB and CxC, and between estimates of BxC and the average of BxB and CxC were not significant for any of the traits (Model 2). The two contrasts associated with the smallest p-values included the difference between BxB and CxC yearling weight estimates ($P = 0.14$), and the difference between BxC and the average BxB and CxC estimates for weaning weight ($P=0.28$). Surprisingly, maternal heterosis was not significant for any of the traits analyzed.

Breed-Specific Heterosis Effects

The breed x breed variance component from Model 2 only explained 1% of the phenotypic variance, averaged across all traits, and was not significantly different from zero. Estimates of breed-specific heterosis are in Table 4. All of the breed-specific heterosis estimates for birth weight were smaller than their respective standard errors.

This was true for a large portion of the breed-specific combinations for weaning and yearling weights. Model 2 estimates of heterosis for the fixed biological type covariates were similar to Model 1. BxC heterosis estimates were significant for birth, weaning and yearling weights with estimates of 0.75 (0.32), 8.21 (1.76) and 14.04 (3.11) kg, respectively. BxB proportions were significant for weaning and yearling weights with estimates of 6.10 (2.41) and 18.48 (4.34) kg, respectively. CxC proportions were different from zero for weaning weight with an estimate of 6.00 (2.84) kg.

The breed x breed effects presented are with respect to the fixed biological type estimates that they were nested within. The exception is the AN x AR estimate. Angus and Red Angus were considered the same breed in the formation of the BxB biological type covariate, consequently the AN x AR estimates are with respect to an assumed heterosis of zero. The largest breed x breed estimates for birth weight were from CH x MARC III, GV x MARCIII, and HH x SM crosses with estimates of 0.42E-05 (0.99E-03), 0.22E-05 (0.99E-03), and .21E-05 (0.99E-03) kg, respectively. The largest estimates for weaning weight were from HH x MARC III, AN x SM, AR x SM and CH x GV crosses with estimates of 2.76 (1.70), 2.09 (1.77), 2.59 (2.27) and 2.51 (2.32) kg, respectively. The weaning weight estimate for AN x AR was -2.69 (1.97). The AN x MARCIII yearling weight estimate was -5.18 (2.93) kg. Positive estimates for yearling weight were 5.07 (3.80), 6.35 (3.14), and 5.10 (4.30) kg for HH x AR, HH x MARCIII and AR x SM, respectively. The estimate for AN x AR for yearling weight was -6.35 (3.66) kg. Estimates for the majority of the specific breed crosses are difficult to estimate, indicated by the large standard errors, due to the structure of the data and limited numbers of animals representing

each breed cross. The breed-specific analysis indicated that there are differences in heterosis based on biological type, and the estimates for specific breed combinations indicate that most of the differences between breed combinations can be accounted for in the biological types. A grading up breeding scheme, to increase the proportion of purebred animals in the data, would allow for better estimation of specific breed combination estimates and is currently being conducted at USMARC.

Correlations among the fixed effects and the (co)variance components for birth, weaning and yearling weight are presented in Tables 5-10. For all three traits low to moderate correlations were observed between the fixed effects of BxB, BxC, and CxC. The moderate correlations among the estimates of those effects indicate slight confounding. The correlations among other fixed effects were low.

For birth weight, correlations among the variance components show partial confounding between the direct additive and the direct-maternal covariance. The maternal additive variance was partially confounded with the direct-maternal covariance and permanent environmental variance. The correlation of unity between the residual variance and breed-specific heterosis variance is an artifact of the near zero variance component estimate for breed-specific heterosis.

For weaning weight and yearling weight, the pattern of correlations among variance component estimates (and hence, confounding among those estimates) was similar, except that the estimate of breed-specific heterosis variance was uncorrelated to all other estimates.

The heterosis estimates presented here were similar to birth, weaning and yearling weight estimates in previous studies by Gregory et al., (1991a,b). Gregory et al. (1991b) found that mean heterosis for the MARC composite populations was similar in both sexes and the level of heterosis retained in the combined F₃ and F₄ generations was greater than expected for birth, ADG from weaning to 368 d and 368-d weight based on expected breed heterozygosity. Estimates of heterosis from the current study and previous studies indicate that heterosis in composite populations is underestimated based on expected breed heterozygosity.

Similarly to the current study, Gregory and et al. (1991b) found greater than expected levels of heterosis were found in the composite populations and suggest this change in expectation may be due to favorable epistatic recombination effects being of greater importance than unfavorable effects. The results of the current study indicate greater levels of heterosis achieved in the composites and confirm that retained heterosis in composite populations is not entirely proportional to breed heterozygosity. Epistatic effects are ignored in the current model and the results indicate an effect that increases heterosis is found in the composite populations. A possible explanation for the higher than expected heterosis could include the theory of parental epistasis involving duplicate genes that lead to greater than expected levels of heterosis which can be attributed to different homozygous epistatic gene combinations present in the parental lines being passed across to the crossbred could be attributed to the increase in expected heterosis (Sheridan, 1981).

Implications

The current study illustrated that differences between breeds and biological types exist relative to levels of heterosis. Further investigation of breed-specific estimates of heterosis will provide valuable estimates for multibreed evaluations and aid in the selection of breeds in forming composites or crossbreeding systems. Growth traits will provide a valuable starting point in estimating breed-specific heterosis because of the availability of data. Differences among breeds based on biological type and differences in breed characteristics for growth performance and size seem to affect the amount of heterosis expressed based on specific crosses according to biological type. Estimates of heterosis based on biological type indicate that heterosis based on breed heterozygosity is underestimating the amount of heterosis retained in composite populations. Further understanding of the favorable epistatic effects in composite and crossbred populations could help to understand the genetic basis of heterosis and better utilize breeds and composite populations.

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Table 1. Number of observations (N) and mean (SD) for birth, weaning and yearling weight.

¹ Trait	N	Mean
BWT, kg	6805	40.6 (4.8)
WT205D, kg	6452	245 (34.3)
WT365D, kg	6293	427 (66.4)

¹BWT=birth weight, WT205D= adjusted weaning weight, WT365D= adjusted yearling weight.

Table 2. Variance component and parameter estimates (SE) for birth weight (BWT), weaning weight (WT205D) and yearling weight (WT365D) for biological type and breed-specific heterosis (Model 1 and 2).

¹ Model item	² BWT, kg ²	WT205D, kg ²	WT365D, kg ²
Biological type analysis (Model 1)			
Variance Component			
V _p	25.19 (0.52)	589.14 (12.55)	1505.80 (31.56)
V _a	10.68 (1.20)	128.72 (20.95)	579.97 (81.26)
Cov _{a,m}	0.47 (0.61)	-37.99 (18.24)	-80.99 (48.00)
V _m	1.15 (0.71)	97.75 (28.98)	77.63 (54.28)
V _{pe}	1.05 (0.52)	140.35 (20.38)	158.76 (38.22)
V _e	11.85 (0.76)	260.30 (14.17)	770.42 (51.96)
Heritabilities			
h ² _a	0.42 (0.44)	0.22 (0.03)	0.39 (0.05)
h ² _m	0.05 (0.03)	0.17 (0.05)	0.05 (0.04)
c ²	0.04 (0.02)	0.24 (0.03)	0.11 (0.03)
Breed-specific heterosis (Model 2)			
Variance Component			
V _p	25.19 (0.52)	593.97 (13.28)	1523.30 (34.43)
V _a	10.68 (1.20)	127.81 (20.88)	575.89 (80.87)
Cov _{a,m}	0.46 (0.61)	-37.50 (18.17)	-77.74 (47.48)
V _m	1.15 (0.71)	98.22 (28.92)	73.87 (53.61)
V _{pe}	1.05 (0.52)	139.13 (20.33)	157.94 (37.98)
V _e	11.85 (0.76)	259.93 (14.14)	769.34 (51.77)
V _{B-S}	1.0E-06 (0.6E-07)	6.37 (4.76)	23.99 (14.84)
Heritabilities			
h ² _a	0.42 (0.04)	0.22 (0.03)	0.38 (0.05)
h ² _m	0.05 (0.03)	0.17 (0.05)	0.05 (0.04)
c ²	0.04 (0.02)	0.23 (0.03)	0.10 (0.02)

¹V_p = phenotypic variance, V_a = direct genetic variance, Cov_{a,m} = direct by maternal covariance, V_m = maternal genetic variance, V_{pe} = permanent environmental variance, V_e = residual variance, V_{B-S} = Random Breed-specific heterosis variance h²_a = direct heritability, h²_m = maternal heritability, c² = proportion of phenotypic variance due to permanent environmental effects.

Table 3. Estimates of breed specific heterosis (SE) (British x British, British x Continental and Continental x Continental) for birth, weaning and yearling weight (Model 1).

¹ Covariate	² BWT,kg	WT205D, kg	WT365D, kg
BxB	0.47 (0.37)	6.43 (1.80)**	17.59 (3.06)**
BxC	0.75 (0.32)*	8.65 (1.54)**	13.88 (2.63)**
CxC	0.73 (0.54)	5.86 (2.57) *	9.12 (4.34) *
Maternal heterosis	0.41 (0.31)	0.34 (1.84)	3.44 (2.66)

¹B=British, C=Continental

²BWT=birth weight, WT205D= adjusted weaning weight, WT365D= adjusted yearling weight.

* $P < 0.05$

** $P < 0.01$

Table 4. Estimates of breed specific heterosis (SE) (British x British, British x Continental and Continental x Continental and breed x breed (nested random) heterozygosity) for birth, weaning and yearling weight (Model 2).

¹ Model term	² BWT, kg	WT205D, kg	WT365D, kg
BxB	0.47 (0.37)	6.10 (2.41)**	18.48 (4.34)***
BxC	0.75 (0.32)**	8.21 (1.76)***	14.04 (3.11)***
CxC	0.73 (0.54)	6.00 (2.83)**	9.32 (4.92)*
Maternal Heterosis	0.41 (0.31)	0.27 (1.84)	3.32 (2.67)
ANxHH	0.17E-05 (0.99E-03)	1.31(1.99)	1.14(3.72)
ANxAR	0.88E-07(0.99E-03)	-2.69(1.97)	-6.35(3.66)
ANxCH	-0.15E-05(0.99E-03)	0.14(1.80)	-2.76(3.29)
ANxGV	-0.28E-05(0.99E-03)	-0.68(1.88)	-3.26(3.47)
ANxSM	0.46E-06(0.99E-03)	2.09(1.77)	2.02(3.23)
ANxLM	0.20E-06(0.99E-03)	-0.02(1.89)	2.72(3.49)
ANxMARCIII	-0.19E-05(0.99E-03)	-0.54(1.59)	-5.18(2.93)
HHxAR	-0.88E-06(0.99E-03)	1.32(2.03)	5.07(3.80)
HHxCH	0.60E-06(0.99E-03)	-1.17(1.95)	-1.10(3.59)
HHxGV	0.30E-06(0.99E-03)	0.66(2.01)	-1.75(3.72)
HHxSM	0.21E-05(0.99E-03)	1.24(1.89)	2.25(3.47)
HHxLM	-0.40E-06(0.99E-03)	-1.23(2.01)	0.60(3.73)
HHxMARCIII	0.15E-05(0.99E-03)	2.76(1.70)	6.35(3.14)
ARxCH	-0.74E-06(0.99E-03)	-0.89(2.34)	-3.94(4.43)
ARxGV	-0.37E-06(0.99E-03)	-1.68(2.40)	1.12(4.61)
ARxSM	0.13E-05(0.99E-03)	2.59(2.27)	5.10(4.30)
ARxLM	-0.37E-07(0.99E-03)	-1.29(2.41)	-1.21(4.63)
ARxMARCIII	-0.90E-06(0.99E-03)	-0.99(1.83)	-1.85(3.39)
CHxGV	0.41E-06 (0.99E-03)	2.51(2.32)	3.67(4.41)
CHxSM	0.13E-05 (0.99E-03)	-0.81(2.18)	0.03(4.10)
CHxLM	-0.89E-06(0.99E-03)	-1.84(2.32)	-3.15(4.40)
CHxMARCIII	0.42E-05 (0.99E-03)	1.49(1.82)	0.00(3.37)
GVxSM	-0.17E-06(0.99E-03)	-0.48(2.31)	-1.18(4.39)
GVxLM	-0.52E-06(0.99E-03)	-1.14(2.39)	-2.08(4.59)
GVxMARCIII	0.22E-05(0.99E-03)	0.23(1.81)	0.62(3.37)
SMxLM	-0.60E-06(0.99E-03)	1.83(2.29)	2.92(4.36)
SMxMARCIII	-0.25E-05(0.99E-03)	-0.41(1.82)	-0.90(3.38)
LMxMARCIII	-0.21E-05(0.99E-03)	-1.58(1.82)	-0.56(3.38)

¹B=British, C=Continental; AN =Angus, HH=Hereford, AR=Red Angus, CH=Charolais, GV=Gelbvieh, SM=Simmental, LM=Limousin, MARCIII = (1/4 AN, 1/4 HH, 1/4 Red Poll, 1/4 Pinzgauer).

²BWT=birth weight, WT205D= adjusted weaning weight, WT365D= adjusted yearling weight.

* $P < 0.10$

** $P < 0.05$

*** $P < 0.01$

Table 5. Estimates, standard errors (SE), and correlations among fixed effects for birth weight.

¹ Effect	² Level	Est., kg	SE, kg	P<	Mean	Sex F	Sex M	BxC	BxB	CxC	Mat. het.
Mean	1	0.00	0.00	0.000	0	0	0	0	0	0	0
Sex	F	-3.32	0.11	0.000	0	1	0	-0.01	0.01	-0.01	-0.01
Sex	M	0.00	0.00	0.000	0	0	0	0	0	0	0
BxC	1	0.75	0.32	0.019	0	-0.01	0	1	0.39	0.40	-0.05
BxB	1	0.47	0.37	0.211	0	0.01	0	0.39	1	0.08	0.03
CxC	1	0.73	0.54	0.175	0	-0.01	0	0.40	0.08	1	-0.09
Mat. het.	1	0.41	0.31	0.188	0	-0.01	0	-0.05	0.03	-0.09	1

¹B=British, C=Continental, Mat. het. = maternal heterosis

²F=female, M=male

Table 6. Estimates, standard errors (SE), and correlations among (co)variance components for birth weight.

¹ Parm.	Est., kg ²	SE, kg ²	σ^2_R	σ^2_A	σ_{AM}	σ^2_M	σ^2_{PE}	σ^2_{B-S}
σ^2_R	11.85	0.76	1	-0.87	0.52	-0.04	-0.23	1.00
σ^2_A	10.68	1.20	-0.87	1	-0.58	0.01	0.14	-0.87
σ_{AM}	0.47	0.61	0.52	-0.58	1	-0.46	0.03	0.52
σ^2_M	1.15	0.71	-0.04	0.01	-0.46	1	-0.72	-0.04
σ^2_{PE}	1.05	0.52	-0.23	0.14	0.03	-0.72	1	-0.23
σ^2_{B-S}	0.00	0.00	1.00	-0.87	0.52	-0.04	-0.23	1

¹ σ^2_R = Residual variance, σ^2_A = Direct genetic variance, σ_{AM} = Direct by maternal covariance, σ^2_M = Maternal genetic variance, σ^2_{PE} = Permanent environmental variance, σ^2_{B-S} = variance component for the breed-specific heterosis covariates nested within the fixed biological type covariates.

Table 7. Estimates, standard errors (SE), and correlations among fixed effects for weaning weight.

¹ Effect	² Level	Est., kg	SE, kg	P<	Mean	Sex B	Sex H	Sex S	BxC	BxB	CxC	Mat het.
Mean	1	0.00	0.00		0	0	0	0	0	0	0	0
Sex	B	9.39	2.16	0.00	0	1	0.22	0	0.00	0.02	0.01	0.08
Sex	H	15.85	0.54	0.00	0	0.22	1	0	-0.01	0.01	-0.01	0.00
Sex	S	0.00	0.00		0	0	0	0	0	0	0	0
BxC	1	8.21	1.76	0.00	0	0.00	-0.01	0	1	0.32	0.31	-0.10
BxB	1	6.09	2.41	0.01	0	0.02	0.01	0	0.32	1	0.10	-0.02
CxC	1	5.99	2.83	0.03	0	0.01	-0.01	0	0.31	0.10	1	-0.09
Mat het.	1	0.27	1.84	0.88	0	0.08	0.00	0	-0.10	-0.02	-0.09	1

¹B=British, C=Continental, Mat het. = maternal heterosis

²F=female, M=male

Table 8. Estimates, standard errors (SE), and correlations among (co)variance components for weaning weight.

¹ Parm.	Est., kg ²	SE, kg ²	σ^2_R	σ^2_A	σ_{AM}	σ^2_M	σ^2_{PE}	σ^2_{B-S}
σ^2_R	259.93	14.14	1	-0.84	0.41	-0.10	-0.11	-0.01
σ^2_A	127.81	20.89	-0.84	1	-0.48	0.10	0.02	-0.01
σ_{AM}	-37.50	18.18	0.41	-0.48	1	-0.68	0.23	0.00
σ^2_M	98.22	28.92	-0.10	0.10	-0.68	1	-0.73	0.01
σ^2_{PE}	139.13	20.33	-0.11	0.02	0.23	-0.73	1	-0.01
σ^2_{B-S}	6.37	4.76	-0.01	-0.01	0.00	0.01	-0.01	1

¹ σ^2_R = Residual variance, σ^2_A = Direct genetic variance, σ_{AM} = Direct by maternal covariance, σ^2_M = Maternal genetic variance, σ^2_{PE} = Permanent environmental variance, σ^2_{B-S} = variance component for the breed-specific heterosis covariates nested within the fixed biological type covariates.

Table 9. Estimates, standard errors (SE), and correlations among fixed effects for yearling weight.

¹ Effect	² Level	Est., kg	SE, kg	P<	Mean	Sex B	Sex H	Sex S	BxC	BxB	CxC	Mat het.
Mean	1	0.00	0.00		0	0	0	0	0	0	0	0
Sex	B	-9.29	3.57	0.01	0	1	0.23	0	0.00	0.02	0.01	0.08
Sex	H	-98.33	0.94	0.00	0	0.23	1	0	-0.01	0.01	-0.01	0.00
Sex	S	0.00	0.00		0	0	0	0	0	0	0	0
BxC	1	14.04	3.11	0.00	0	0.00	-0.01	0	1	0.30	0.29	-0.09
BxB	1	18.48	4.34	0.01	0	0.02	0.00	0	0.30	1	0.10	0.00
CxC	1	9.32	4.92	0.03	0	0.01	-0.01	0	0.29	0.10	1	-0.09
Mat het.	1	3.32	2.67	0.88	0	0.08	0.00	0	0.09	0.00	-0.09	1

¹B=British, C=Continental, Mat het. = maternal heterosis

²F=female, M=male

Table 10. Estimates, standard errors (SE), and correlations among (co)variance components for yearling weight.

¹ Parm.	Est., kg ²	SE, kg ²	σ^2_R	σ^2_A	σ_{AM}	σ^2_M	σ^2_{PE}	σ^2_{B-S}
σ^2_R	769.34	51.77	1	-0.88	0.58	-0.16	-0.17	-0.01
σ^2_A	575.89	80.88	-0.88	1	-0.64	0.15	0.08	0.00
σ_{AM}	-77.74	47.49	0.58	-0.64	1	-0.63	0.09	0.00
σ^2_M	73.87	53.61	-0.16	0.15	-0.63	1	-0.66	-0.01
σ^2_{PE}	157.94	37.99	-0.17	0.08	0.09	-0.66	1	0.00
σ^2_{B-S}	23.99	14.84	-0.01	0.00	0.00	-0.01	0.00	1

¹ σ^2_R = Residual variance, σ^2_A = Direct genetic variance, σ_{AM} = Direct by maternal covariance, σ^2_M = Maternal genetic variance, σ^2_{PE} = Permanent environmental variance, σ^2_{B-S} = variance component for the breed-specific heterosis covariates nested within the fixed biological type covariates.