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1-9-2015

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Schiermiester, Lauren N.; Thallman, R. M.; Kuehn, Larry; Kachman, Stephen D.; and Spangler, Matthew L., "Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle" (2015). *Faculty Papers and Publications in Animal Science*. 869. <http://digitalcommons.unl.edu/animalscifacpub/869>

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## Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle<sup>1</sup>

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**ABSTRACT:** Heterosis, assumed proportional to expected breed heterozygosity, was calculated for 6834 individuals with birth, weaning and yearling weight records from Cycle VII and advanced generations of the U.S. Meat Animal Research Center (USMARC) Germplasm Evaluation (GPE) project. Breeds represented in these data included: Angus, Hereford, Red Angus, Charolais, Gelbvieh, Simmental, Limousin and Composite MARC III. Heterosis was further estimated by proportions of British  $\times$  British (B  $\times$  B), British  $\times$  Continental (B  $\times$  C) and Continental  $\times$  Continental (C  $\times$  C) crosses and by breed-specific combinations. Model 1 fitted fixed covariates for heterosis within biological types while Model 2 fitted random breed-specific combinations nested within the fixed biological type covariates. 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). The B  $\times$  B, B  $\times$  C, and C  $\times$  C heterosis estimates for birth weight were 0.47 (0.37), 0.75 (0.32), and 0.73 (0.54) kg, respectively. The B  $\times$  B, B  $\times$  C, and C  $\times$  C 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 B  $\times$  B, B  $\times$  C, and C  $\times$  C heterosis were 17.59(3.06), 13.88 (2.63), and 9.12 (4.34) kg, respectively. Differences did exist among estimates of breed-specific 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.

**Key words:** cattle, genetics, heterosis

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J. Anim. Sci. 2015.93:46–52  
doi:10.2527/jas2014-8493

### 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*  $\times$  *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 *B. indicus* breeds and *B. taurus* breeds than among *B. taurus* breeds. Current estimates for commonly used combinations of beef breeds could provide strategies to utilize popular beef breeds in crossbreeding systems for optimal 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 produc-

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Received September 8, 2014.  
Accepted November 13, 2014.

tion environments. Differences in estimates of heterosis based on breed combinations could also be useful in multibreed evaluations as estimates of 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 AI to AN, HH, and composite MARC III (1/4 AN, 1/4 HH, 1/4 Pinzgauer [PZ], 1/4 Red Poll [RP]) 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 harvest. 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 that were of varying proportions of the 7 breeds used in Cycle VII produced through continuous sampling of industry sires from these breeds. 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 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 harvest 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  $> 3$  SD from the mean after correcting for systematic effects of sex, age of dam, and year and season of birth. There were 6,804 birth weight records, 6,451 weaning weight records, and 6,293 yearling weight records. Means (SD) after removal of outliers were 40.6 (4.8), 245 (34.3), and 427 (66.4) kg for birth, weaning, and yearling weight, respectively. 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 and natural service sires were assigned to different genetic groups than the AI sires (i.e., Hereford dams were assigned to different genetic groups than Hereford AI sires). A 4-generation pedigree containing 9,211 animals was used. Founder animals representing the 13 genetic groups were included: 7 AI sire groups (AN, AR, HH, CH, GV, LM, and SM), commercial AN, commercial HH, commercial SM, commercial CH, commercial AR  $\times$  SM, 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 1 minus the product of the proportion of the same breed from the sire and dam. Probabilities of heterozygosity were then partitioned among British (AN, AR, or HH) or Continental (CH, GV, LM, or SM) to form the fixed linear heterosis covariates of British  $\times$  British (**B**  $\times$  **B**), Continental  $\times$  Continental (**C**  $\times$  **C**) or British  $\times$  Continental (**B**  $\times$  **C**). Maternal and AI (i.e., Angus, Simmental, Hereford, Charolais) genetic groups of the same breed were combined for expected heterosis derivations. 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 3 biological type classifications (**B**  $\times$  **B**, **C**  $\times$  **C**, and **B**  $\times$  **C**). Expected breed-heterozygosity was also evaluated through breed  $\times$  breed random covariates 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 **B**  $\times$  **B**, **B**  $\times$  **C**, and **C**  $\times$  **C** and Model 2- including breed  $\times$  breed random covariates nested within the fixed covariates of **B**  $\times$  **B**, **B**  $\times$  **C**, and **C**  $\times$  **C**. In both models, sex (heifer, bull, steer), breed (fitted as genetic groups), maternal heterosis (non-specific), and 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. Additive and maternal variance structures were modeled as the direct product of the numerator relationship matrix and a  $2 \times 2$

**Table 1.** 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)

Model item <sup>1</sup>	BWT <sup>2</sup> , kg <sup>2</sup>		WT205D <sup>2</sup> , kg <sup>2</sup>		WT365D <sup>2</sup> , kg <sup>2</sup>	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
$V_p$	25.19 (0.52)	25.19 (0.52)	589.14 (12.55)	593.97 (13.28)	1,505.80 (31.56)	1,523.30 (34.43)
$V_a$	10.68 (1.20)	10.68 (1.20)	128.72 (20.95)	127.81 (20.88)	579.97 (81.26)	575.89 (80.87)
$Cov_{a,m}$	0.47 (0.61)	0.46 (0.61)	-37.99 (18.24)	-37.50 (18.17)	-80.99 (48.00)	-77.74 (47.48)
$V_m$	1.15 (0.71)	1.15 (0.71)	97.75 (28.98)	98.22 (28.92)	77.63 (54.28)	73.87 (53.61)
$V_{pe}$	1.05 (0.52)	1.05 (0.52)	140.35 (20.38)	139.13 (20.33)	158.76 (38.22)	157.94 (37.98)
$V_e$	11.85 (0.76)	11.85 (0.76)	260.30 (14.17)	259.93 (14.14)	770.42 (51.96)	769.34 (51.77)
$V_{B-S}$	–	0	–	6.37 (4.76)	–	23.99 (14.84)
$h^2$						
$h_a^2$	0.42 (0.44)	0.42 (0.04)	0.22 (0.03)	0.22 (0.03)	0.39 (0.05)	0.38 (0.05)
$h_m^2$	0.05 (0.03)	0.05 (0.03)	0.17 (0.05)	0.17 (0.05)	0.05 (0.04)	0.05 (0.04)
$c^2$	0.04 (0.02)	0.04 (0.02)	0.24 (0.03)	0.23 (0.03)	0.11 (0.03)	0.10 (0.02)

<sup>1</sup> $V_p$  = 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  $h_a^2$  = direct heritability,  $h_m^2$  = maternal heritability,  $c^2$  = proportion of phenotypic variance due to permanent environmental effects.

<sup>2</sup>BWT = adjusted birth weight, WT205D = adjusted weaning weight, WT365D = adjusted yearling weight.

co-variance matrix of direct and maternal (co)variances. The residuals were assumed to be independent.

To determine the extent to which heterosis estimates were confounded with each other or with other fixed effects, correlations among fixed effect estimates were computed by dividing the rows and columns of the block of the inverse mixed model equations corresponding to those fixed effects by the standard errors corresponding to those rows and columns, respectively as in Thallman et al. (2014). Correlations with absolute value close to one would indicate confounding. Similarly, to identify colinearities among (co)variance components, correlations among (co)variance component estimates were computed by dividing the rows and columns of the inverse approximate information matrix by the standard errors of (co)variance component estimates corresponding to those rows and columns, respectively.

Overall direct heterosis was not included in either model as the sum of the covariates accounting for biological type heterozygosity are equivalent to the overall direct heterosis. Contrasts among heterosis estimates of breed groups were obtained.

## RESULTS AND DISCUSSION

### Genetic Parameters

Genetic parameters and variance component estimates were similar for both models (Table 1). 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  $\times$  breed random

covariate was not significant ( $P = 0.175$ ). 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 2 were the same as Model 1 except yearling weight heritability was 0.38 (0.05). The estimates of heritability reported here are slightly lower 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). The direct-maternal genetic correlations were 0.13, -0.34, and -0.38 for birth, weaning, and yearling weights, respectively, in Model 1 and the same in Model 2 except the correlation for weaning weight was -0.33.

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 B  $\times$  B, B  $\times$  C, and C  $\times$  C covariates are presented in Table 2. The birth weight heterosis estimates for B  $\times$  B and C  $\times$  C proportions were 0.47 (0.37) and 0.73 (0.54) kg, respectively, but were not significant. The B  $\times$  C estimate for birth



**Table 2.** Estimates of biological type heterosis (SE) (British x British, British x Continental and Continental x Continental) for birth, weaning and yearling weight (Model 1)

Covariate <sup>1</sup>	BWT <sup>2</sup> , kg	WT205D <sup>2</sup> , kg	WT365D <sup>2</sup> , kg
B × B	0.47 (0.37)	6.43 (1.80)**	17.59 (3.06)**
B × C	0.75 (0.32)*	8.65 (1.54)**	13.88 (2.63)**
C × C	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)

<sup>1</sup>B = British, C = Continental.

<sup>2</sup>BWT = adjusted birth weight, WT205D = adjusted weaning weight, WT365D = adjusted yearling weight.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

weight was 0.75 (0.32) kg ( $P = 0.02$ ), which is similar to the B × C heterosis estimate reported by Williams et al. (2010) of 0.70 (0.05) kg for birth weight. Williams et al. (2010) reported a larger B × B estimate of 0.90 (0.06) and a smaller C × C estimate of 0.63 (0.23) kg for birth weight. Heterosis estimates for birth weight were similar to those reported by Gregory et al. (1991b), which evaluated composite animals including the MARCIII population. However, the individual heterosis estimated in the current study for birth weight was less than that reported by Cunningham and Magee (1988) who utilized Angus, Hereford, Simmental, and Holstein-Friesian germplasm. The B × B, B × C, and C × C 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 B × B, B × C, and C × C crosses for weaning weight of 8.22 (0.25), 5.79 (0.25), and 3.47 (1.28) kg, respectively. Cunningham and Magee (1988) reported an average direct heterosis estimate of 26.3 (12.9) kg. from the rotational crosses of Angus, Hereford, Holstein-Friesian, and Simmental; within the range of the estimates of the current study. Both the results from the current study and those from Williams et al. (2010) suggest that the C × C heterosis estimates are the smallest among the 3 biological type combinations for birth and weaning weights. The fact that heterosis was greater for weaning weight than for birth weight is not surprising, and agrees with results from Brinks et al. (1967). Biological type heterosis estimates for yearling weight were 17.59 (3.06), 13.88 (2.63), and 9.12 (4.34) kg for B × B, B × C, and C × C, respectively, and were all significantly different from 0. The weaning and yearling weight heterosis estimates were greater than those reported by Gregory et al. (1991b). 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.

Heterosis due to B × B and C × C differed by 8.5 (5.0) kg of yearling weight. The same comparison for birth and weaning weight were -0.25 (0.63) and 0.57 (2.98), respectively. The differences between B × C and C × C for birth, weaning and yearling weight were 0.02 (0.50), 2.78 (2.41) and 4.8 (7.5) kg, respectively. The differences between B × B and B × C covariates indicated heavier birth and weaning weights for B × C heterosis while yearling weight heterotic effects were greater for B × B crosses with estimates of 0.26 (0.38), 2.22(1.80) and -3.70 (3.1), respectively. Two degrees of freedom orthogonal contrasts were estimated as the difference between crosses of British breeds and those of Continental breeds (B × B - C × C) and between crosses including both British and Continental breeds and the average of British only and Continental only crosses  $\{B \times C - [(B \times B + C \times C)/2]\}$ , the latter of which indicates asymmetry or a significant advantage or disadvantage of crosses comprised of more biologically diverse breeds. The overall contrasts were not significant for any of the traits analyzed, thus contrast estimates are not presented. Surprisingly, maternal heterosis was not significant for any of the traits analyzed. This may be because 75% of the dams were crossbred, meaning contrasts on maternal heterosis were limited.

Correlations among the estimates of fixed effects for yearling weight are presented in Table 3 to provide an assessment of the degree of confounding between various fixed effects in the model. For all 3 traits low to moderate correlations were observed between the fixed effects of B × B, B × C, and C × C. The moderate correlations among the estimates of those effects indicate slight confounding. The correlations among other fixed effects were low.

### ***Breed-Specific Heterosis Effects***

Breed specific estimates of heterosis are reported in Table 4. The breed-specific heterosis variance for birth weight from Model 2 was estimated to be 0. Because this component was the only difference between Models 1 and 2, results for Model 2 are not presented for birth weight. The breed × breed variance component from Model 2 only explained 1.07 and 1.57% of the phenotypic variance for weaning and yearling weights, respectively; neither was significantly different from 0.

Most of the breed-specific heterosis estimates were smaller than their respective standard errors. Model 2

**Table 3.** Estimates, standard errors (SE), and correlations among fixed effects for yearling weight (Model 2)

Effect <sup>1</sup>	Level <sup>2</sup>	Est., kg	SE, kg	P <	Mean	SexB	SexH	Sex S	B × C	B × B	C × C	Mat het.
Mean	I	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
B × C	I	14.04	3.11	0.00	0	0.00	-0.01	0	1	0.30	0.29	-0.09
B × B	I	18.48	4.34	0.01	0	0.02	0.00	0	0.30	1	0.10	0.00
C × C	I	9.32	4.92	0.03	0	0.01	-0.01	0	0.29	0.10	1	-0.09
Mat het.	I	3.32	2.67	0.88	0	0.08	0.00	0	0.09	0.00	-0.09	1

<sup>1</sup>B = British, C = Continental, Mat het. = maternal heterosis.

<sup>2</sup>B = bull, H = heifer, S = steer.

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

Model term <sup>1</sup>	WT205D <sup>2</sup> , kg	WT365D <sup>2</sup> , kg
B × B	6.10 (2.41)**	18.48 (4.34)***
B × C	8.21 (1.76)***	14.04 (3.11)***
C × C	6.00 (2.83)**	9.32 (4.92)*
Maternal heterosis	0.27 (1.84)	3.32 (2.67)
AN × HH	1.31 (1.99)	1.14 (3.72)
AN × AR	-2.69 (1.97)	-6.35 (3.66)
AN × CH	0.14 (1.80)	-2.76 (3.29)
AN × GV	-0.68 (1.88)	-3.26 (3.47)
AN × SM	2.09 (1.77)	2.02 (3.23)
AN × LM	-0.02 (1.89)	2.72 (3.49)
AN × MARCIII	-0.54 (1.59)	-5.18 (2.93)
HH × AR	1.32 (2.03)	5.07 (3.80)
HH × CH	-1.17 (1.95)	-1.10 (3.59)
HH × GV	0.66 (2.01)	-1.75 (3.72)
HH × SM	1.24 (1.89)	2.25 (3.47)
HH × LM	-1.23 (2.01)	0.60 (3.73)
HH × MARCIII	2.76 (1.70)	6.35 (3.14)
AR × CH	-0.89 (2.34)	-3.94 (4.43)
AR × GV	-1.68 (2.40)	1.12 (4.61)
AR × SM	2.59 (2.27)	5.10 (4.30)
AR × LM	-1.29 (2.41)	-1.21 (4.63)
AR × MARCIII	-0.99 (1.83)	-1.85 (3.39)
CH × GV	2.51 (2.32)	3.67 (4.41)
CH × SM	-0.81 (2.18)	0.03 (4.10)
CH × LM	-1.84 (2.32)	-3.15 (4.40)
CH × MARCIII	1.49 (1.82)	0.00 (3.37)
GV × SM	-0.48 (2.31)	-1.18 (4.39)
GV × LM	-1.14 (2.39)	-2.08 (4.59)
GV × MARCIII	0.23 (1.81)	0.62 (3.37)
SM × LM	1.83 (2.29)	2.92 (4.36)
SM × MARCIII	-0.41 (1.82)	-0.90 (3.38)
LM × MARCIII	-1.58 (1.82)	-0.56 (3.38)

<sup>1</sup>B=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).

<sup>2</sup>WT205D= adjusted weaning weight, WT365D= adjusted yearling weight.

\* P < 0.10.

\*\* P < 0.05.

\*\*\* P < 0.01

estimates of heterosis for the fixed biological type covariates were similar to Model 1. The B × C 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. The B × B proportions were significant for weaning and yearling weights with estimates of 6.10 (2.41) and 18.48 (4.34) kg, respectively. The C × C proportions were different from zero for weaning weight with an estimate of 6.00 (2.83) kg.

The breed × breed effects presented are deviations from the fixed biological type estimates that they were nested within. The largest estimates for weaning weight were from HH × MARC III, AN × SM, AR × SM, and CH × 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 × AR was -2.69 (1.97). The AN × 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 × AR, HH × MARCIII, and AR × SM, respectively. The estimate for AN × AR for yearling weight was -6.35 (3.66) kg. Estimates for the majority of the specific breed crosses were difficult to estimate, as indicated by the large standard errors, due to the structure of the data and limited numbers of animals representing each breed cross. The difficulty in estimation of the breed-specific heterosis variance component was not seemingly due to confounding. For yearling weight, correlations among the variance component estimates for Model 2 are presented in Table 5. They 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 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 breeding scheme in which more purebred or high-grade cattle are produced as contemporaries of the crossbreds would

**Table 5.** Estimates, standard errors (SE), and correlations among (co)variance components for yearling weight (Model 2)

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

<sup>1</sup> $\sigma^2_R$  = residual variance,  $\sigma^2_A$  = direct genetic variance,  $\sigma_{AM}$  = direct by maternal covariance,  $\sigma^2_M$  = maternal genetic variance,  $\sigma^2_{PE}$  = permanent environmental variance,  $\sigma^2_{B-S}$  = variance component for the breed-specific heterosis covariates nested within the fixed biological type covariates.

allow for better estimation of breed-specific heterosis and is currently being conducted at USMARC.

### ***Assumption of Heterosis Proportional to Breed Heterozygosity***

The heterosis estimates presented here are based primarily on comparisons between 3- and 4-way crosses and  $F_2$  and between  $F_1$  and backcrosses. There were relatively few purebred or high percentage cattle that were contemporaries of  $F_1$  cattle. Therefore, these heterosis estimates are quite dependent on the assumption that heterosis is proportional to expected breed heterozygosity.

The heterosis estimates presented here were similar to birth and weaning and larger than 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  $F_3$  and  $F_4$  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 previous studies suggest that heterosis in composite populations is underestimated based on expected breed heterozygosity.

Gregory et al. (1991b) found greater than expected levels of heterosis 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. 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).

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. 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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