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Covariance Components and Prediction for Additive and Nonadditive Preweaning Growth Genetic Effects in an Angus-Brahman Multibreed Herd¹

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ABSTRACT: Estimates of covariances and sire expected progeny differences of additive and nonadditive direct and maternal genetic effects for birth and weaning weights were obtained using records from 1,581 straightbred and crossbred calves from the Angus-Brahman multibreed herd at the University of Florida. Covariances were estimated by Restricted Maximum Likelihood, using a Generalized Expectation-Maximization algorithm applied to multibreed populations. Estimates of heritabilities and additive genetic correlations for straightbred and crossbred groups were within the ranges of values found in the literature for these traits. Maximum values of interactivities (ratios of nonadditive genetic variances to

phenotypic variances) and nonadditive correlations were somewhat smaller than heritabilities and additive genetic correlations. Sire additive and total direct and maternal genetic predictions for birth and weaning weight tended to increase with the fraction of Brahman alleles, whereas nonadditive direct and maternal genetic predictions were similar for sires of all Angus and Brahman fractions. These results showed that it is feasible to evaluate sires for additive and nonadditive genetic effects in a structured multibreed population. Data from purebred breeders and commercial producers will be needed to accomplish the same goal at a national level.

Key Words: Beef Cattle, REML, Genetic Variance, Growth, Populations

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Introduction

Most of the beef in the United States is produced by crossbred animals. The parents of these crossbred animals can be of different breeds or they may be crossbreds themselves. A population composed of straightbred and crossbred animals that interbreed constitutes a multibreed population (Elzo, 1983, 1990b; Elzo and Famula, 1985). In a multibreed population additive and nonadditive genetic effects should be accounted for in the genetic evaluation model. Thus, it seems appropriate that sires be evaluated for their general combining ability (multibreed additive expected progeny difference) and their specific combining abilities when mated to dams

of specific breed groups (multibreed nonadditive expected progeny differences). Currently, national beef cattle sire evaluations use intrabreed genetic prediction procedures, and comparisons of sires across breeds are computed using a table of correction factors obtained using experimental data from the Meat Animal Research Center (Notter and Cundiff, 1991; Van Vleck and Cundiff, 1996). The goal of these intrabreed and interbreed predictions is to compare sires for additive genetic effects. However, if animals of various breeds and crossbred groups participate in a multibreed mating scheme, then they need to be evaluated for additive and nonadditive genetic effects. Ideally a multibreed national cattle evaluation that uses field data and accounts for group and random additive and nonadditive genetic effects would need to be implemented (Elzo, 1996a). To help in the development and validation of genetic evaluation procedures for multibreed populations, an Angus-Brahman multibreed experimental herd was established at the University of Florida in 1988. Thus, the objectives of this study were to estimate genetic covariances and predict sire genetic values for additive and nonadditive direct and maternal genetic effects for birth weight and weaning weight in the Angus-Brahman herd using multibreed procedures.

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Table 1. Numbers of sires, maternal grandsires, dams, and calves by breed-group-of-sire × breed-group-of-dam combination

Breed group of dam	Breed group of sire					
	Angus (A)	$\frac{3}{4}$ A $\frac{1}{4}$ B	$\frac{1}{2}$ A $\frac{1}{2}$ B	$\frac{1}{4}$ A $\frac{3}{4}$ B	Brahman (B)	Brangus
Angus	16 ^a	7	9	10	15	16
	31 ^b	2	4	7	6	11
	69 ^c	24	22	28	40	40
	117 ^d	25	24	31	45	51
$\frac{3}{4}$ A $\frac{1}{4}$ B	13	9	9	9	17	13
	5	6	2	4	5	6
	13	20	23	22	24	29
	29	21	25	24	27	32
$\frac{1}{2}$ A $\frac{1}{2}$ B	16	11	9	11	18	15
	12	6	3	6	7	12
	50	36	38	47	54	50
	62	41	46	57	65	66
$\frac{1}{4}$ A $\frac{3}{4}$ B	11	6	7	7	12	10
	3	1	2	2	1	1
	21	16	23	16	25	24
	24	20	24	19	32	28
Brahman	13	11	9	11	20	16
	10	4	6	5	38	9
	45	40	36	43	107	44
	53	44	39	49	195	50
Brangus	10	7	8	10	12	16
	3	3	2	4	5	14
	21	15	19	23	23	66
	23	16	19	26	25	106
Total	16	11	10	11	20	17
	35	12	9	10	38	21
	229	150	162	178	271	250
	308	167	179	206	388	333

^aNumber of sires.^bNumber of known maternal grandsires.^cNumber of dams.^dNumber of calves.

Materials and Methods

Animals, Mating Strategy, and Records

The data set used consisted of 1,581 birth weight (**BW**) and 1,449 weaning weight (**WW**) records from 1,581 straightbred and crossbred calves born between 1989 and 1996 in the Angus (**A**)-Brahman (**B**) multibreed herd of the University of Florida. Calves were the product of a diallel mating strategy involving 16 A, 11 $\frac{3}{4}$ A $\frac{1}{4}$ B, 10 $\frac{1}{2}$ A $\frac{1}{2}$ B, 11 $\frac{1}{4}$ A $\frac{3}{4}$ B, 20 B, and 17 Brangus ($\frac{5}{8}$ A $\frac{3}{8}$ B) sires mated to 124 A, 78 $\frac{3}{4}$ A $\frac{1}{4}$ B, 127 $\frac{1}{2}$ A $\frac{1}{2}$ B, 68 $\frac{1}{4}$ A $\frac{3}{4}$ B, 160 B, and 94 Brangus dams. The representation of the different breed groups of sires and dams in the multibreed herd was primarily the result of availability of animals. A conscious effort was made to use semen and sires of different sources and parts of the country, but the resulting sets of sires within breed groups were not random samples. Semen was either donated by, or purchased from, AI organizations. Only semen from inexpensive bulls (less than \$20 per straw) was purchased. Most cleanup sires were either donated by, or purchased from, cooperat-

ing cattle producers. Semen was also collected from cleanup sires. A few crossbred AI and(or) cleanup sires were produced in the multibreed herd. Similarly, initial sets of dams were those available from other breeding experiments or donated by cooperating producers. Between two and five sires per breed group of sire were used in the mating program per year. Sires were used for 2 yr to create connectedness across years. The number of dams mated per breed group per year ranged from 14 ($\frac{3}{4}$ A $\frac{1}{4}$ B in 1990) to 74 (B in 1995). Table 1 shows the distribution of sires, maternal grandsires, dams, and calves per breed-group-of-sire × breed-group-of-dam subclass. The total number of bulls represented in the data set was 144. There were 29 bulls represented as sires only, 60 bulls appeared as maternal grandsires only, and 55 bulls were sires and maternal grandsires.

Cow-Calf Management and Contemporary Groups

Cows were maintained on bahiagrass (*Paspalum notatum*) pastures throughout the year with mineral supplementation. In winter (mid-December to

March), as part of a nutrition study, second-calf and older cows within a breed-group-of-dam \times breed-group-of-sire subclass were allocated to six replicated forage supplementation regimens and one control (13 supplementation groups). Supplementation was bermudagrass (*Cynodon dactylon*) hay wilted to several percentages of DM, urea, and molasses (Odenya et al., 1992). Heifers were not part of the winter supplementation study. Because none of the winter supplementation regimens was stressful to cows, it was assumed that their impact on maternal effects was negligible. Thus, dam winter supplementation group was only included as part of the definition of calf weaning contemporary groups. This was done to account for potential differences in weaning weight that might be attributable to differential calf consumption of winter supplemental feed supplied to their dams (e.g., molasses).

Estrus was synchronized in cows with PGF_{2 α} in March (A and crossbred AB) and April (B). Cows were artificially inseminated twice then assigned to one of six cleanup herds (one cleanup herd per breed group of sire) and exposed to a cleanup sire for 60 d. Estrus was synchronized in heifers, which were inseminated 2 wk earlier than cows. Braham dams were bred later than A and AB dams because of concerns with calf mortality of straightbred B calves. Cows that calved less than 45 d before the synchronization date were assigned to a second synchronization group (one for A and AB dams, and another for B dams). Thus, the insemination dates of A and AB dams overlapped with that of B dams. The cleanup periods for A and AB and for B dams also overlapped, and this caused the calving dates for all breed groups of dams to overlap as well. The staggered estrus synchronization and insemination (AI and natural service) system used in this multibreed herd created a continuous, albeit long, mating season, and consequently a single long calving season.

Calves were born from late December to March and weaned in September (calves from A and crossbred AB dams) and October (calves from B dams). Calves from B dams were weaned later to give them the opportunity to remain with their dams for approximately the same length of time as calves of A and AB dams. It should be emphasized that sires of all breed groups that were used as AI sires, cleanup sires, or as AI and cleanup sires in a breeding season were mated to dams of *all* breed groups (A, AB crossbred, and B dams). This mating strategy created connections among sires across all breed groups of dams within a breeding season. Because calves were born and weaned within a 3-mo period, and sires were well connected across all breed groups of dams within a breeding season, comparisons among sires could be fairly made across all breed groups of dams.

Multibreed contemporary groups were defined similarly to intrabreed contemporary groups (BIF, 1996), except that calves of all breed group combinations

were allowed in a contemporary group. Thus, multibreed contemporary groups were defined as follows: 1) birth contemporary group: group of calves that were born in the same calving year (1989 to 1996), within a period of 3 mo, and were of the same sex (1 = bull, 2 = heifer), and 2) weaning contemporary group: group of calves that were born in the same calving year (1989 to 1996), were of the same sex (1 = bull, 2 = heifer, 3 = steer), whose dams were in the same winter management group (13 winter supplementation groups), and were born, and also weaned, within a 3-mo period.

Multibreed Covariance Component Estimation and Genetic Prediction Procedures

Covariance components were estimated by Restricted Maximum Likelihood procedures (Harville, 1977) that used a Generalized Expectation-Maximization (**GEM**) algorithm (Dempster et al., 1977) applied to multibreed populations (**MREMLEM**, Elzo, 1994). Computations were performed using an in-house FORTRAN program compiled using XL FORTRAN for AIX, and run in an IBM RS6000 workstation, model 580. To ensure that estimates of covariance matrices were positive definite, the MREMLEM procedure computed the Cholesky elements of each covariance matrix first, and then each Cholesky matrix was multiplied by its transpose to obtain the matrices of covariance estimates (Elzo, 1996b).

Multibreed Model. The model used was a two-trait (BW and WW) multibreed sire-maternal grandsire model. Each trait was assumed to have both direct (**D**) and maternal (**M**) genetic effects.

Fixed environmental effects in the model were contemporary group and a covariate for age of dam within sex of calf and breed group of dam, where breed group was modeled as a regression on the fraction of A in the dam. The fixed regression group genetic effects were as follows: 1) intrabreed additive direct (as a function of the expected fraction of A alleles in all sires plus .5 the expected fraction of A alleles in all maternal grandsires), 2) intrabreed additive maternal (as a function of the expected fraction of A alleles in all maternal grandsires), 3) interbreed AB additive direct (as a function of the probability of A and B alleles in the parents of all sires plus .5 the probability of A and B alleles in the parents of all maternal grandsires), 4) interbreed AB additive maternal (as a function of the probability of A and B alleles in the parents of all maternal grandsires), 5) intralocus interbreed A/B nonadditive direct (as a function of the probability of A and B alleles at one locus of the progeny of all sires), 6) intralocus interbreed A/B nonadditive maternal (as a function of the probability of A and B alleles in one locus of the female progeny of all maternal grandsires, i.e., dams of calves), and 7) a combination of direct and maternal group genetic effects due to all maternal granddams (as a function

of the expected fraction of A alleles in the maternal granddam of the calf). Intrabreed additive genetic regression effects estimated the deviation between A and B group additive genetic effects. Interbreed additive genetic regression effects estimated the deviation between interbreed AB additive genetic group effects and intrabreed AA and BB as a function of the probability of A and B alleles being present in the *parents* of sires and maternal grandsires. Intralocus interbreed A/B nonadditive genetic regression effects estimated the difference between interbreed A/B and intrabreed A/A and B/B group genetic effects as a function of the probability of A and B alleles from different parents being paired at one locus in the *progeny* of sires and maternal grandsires.

Random effects in the model were as follows: 1) direct additive sire genetic effect, 2) direct additive maternal grandsire genetic effect, 3) maternal additive maternal grandsire genetic effect, 4) direct nonadditive sire genetic effect (as a function of intralocus interbreed A/B interactions in the progeny of a sire), 4) maternal nonadditive maternal grandsire genetic effect (as a function of intralocus interbreed A/B interactions in the dam), and 5) residual.

In matrix notation, the multibreed mixed model was as follows:

$$y = Xb + Z_g a g_a + Z_{gn} g_n + Z_{mgd} g_{mgd} + Z_a s_a + Z_n s_n + v$$

$$\begin{bmatrix} y \\ s_a \\ s_n \\ v \end{bmatrix} \sim MVN$$

$$\left\{ \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} Z_a G_a Z_a' + Z_n G_n Z_n' + R & Z_a G_a & Z_n G_n & R \\ & G_a & 0 & 0 \\ & G_a Z_n' & G_n & 0 \\ & R & 0 & 0 \end{bmatrix} \right\} \quad [1]$$

where

- y = vector of BW and WW calf records ordered by traits within calves,
- b = vector of contemporary groups (b_{cg}) and age of dam within sex of calf (b_{adx}) effects,
- g_a = vector of intrabreed A direct (g_{Aad}), intrabreed A maternal (g_{Aam}), interbreed AB direct (g_{ABad}), and interbreed AB maternal (g_{ABam}) additive genetic group effects,
- g_n = vector of interbreed A/B nonadditive direct ($g_{A/Bnd}$) and maternal ($g_{A/Bnm}$) genetic group effects,
- g_{mgd} = vector of maternal granddam genetic group effects,
- s_a = vector of sire additive direct (s_{ad}) and maternal (s_{am}) genetic effects,

s_n = vector of sire nonadditive direct (s_{nd}) and maternal (s_{nm}) genetic effects,

v = vector of residuals,

X = matrix that relates calf records to 1) to elements of b_{cg} (1s and 0s), and 2) to elements of b_{adx} through the age of the dam and the expected fraction of A alleles in the dam of the calf,

Z_{ga} = matrix that relates calf records to 1) elements of g_{Aad} through the expected fraction of A alleles in the sire and the maternal grandsire of the calf ($p_{As} + .5p_{Am}$), 2) elements of g_{Aam} through the expected fraction of A alleles in the maternal grandsire of the calf (p_{Am}), 3) elements of g_{ABad} through the probability of A and B alleles in the parents of the sire and of the maternal grandsire of the calf [$(p_{Ass} p_{Bss} + p_{Ads} p_{Bds}) + .5(p_{Asd} p_{Bsd} + p_{Add} p_{Bdd})$], and 4) elements of g_{ABam} through the probability of A and B alleles in the parents of the maternal grandsire of the calf ($p_{Asd} p_{Bsd} + p_{Add} p_{Bdd}$), where p = probability, and the subscripts A = Angus, B = Brahman, s = sire, m = maternal grandsire, ss = sire of sire, ds = dam of sire, sd = sire of dam (= maternal grandsire), dd = dam of dam,

Z_{gn} = matrix that relates calf records to 1) elements of g_{nd} through the probability of intralocus A and B alleles in the calf ($p_{As} p_{Bd} + p_{Bs} p_{Ad}$), and 2) elements of g_{nm} through the probability of intralocus A and B alleles in the dam of the calf ($p_{Asd} p_{Bdd} + p_{Bsd} p_{Add}$),

Z_a = matrix that relates calf records to 1) elements of s_{ad} through the sire (1) and the maternal grandsire (.5), and 2) elements of s_{am} through the maternal grandsire (1),

Z_n = matrix that relates calf records to 1) elements of s_{nd} through the probability of intralocus A and B alleles in the calf ($p_{As} p_{Bd} + p_{Bs} p_{Ad}$), and 2) elements of s_{nm} through the probability of intralocus A and B alleles in the dam of the calf ($p_{Asd} p_{Bdd} + p_{Bsd} p_{Add}$), and

Z_{mgd} = matrix that relates calf records to elements of g_{mgd} through the expected fraction of A alleles in the maternal granddam.

The multibreed model accounted for covariances among direct and maternal sire additive genetic effects. Similarly, covariances among direct and maternal sire nonadditive genetic effects were allowed. Thus, neither G_a nor G_n was block-diagonal. However, the residual covariance matrix R was block-diagonal, with 2×2 blocks, where 2 is the number of traits.

Multibreed Mixed Model Equations (MMME). The MMME for model [1] were as follows:

$$\begin{bmatrix}
 X'R^{-1}X & X'R^{-1}Z_{ga} & X'R^{-1}Z_{gn} & X'R^{-1}Z_{mgd} & X'R^{-1}Z_a & X'R^{-1}Z_n \\
 Z_{ga}'R^{-1}X & Z_{ga}'R^{-1}Z_{ga} & Z_{ga}'R^{-1}Z_{gn} & Z_{ga}'R^{-1}Z_{mgd} & Z_{ga}'R^{-1}Z_a & Z_{ga}'R^{-1}Z_n \\
 Z_{gn}'R^{-1}X & Z_{gn}'R^{-1}Z_{ga} & Z_{gn}'R^{-1}Z_{gn} & Z_{gn}'R^{-1}Z_{mgd} & Z_{gn}'R^{-1}Z_a & Z_{gn}'R^{-1}Z_n \\
 Z_{mgd}'R^{-1}X & Z_{mgd}'R^{-1}Z_{ga} & Z_{mgd}'R^{-1}Z_{gn} & Z_{mgd}'R^{-1}Z_{mgd} & Z_{mgd}'R^{-1}Z_a & Z_{mgd}'R^{-1}Z_n \\
 Z_a'R^{-1}X & Z_a'R^{-1}Z_{ga} & Z_a'R^{-1}Z_{gn} & Z_a'R^{-1}Z_{mgd} & Z_a'R^{-1}Z_a + G_a^{-1} & Z_a'R^{-1}Z_n \\
 Z_n'R^{-1}X & Z_n'R^{-1}Z_{ga} & Z_n'R^{-1}Z_{gn} & Z_n'R^{-1}Z_{mgd} & Z_n'R^{-1}Z_a & Z_n'R^{-1}Z_n + G_n^{-1}
 \end{bmatrix}
 \begin{bmatrix}
 b \\
 g_a \\
 g_n \\
 g_{mgd} \\
 s_a \\
 s_n
 \end{bmatrix}
 =
 \begin{bmatrix}
 X'R^{-1}y \\
 Z_{ga}'R^{-1}y \\
 Z_{gn}'R^{-1}y \\
 Z_{mgd}'R^{-1}y \\
 Z_a'R^{-1}y \\
 Z_n'R^{-1}y
 \end{bmatrix} \quad [2]$$

To facilitate computations, 1) equations for environmental effects were ordered by trait (BW, WW) within each environmental effect (b), and 2) equations for genetic effects were ordered by trait and effect (i.e., BW direct, WW direct, BW maternal, WW maternal) within each group (g_a, g_n, g_{mgd}) and sire (s_a, s_n) genetic effect.

Inverses of Covariance Matrices of Random Effects. The MMME require the inverses of G_a, G_n, and R. The inverse of G_a was obtained using the computational rules described in Elzo (1990b). The multibreed direct and maternal additive genetic covariances between BW and WW needed to obtain the coefficients used by the computational rules were computed using formula 1 in Elzo (1994). For the case of two breeds this formula becomes:

$$\text{cov}_a(w, z)_i = p_{Ai}(\sigma_{awz})_A + p_{Bi}(\sigma_{awz})_B + (p_{As}p_{Bs} + p_{Ad}p_{Bd})(\sigma_{awz})_{AB} \quad [3]$$

where w, z = two traits direct and(or) maternal (e.g., BW direct and BW direct, BW direct and WW maternal), the subscripts a = additive, A = Angus, B = Brahman, i = animal, s = sire of i, d = dam of i, and p_{Ax} = expected fraction of A in animal x, x = i, s, d, (σ_{awz})_X = intrabreed (X = A, B) additive genetic covariance between w and z, (σ_{awz})_{AB} = interbreed AB additive genetic covariance between traits w and z.

The inverse of G_n was computed using the recursive procedure for regression models (Elzo, 1990a) applied to the one locus case. The covariances used for the computation of G_n⁻¹ were direct and maternal intralocus interbreed A/B genetic covariances.

The inverse of R was computed directly because R is a block-diagonal, with 2 × 2 matrices of multibreed residual covariances for BW and WW. Multibreed residual covariances were computed as linear combinations of multibreed additive direct and maternal, nonadditive maternal (if the maternal grandsire was unknown), and multibreed environmental covariances (Elzo, 1994, 1996a).

Nonadditive maternal covariances included in the residual covariance due to unknown maternal grandsires were computed using formula 5 (Elzo, 1996a) applied to the case of two breeds; thus,

$$\text{cov}_n(w, z)_m = (p_{Asd}p_{Bdd} + p_{Bsd}p_{Add})(\sigma_{nwz})_{A/B} \quad [4]$$

where w, z = two traits (BW maternal, WW maternal), the subscripts n = nonadditive, m = maternal grandsire, A = Angus, B = Brahman, sd = sire of dam, dd = dam of dam, and p_{Axy} = expected fraction of A in animal xy, xy = ss, sd, and (σ_{nwz})_{AB} = intralocus interbreed A/B environmental covariance between traits w and z.

Multibreed environmental covariances were obtained by formula 2 (Elzo, 1994) for the case of two breeds; thus,

$$\text{cov}_3(w, z)_i = p_{Ai}(\sigma_{ewz})_A + p_{Bi}(\sigma_{ewz})_B + (p_{As}p_{Bs} + p_{Ad}p_{Bd})(\sigma_{ewz})_{AB} \quad [5]$$

where w, z = two traits (BW, WW), the subscripts e = environmental, A = Angus, B = Brahman, i = calf, s = sire of i, d = dam of i, and p_{Ax} = expected fraction of A in animal x, x = i, s, d, (σ_{ewz})_X = intrabreed (X = A, B) environmental covariance between w and z, and (σ_{ewz})_{AB} = interbreed AB environmental covariance between traits w and z.

The formula for the residual covariance between two traits (w and z) is a linear combination of direct and maternal additive (formula [3]), maternal nonadditive (formula [4]), and environmental (formula [5]) multibreed covariances; thus,

$$\text{cov}_v(w, z)_i = \text{cov}_a(w, z)_i - (\delta_s).25\text{cov}_a(w, z)_s - (\delta_m).0625\text{cov}_a(w, z)_m + (1 - \delta_m)\text{cov}_n(w, z)_m + \text{cov}_e(w, z)_i \quad [6]$$

where the superscripts i, s, and m refer to a calf, its sire, and its maternal grandsire, the subscripts v, a, n, and e represent residual, additive genetic, nonadditive genetic and environmental, and

$$\begin{aligned}
 \delta_x &= 1 \text{ if animal } x \text{ is identified, and zero otherwise, for } x = s, m, \\
 \text{cov}_a(w, z)_i &= \text{cov}_a(w_D, z_D)_i + \text{cov}_a(w_M, z_M)_d + .5 \text{cov}_a(w_D, z_M)_d + .5 \text{cov}_a(w_M, z_D)_d, \\
 &\text{where the subscripts } D = \text{direct, and } M = \text{maternal,} \\
 \text{cov}_a(w, z)_s &= \text{cov}_a(w_D, z_D)_s, \\
 \text{cov}_a(w, z)_m &= \text{cov}_a(w_D, z_D)_m + 4 \text{cov}_a(w_M, z_M)_m + 2 \text{cov}_a(w_D, z_M)_m + 2 \text{cov}_a(w_M, z_D)_m, \\
 \text{cov}_n(w, z)_m &= \text{cov}_n(w_M, z_M)_{sd},
 \end{aligned}$$

and cov_e(w, z)_i is computed by formula [5].

Computational Strategy. The MREMLEM algorithm (Elzo, 1994, 1996b) assumed that covariances among sire additive genetic effects, and among sire nonadditive genetic effects, were zero. This time, however, additive and nonadditive genetic covariances among sires were permitted in the multibreed model. Thus, instead of sire additive and nonadditive genetic predictions, residual sire additive and nonadditive genetic predictions were used to estimate covariance components. Because covariances among residual sire additive and nonadditive genetic effects across sires are zero the MREMLEM algorithm could now be used.

Consequently, an additional set of computations was added to the expectation step of the MREMLEM algorithm. First, as previously done (Elzo, 1994, 1996b), the inverse of the left-hand side of the MMME (Eq. [2]), and the predicted values of s_a and s_n , were obtained by sparse matrix techniques (FSPAK, Perez-Enciso et al., 1994). Second, the residual sire additive and nonadditive genetic predictions and their corresponding variances of prediction errors were computed as follows:

$$\hat{\varphi}_s = [1 \quad -.5 \quad -.25] \begin{bmatrix} \hat{s}_s \\ \hat{s}_{ss} \\ \hat{s}_{ms} \end{bmatrix}$$

$$\text{var}(\hat{\varphi}_s - \varphi_s) = [1 \quad -.5 \quad -.25] \begin{bmatrix} c_{s,s} & c_{s,ss} & c_{s,ms} \\ c_{ss,s} & c_{ss,ss} & c_{ss,ms} \\ c_{ms,s} & c_{ms,ss} & c_{ms,ms} \end{bmatrix} \begin{bmatrix} 1 \\ -.5 \\ -.25 \end{bmatrix} \quad [7]$$

where the subscripts s = sire, ss = sire of sire, ms = maternal grandsire of sire, \hat{s}_x = expected progeny difference of x , $x = s, ss$, and ms , for a particular trait and genetic effect (e.g., BW additive direct, WW nonadditive maternal), and $c_{x,x'}$ = x, x' th element of the inverse of the left-hand side of the MMME [2], for $x, x' = s, ss$, and ms , for a given trait and genetic effect. Predicted multibreed residuals and their error variances of prediction were computed as indicated in Elzo (1994). The remainder of the computations in the MREMLEM program followed the Cholesky maximization strategy outlined in Elzo (1996b).

Priors. Initial values used to start the two-trait MREMLEM iterations were single-trait MREMLEM estimates of covariances between direct and maternal genetic effects for BW and WW, and zeroes for all direct and maternal covariances between BW and WW. Convergence was reached when the ratio of the difference between the sum of squares of the absolute values between two successive GEM iterations relative to the sum of squares of the covariances of the previous GEM iteration was less than 10^{-4} in two consecutive GEM iterations.

Estimates of Genetic, Environmental, and Phenotypic Covariances. The MREMLEM procedure estimated the

upper triangular elements of the following *base* genetic and environmental covariance matrices at each GEM iteration: 1) three 4×4 additive direct and maternal (intra-breed A, intra-breed B, and interbreed AB), 2) one 4×4 nonadditive direct and maternal (interbreed A/B), and 3) three 2×2 environmental (intra-breed A, intra-breed B, and interbreed AB). Base intra-breed and interbreed environmental contained direct and maternal environmental effects. The elements of each estimated base additive and nonadditive genetic covariance matrix were $\text{var}(\text{BWD})$, $\text{cov}(\text{BWD}, \text{WWD})$, $\text{cov}(\text{BWD}, \text{BWM})$, $\text{cov}(\text{BWD}, \text{WWM})$, $\text{var}(\text{WWD})$, $\text{cov}(\text{WWD}, \text{WWD})$, $\text{cov}(\text{WWD}, \text{BWM})$, $\text{cov}(\text{WWD}, \text{WWM})$, $\text{var}(\text{BWM})$, $\text{cov}(\text{BWM}, \text{WWM})$, and $\text{var}(\text{WWM})$, where D = direct, and M = maternal. The elements of each estimated base environmental covariance matrix were $\text{var}(\text{BWE})$, $\text{cov}(\text{BWE}, \text{WWE})$, and $\text{var}(\text{WWE})$, where E = environmental.

Estimates of base covariance matrices were used to compute the multibreed covariance matrices needed by the MMME at every GEM iteration. Multibreed genetic and environmental covariance matrices for animals of all breed groups were computed as weighted sums of intra-breed and interbreed base covariances (formulas [3] and [5] above). Intra-breed weights were the expected breed composition of an animal, and interbreed weights were the sum of the products of the expected fractions of A and B in the parents of an animal. For example, if the additive intra-breed A, intra-breed B, and interbreed AB covariances for direct BW genetic effects are 9, 12, and 4 kg^2 , then, by formula [3], the multibreed additive genetic covariance for a $\frac{3}{4}A \frac{1}{4}B$ sire will be equal to $[(.75)(9) + (.25)(12) + [(1)(0) + (.5)(.5)](4)](4) = 10.75 \text{ kg}^2$. A similar set of computations was done to obtain multibreed environmental covariances (formula [5]) for each animal with records.

Random nonadditive genetic effects due to sire \times breed-group-of-dam interactions were assumed to be a function of intralocus interbreed A/B interactions occurring in all sire \times breed-group-of-dam subclasses from a particular sire. Consequently, the nonadditive covariance matrix used for all sires was equal to the base nonadditive covariance matrix. Had a subclass approach been used to model sire \times breed-group-of-dam interactions, multibreed nonadditive covariances would have been computed as a weighted sum of base nonadditive covariances (Elzo, 1996b). In general, multibreed covariances (additive, nonadditive, and environmental) would be computed as weighted sums of base covariances for random subclass effects, and they would be equal to base covariances for random regression effects.

Genetic Parameters. Ratios of additive genetic variances to phenotypic variances (heritabilities), ratios of nonadditive genetic variances to phenotypic variances (interactibilities), additive and nonadditive

genetic correlations, environmental correlations, and phenotypic correlations were computed for five parental breed group combinations (A × A, B × B, A × B, ½A ½B × A, and ½A ½B × ¾A ¼B). The required multibreed additive direct and maternal genetic covariances were computed as described above.

Nonadditive covariances for specific sire × breed-group-of-dam combinations were computed as the product of the probability of intralocus interbreed combinations in this mating times the base nonadditive covariance matrix (formula [4]). For example, if the base nonadditive intralocus interbreed covariance for BW direct were 7 kg², then by formula [4], the nonadditive covariance for BW direct in the progeny of A × B matings would be [(1)(1) + (0)(0)](7) = 7 kg².

Phenotypic covariances were computed by adding the appropriate additive, and nonadditive direct and maternal variances and covariances, and environmental covariances; thus,

$$\begin{aligned} \text{cov}_p(w, z) = & \text{cov}_a(w_{D,ZD})_i + \text{cov}_a(w_{M,ZM})_d + .5 \\ & \text{cov}_a(w_{D,ZM})_d + .5 \text{cov}_a(w_{M,ZD})_d + \\ & \text{cov}_n(w_{D,ZD})_s + \text{cov}_n(w_{M,ZM})_m + .5 \\ & \text{cov}_n(w_{D,ZM})_m + .5 \text{cov}_n(w_{M,ZD})_m + \\ & \text{cov}_e(w, z) \end{aligned} \quad [8]$$

where w and z are two traits (e.g., BW and WW), and the subscripts p = phenotypic, a = additive, n = nonadditive, e = environmental, i = calf, d = dam, s = sire, m = maternal grandsire, D = direct, M = maternal. Direct and maternal additive genetic covariances in formula [8] are obtained by formula [3], direct and maternal nonadditive genetic covariances by formula [4], and environmental covariances by formula [5]. As an example, consider the computation of the phenotypic variance of BW for calves of breed group ¾A ¼B, which are progeny of unrelated A sires and ½A ½B (F₁) dams. Assume that 1) the additive intrabreed A, intrabreed B, and interbreed AB covariances a) for direct BW genetic effects are 9 kg², 12 kg², and 4 kg², b) for maternal BW genetic effects are 6, 14, and 2 kg², and c) between BW direct and maternal genetic effects are 0, -2, and -4 kg², 2) the nonadditive interbreed A/B covariance a) for direct BW genetic effects is 7 kg², b) for maternal BW genetic effects is 6 kg², and c) between direct and maternal BW genetic effects is 0 kg², and 3) the environmental intrabreed A, intrabreed B, and interbreed AB variances for BW are 18, 22, and 16 kg², respectively. The values of the covariances needed to compute the phenotypic variance of BW for the ¾A ¼B calf are as follows: 1) $\text{cov}_a(w_{D,ZD})_i = [.75](9) + [.25](12) + [(1)(0) + (.5)(.5)](4) = 10.75 \text{ kg}^2$, 2) $\text{cov}_a(w_{M,ZM})_d = [.5](6) + [.5](14) + [0](2) = 10.0 \text{ kg}^2$, 3) $\text{cov}_a(w_{D,ZM})_d = \text{cov}_a(w_{M,ZD})_d = [[.5](0) + [.5](-2) + [(1)(0) + (0)(1)](-4)] = -1.0 \text{ kg}^2$, 4) $\text{cov}_n(w_{D,ZD})_s = [(1.0)(.5) + (.0)(.5)](7) = 3.5 \text{ kg}^2$, 5)

$\text{cov}_n(w_{M,ZM})_m = [(1.0)(1.0) + (0)(0)](6) = 6.0 \text{ kg}^2$, 6) $\text{cov}_n(w_{D,ZM})_m = \text{cov}_n(w_{M,ZD})_m = [(1)(0) + (0)(1)](0) = 0 \text{ kg}^2$, and 7) $\text{cov}_e(w, z) = [.75](18) + [.25](22) + [(1)(0) + (.5)(.5)](16) = 23.0 \text{ kg}^2$. Thus, by formula [8], the phenotypic variance of BW for the ¾A ¼B calf is equal to $[10.75 + 10.0 + 2(.5)(-1.0) + 3.5 + 6.0 + 2(.5)(0) + 23.0] = 52.25 \text{ kg}^2$.

Multibreed Genetic Predictions. Additive and nonadditive direct and maternal multibreed expected progeny differences (**MEPD**) for sires were obtained by solving the MMME with the estimates of covariances obtained at convergence.

Additive and nonadditive direct and maternal sire MEPD were obtained as the sum of a genetic group component (fixed) and a deviation from it (random). Genetic groups were defined in terms of the genetic components contained in the additive and nonadditive direct and maternal random genetic effects. Sire additive genetic groups were defined as a linear function of intrabreed (g_{Aa}) and interbreed (g_{ABa}) additive genetic group effects. Similarly, sire nonadditive genetic groups were defined as a linear function of intralocus interbreed nonadditive (g_n) genetic group effects. Thus, additive and nonadditive genetic groups were computed as linear functions of the estimates of regression genetic group effects from the MMME. However, sire additive (s_a) and nonadditive (s_n) deviations were obtained directly from the solutions to the MMME.

The linear function used to compute sire MEPD for additive direct and maternal genetic effects was a weighted sum of direct and maternal sire additive intrabreed and interbreed group genetic effects, plus sire additive random genetic effects. Intrabreed additive weights were the expected fractions of A alleles in the sires themselves. Interbreed additive weights were the sum of the products of expected A and B fractions in the parents of each sire. Thus,

$$\hat{u}_{ai} = p_{Ai}\hat{g}_{Aa} + (p_{As}p_{Bs} + p_{Ad}p_{Bd})\hat{g}_{ABa} + \hat{s}_{ai} \quad [9]$$

where \hat{u}_{ai} = direct or maternal additive MEPD for sire i , p_{Xk} = expected fraction of breed X (X = A, B) in the breed group of animal k , $k = i, s$ (sire of sire i), d (dam of sire i), \hat{g}_{Aa} = generalized least squares estimate of $g_{Aa} - g_{Ba}$, \hat{g}_{ABa} = generalized least squares estimate of $g_{ABa} - .5(g_{AAa} + g_{BBa})$, and \hat{s}_{ai} = best linear unbiased predictor of s_{ai} .

Nonadditive direct and maternal sire MEPD were computed as the sum of their direct and maternal nonadditive intrabreed intralocus group and random genetic effects. Thus,

$$\hat{u}_{ni} = (p_{Ai}p_{Bd} + p_{Bi}p_{Ad})(\hat{g}_n + \hat{s}_{ni}) \quad [10]$$

where \hat{u}_{ni} = direct or maternal nonadditive MEPD for sire i , p_{Xi} = expected fraction of breed X (X = A, B) in

Table 2. Estimates of base additive and nonadditive genetic covariances for birth weight and weaning weight

Trait pair ^a	Genetic covariances, kg ²			
	Additive intrabreed A	Additive intrabreed B	Additive interbreed AB	Additive interbreed A/B
BWD, BWD	6.41	7.60	.21	5.47
BWD, WWD	7.09	10.50	1.35	4.97
BWD, BWM	.03	-.32	-2.66	.14
BWD, WWM	-.90	1.62	-8.26	-.36
WWD, WWD	138.01	208.53	8.64	138.78
WWD, BWM	.89	2.80	-17.05	1.10
WWD, WWM	-32.70	-39.91	-51.52	3.11
BWM, BWM	4.90	5.87	33.74	5.95
BWM, WWM	1.09	2.82	105.61	3.52
WWM, WWM	100.44	151.69	751.69	154.82

^aD = direct; M = maternal.

sire i , p_{Xd} = expected fraction of breed X ($X = A, B$) in dams of breed group d mated to sire i , \hat{g}_n = generalized least squares estimate of $g_{A/Bn} - .5(g_{A/An} + g_{B/Bn})$, and \hat{s}_{ni} = best linear unbiased predictor of S_{ni} .

Total sire MEPD were computed as the sum of sire additive MEPD and sire nonadditive MEPD:

$$\hat{u}_{ti} = \hat{u}_{ai} + \hat{u}_{ni} \quad [11]$$

Nonadditive and total MEPD were computed here assuming that sires had been mated to $\frac{1}{2}A \frac{1}{2}B$ dams. Dams of breed group $\frac{1}{2}A \frac{1}{2}B$ were chosen because the probabilities of intralocus interbreed A/B interactions are the same (.5) for sires of any A and B fractions. Thus, sires of any A and B fractions can be compared on an equal basis for all direct and maternal genetic effects (additive, nonadditive, and total).

To illustrate the computation of additive, nonadditive, and total MEPD, assume that 1) the additive intrabreed and interbreed, and the nonadditive interbreed genetic values for WW are -8, -14, and 20 kg, 2) the intragroup additive and nonadditive predictions of a $\frac{1}{4}A \frac{3}{4}B$ sire are 6 and 9 kg, and 3) the $\frac{1}{4}A \frac{3}{4}B$ sire will be mated to A dams. This sire's additive direct MEPD (formula [9]) is equal to $[(.25)(-8) + [(.5)(.5) + (0)(0)](-14) + (6) = .5$ kg, its nonadditive MEPD (formula [10]) is $[(.25)(0) + (.75)(1)](20) + [(.25)(0) + (.75)(1)](9) = 21.75$ kg, and its total MEPD (formula [11]) is $.5 + 21.75 = 22.25$ kg.

Results and Discussion

Covariance Components and Genetic Parameters

The MREMLEM estimates of base intrabreed and interbreed additive, and interbreed nonadditive genetic covariances are shown in Table 2, and those of base intrabreed and interbreed environmental covariances are in Table 3. It took 5 GEM iterations and

11.7 min for the MREMLEM program to achieve convergence. Tables 4 and 5 contain genetic parameters for straightbred and crossbred groups. Table 4 contains heritabilities, and additive genetic, environmental, and phenotypic correlations for five parental breed group combinations ($A \times A$, $B \times B$, $A \times B$, $\frac{1}{2}A \frac{1}{2}B \times A$, and $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$). These breed group combinations were chosen to illustrate estimates of genetic parameters in straightbred animals (progeny of $A \times A$, and $B \times B$ parents), crossbred animals without interbreed additive but with nonadditive direct genetic effects (progeny of $A \times B$ parents), crossbred animals with interbreed additive and nonadditive direct genetic effects (progeny of $\frac{1}{2}A \frac{1}{2}B \times A$ parents), and crossbred animals with interbreed additive and nonadditive direct and maternal genetic effects (progeny of $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$ parents). Table 5 contains the ratios of nonadditive genetic variances to phenotypic covariances (interactibilities) and nonadditive genetic correlations for three parental breed group combinations whose progeny are expected to show intralocus interbreed A/B interaction effects ($A \times B$, $\frac{1}{2}A \frac{1}{2}B \times A$, and $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$).

Intrabreed heritability estimates were of medium size for direct and maternal effects of BW and WW, although they were somewhat larger for direct genetic effects (.22 (A) and .23 (B) for BWD, and .25 (A) and .29 (B) for WWD) than for maternal genetic effects (.17 (A) and .18 (B) for BWM, and .18 (A)

Table 3. Estimates of base environmental covariances for birth weight and weaning weight

Trait pair	Environmental covariances, kg ²		
	Intrabreed A	Intrabreed B	Interbreed AB
BW, BW	17.51	19.40	8.19
BW, WW	21.61	23.79	-5.75
WW, WW	356.17	408.24	12.56

Table 4. Estimates of heritabilities, and additive genetic, environmental, and phenotypic correlations for birth weight (BW) and weaning weight (WW)

Parameter ^a	Breed group combination					
	A × A	B × B	A × B	½A ½B × A	½A ½B × ¾A ¼B	
h ² (BWD)	.22	.23	.19	.16	.13	
r _A (BWD, WWD)	.24	.26	.25	.25	.26	
r _A (BWD, BWM)	.01	-.05	-.02	-.08	-.11	
r _A (BWD, WWM)	-.04	.05	.01	-.05	-.06	
h ² (WWD)	.25	.29	.22	.18	.15	
r _A (WWD, BWM)	.03	.08	.06	-.06	-.10	
r _A (WWD, WWM)	-.28	-.22	-.25	-.22	-.21	
h ² (BWM)	.17	.18	.15	.32	.38	
r _A (BWM, WWM)	.05	.09	.07	.44	.51	
h ² (WWM)	.18	.21	.16	.35	.41	
r _E (BW, WW)	.27	.27	.27	.24	.22	
r _P (BW, WW)	.23	.27	.24	.28	.30	

^ah² = heritability; r_A = additive genetic correlation; r_E = environmental correlation; r_P = phenotypic correlation; D = direct; M = maternal.

and .21 (B) for WWM). Estimates of additive genetic correlations were close to zero (-.05 to .09), except for those between BWD and WWD (.24 (A) and .26 (B)), and between WWD and WWM (-.28 (A) and -.22 (B)). Estimates of intrabreed additive genetic covariances, heritabilities and genetic correlations obtained here were similar to those estimated with field data for these two breeds by researchers at the University of Georgia (Kriese et al., 1991; Pollak et al., 1994, reporting covariances estimated at the University of Georgia; A. Nelson, personal communication). Thus, it seems that the animals in the AB multibreed herd had a reasonable representation of the A and B populations in the country.

The pattern of values of interbreed additive genetic covariance estimates were substantially different from intrabreed covariances (Table 2). Additive direct interbreed genetic variances were much smaller than intrabreed ones. Additive maternal genetic variances, however, were much larger than intrabreed ones. Additive interbreed covariances also tended to be of larger absolute value than intrabreed additive covariances. These patterns were observed to a much lesser extent in the covariance estimates from the single-trait runs used as priors. Thus, a factor that must have contributed to these differences is the small size of the data set relative to the large number of covariances (49) being estimated in the two-trait run. Another factor that might be relevant is the fact that only data from progeny of crossbred parents help estimate interbreed additive covariances. Thus, a larger variety of crossbred parents in the multibreed population should yield better estimates of interbreed additive covariances.

Despite seemingly poor estimates of interbreed additive covariances, estimates of genetic parameters in progeny groups from parental mating groups with interbreed additive variation (e.g., progeny from ½A ½B × ¾A ¼B parents, Table 4) were reasonable. Because of the values estimated for interbreed addi-

tive variances, 1) heritability estimates for direct genetic effects were smaller in progeny groups with interbreed additive variation (e.g., .13 for BWD, and .15 for WWD, in progeny from ½A ½B × ¾A ¼B parents) than those in progeny groups without interbreed additive variation (e.g., .19 for BWD, and .22 for WWD, in progeny from A × B parents), and 2) heritability estimates for maternal genetic effects were larger in progeny groups with interbreed additive variation (e.g., .38 for BWM, and .41 for WWM, in progeny from ½A ½B × ¾A ¼B parents) than those of progeny groups without interbreed additive variation (e.g., .15 for BWM, and .16 for WWM, in progeny from A × B parents). Similarly, estimates of additive genetic correlations tended to be larger in progeny groups in which interbreed variation was expected to be present (Table 4).

Estimates of intralocus interbreed A/B nonadditive covariances due to sire × breed-group-of-dam interac-

Table 5. Estimates of interactibilities and nonadditive genetic correlations for birth weight (BW) and weaning weight (WW)

Parameter ^a	A × B	½A ½B × A		½A ½B × ¾A ¼B	
		½A ½B	¾A ¼B	½A ½B	¾A ¼B
i ² (BWD)	.15	.06	.05		
r _N (BWD, WWD)	.18	.18	.18		
r _N (BWD, BWM)	.03	.03	.03		
r _N (BWD, WWM)	-.01	-.01	-.01		
i ² (WWD)	.18	.08	.06		
r _N (WWD, BWM)	.04	.04	.04		
r _N (WWD, WWM)	.02	.02	.02		
i ² (BWM)	.16	.07	.06		
r _N (BWM, WWM)	.12	.12	.12		
i ₂ (WWM)	.20	.09	.07		

^ai² = interactibility (ratio of intralocus interbreed genetic variance to phenotypic variance); r_N = nonadditive genetic correlation; D = direct; M = maternal.

tions yielded estimates similar in size and pattern to additive intrabreed covariances (Table 2). The largest difference between estimates of intrabreed additive and nonadditive genetic covariances were those between WWD and WWM, which were negative for intrabreed additive covariances in A (-32.70 kg^2) and B (-39.91 kg^2), but positive for the A/B nonadditive genetic covariance (3.11 kg^2). These nonadditive covariance estimates represent maximum values, and are attained only in crossbred calves produced by the mating of straightbred parents. Thus, interactibilities must be computed for each mating type. Nonadditive interbreed A/B correlations, however, need to be computed only once because the expected fraction of A/B interactions in the numerator and the denominator will cancel each other out; thus, they will be the same for progeny groups of any AB expected fractions.

Maximum interactibility estimates (i.e., $A \times B$, Table 5) were similar to intrabreed heritabilities (Table 4). However, interactibility estimates showed a pattern opposite to those of heritabilities; interactibility estimates for direct nonadditive genetic effects were somewhat smaller than those for maternal nonadditive genetic effects (e.g., .15 for BWD, .18 for WWD, .16 for BWM, and .20 for WWM, in $A \times B$). Nonadditive interbreed A/B correlations were all low ($-.01$ to .18). Estimates of interactibilities for progeny groups other than those produced by the mating of straightbred parents will be $\leq 50\%$ of the interactibility values of the F_1 breed group (e.g., the interactibility in the progeny group of $\frac{1}{2}A \frac{1}{2}B \times B$ parents drops to .06 for BWD; Table 5).

The main point here is that interactibility estimates were **not** zero. Thus, nonadditive interbreed A/B genetic effects due to sire \times breed-group-of-dam interactions will need to be accounted for when sires are used in crossbreeding programs, because sires from the same breed group will **not** necessarily have the same interbreed combining ability.

Multibreed Genetic Predictions

Sires in a multibreed population can be compared for additive, nonadditive, and total genetic effects. These MEPD can be used to compare sires of *several* AB breed fractions when mated to dams of *any* AB breed composition. However, comparison of sires for nonadditive genetic effects involves the probability of occurrence of interbreed intralocus nonadditive effects in the progeny of a specific mating. This probability will usually be different for sires of various A and B breed fractions unless they are (or assumed to be) mated to $\frac{1}{2}A \frac{1}{2}B$ dams. Thus, to be able to compare the ability of sires of all breed groups for all genetic effects (additive, nonadditive, and total) on an equal basis, they were assumed to be mated to $\frac{1}{2}A \frac{1}{2}B$ dams. This option was used here because it simplified the comparison of nonadditive and total MEPD of sires of different AB breed composition; no mention of

different probabilities of intralocus interbreed interactions for sires of various breed compositions needed to be made. Commercial producers trying to choose bulls for total MEPD should compare sires of various breed compositions when (assumed to be) mated to dams of each breed group present in their herds. For example, if a commercial herd had six mating groups of dams as those defined for the AB multibreed herd (A, $\frac{3}{4}A \frac{1}{4}B$, $\frac{1}{2}A \frac{1}{2}B$, $\frac{1}{4}A \frac{3}{4}B$, B, and Brangus), it would need six separate lists of sire total MEPD (one for each breed group of dams). Simplifying assumptions will probably be needed when defining breed groups of dams in commercial herds to keep the number of sire comparisons within mating type to a minimum.

Table 6 contains means and ranges of sire additive, nonadditive, and total direct and maternal genetic effects for BW and WW, when sires are mated to $\frac{1}{2}A \frac{1}{2}B$ dams. The means (ranges) of the standard error of predictions (SEP), considering all sires in the multibreed herd, were 1.3 (.8, 1.6) kg for BW additive direct, 6.6 (4.3, 7.9) kg for WW additive direct, 1.5 (.7, 2.4) kg for BW additive maternal, 7.3 (3.6, 11.2) kg for WW additive maternal, .5 (.2, .6) kg for BW nonadditive direct, 2.5 (1.4, 2.8) kg for WW nonadditive direct, .5 (.2, .5) kg for BW nonadditive maternal, 2.5 (1.2, 2.8) kg for WW nonadditive maternal, 1.9 (1.1, 2.2) for BW total direct, 9.1 (5.8, 10.7) kg for WW total direct, 2.0 (1.0, 2.9) kg for BW total maternal, and 9.8 (5.2, 14.0) kg for WW total maternal.

Additive Genetic Predictions. Mean MEPD for BW additive direct genetic effects tended to increase along with the B fraction in the sire. Thus, the lowest BW additive direct sire MEPD occurred in A sires, the largest one was that of B sires, and crossbred sires had intermediate values. Brangus sires were comparable to $\frac{1}{2}A \frac{1}{2}B$ sires. A similar trend was observed with the mean WW additive MEPD, but, this time, Brangus sires were closer to $\frac{3}{4}A \frac{1}{4}B$ sires than to $\frac{1}{2}A \frac{1}{2}B$ sires. Ranges of BW and WW additive direct MEPD within breed groups of sires supported these trends. No such trend occurred with the means and ranges of BW additive maternal MEPD, and the ranges showed that there were sires with low as well as high BW additive maternal MEPD values in all breed groups. Mean values were also smaller for A and crossbred sires for WW additive maternal MEPD than for B or Brangus. Despite all these differences in mean BW and WW additive MEPD for direct and maternal genetic effects, except for BW additive direct, there was overlapping of ranges across breed groups of sires. Thus, sires of comparable MEPD existed in these six breed groups, except for BW additive direct genetic effects.

Nonadditive Genetic Predictions. Means and ranges of nonadditive genetic predictions showed a different trend from that found in additive genetic predictions; they tended to be similar across breed groups of sires. All values of means and ranges (except for one lower

Table 6. Means and ranges of additive, nonadditive, and total multibreed expected progeny differences of sires mated to $\frac{1}{2}$ A $\frac{1}{2}$ B dams for birth weight (BW) and weaning weight (WW)

Genetic effect ^a	Breed group of sire					
	Angus (A)	$\frac{3}{4}$ A $\frac{1}{4}$ B	$\frac{1}{2}$ A $\frac{1}{2}$ B	$\frac{1}{4}$ A $\frac{3}{4}$ B	Brahman (B)	Brangus
BWAD	-4.0 ^b (-5.2, -2.6) ^c	-2.6 (-3.2, -1.3)	-2.2 (-3.2, -1.1)	-6 (-1.9, 1.0)	.0 (-1.1, 1.5)	-2.3 (-3.1, -.4)
BWND	1.2 (.5, 1.8)	1.1 (.5, 1.7)	1.1 (.6, 2.0)	1.3 (.1, 2.6)	1.2 (.7, 2.2)	1.2 (.6, 2.8)
BWTD	-2.8 (-4.1, -.8)	-1.6 (-2.8, .3)	-1.2 (-2.5, .9)	.7 (-1.9, 3.6)	1.2 (-.4, 2.9)	-1.1 (-2.6, 2.4)
WWAD	-7.9 (-10.6, -.9)	-6.1 (-9.6, -2.3)	-5.2 (-11.1, -2.2)	-2.2 (-9.4, 2.3)	.2 (-11.2, 9.9)	-6.3 (-10.6, .7)
WWND	11.0 (8.5, 15.9)	9.8 (4.9, 12.9)	9.9 (5.8, 12.8)	10.5 (4.3, 13.3)	10.6 (3.8, 16.4)	10.5 (7.5, 18.0)
WWTD	3.1 (-1.5, 11.1)	3.7 (-2.1, 10.6)	4.8 (-5.4, 10.6)	8.3 (-5.2, 15.6)	10.7 (-7.4, 21.7)	4.2 (-3.2, 18.7)
BWAM	.8 (-.4, 2.2)	-.1 (-1.9, .9)	.4 (-.7, 2.3)	-.3 (-1.1, .4)	.0 (-1.3, 1.2)	.0 (-2.3, 2.4)
BWNM	1.0 (.3, 1.8)	.9 (.2, 1.3)	.8 (-.3, 1.6)	1.0 (.6, 1.8)	.9 (.2, 1.5)	1.0 (.5, 1.5)
BWTM	1.8 (.5, 3.1)	.8 (-1.7, 2.2)	1.2 (-1.0, 3.9)	.7 (-.6, 1.9)	.9 (-.4, 2.1)	1.1 (-1.9, 3.8)
WWAM	-6.3 (-9.8, -3.3)	-11.1 (-18.9, -8.2)	-3.3 (-5.4, -1.0)	-7.9 (-13.4, -3.0)	.0 (-6.1, 6.9)	.0 (-27.2, 1.4)
WWNM	22.8 (18.7, 26.1)	22.6 (18.3, 24.4)	22.5 (20.6, 24.5)	21.9 (17.8, 24.2)	22.7 (19.4, 25.1)	22.8 (18.4, 26.7)
WWTM	16.5 (12.9, 20.8)	11.5 (-.6, 15.8)	19.1 (15.2, 23.5)	14.0 (6.2, 20.6)	22.7 (14.3, 28.4)	9.5 (-8.8, 28.1)

^aAD(M) = additive direct (maternal); ND(M) = nonadditive direct (maternal); TD(M) = total direct (maternal).

^bMean of sire expected progeny differences.

^c(Smallest, largest) sire expected progeny differences.

range for BW nonadditive maternal) were positive, indicating that intralocus interbreed A/B genetic effects would usually cause an increase in BW and WW in the progeny of these sires. Thus, intralocus interbreed A/B genetic effects should be considered if BW needs to be controlled for calving ease purposes. Nonadditive BW direct and maternal MEPD were similar. However, nonadditive WW maternal MEPD were twice as large as nonadditive WW direct MEPD.

Total Genetic Predictions. Because of the similarity of mean nonadditive MEPD genetic values, the pattern of mean total MEPD across breed groups of sires was similar to the pattern found for mean additive MEPD; except for the mean total MEPD for BW maternal, mean total MEPD for BW direct, WW direct, and WW maternal, tended to increase from the A to the B breed group of sires. However, the ranges of total MEPD across breed groups of sires showed that there were sires with low and high total MEPD in the six breed groups of sires.

Relationship Between Additive, Nonadditive, and Total MEPD. Correlations between additive and nonadditive MEPD within traits and effects (Table 7) ranged from low to medium (.25 for BW direct, .20 for WW direct, .40 for BW maternal, and .32 for WW

maternal), those between additive and total MEPD were high (.98 for BW direct, .94 for WW direct, .96 for BW maternal, and .98 for WW maternal), and those between nonadditive and total MEPD were of medium size (.42 for BW direct, .53 for WW direct, .65 for BW maternal, and .52 for WW maternal). Correlations between additive and nonadditive MEPD across traits were smaller than those within traits, particularly those across genetic effects (Table 7). These correlations indicated that, in this multibreed herd, 1) there were sires that had high additive MEPD and low nonadditive MEPD, and vice versa, 2) there were sires with similar additive MEPD, but different nonadditive MEPD, and vice versa, and 3) differences between additive and nonadditive sire MEPD tended to disappear when total MEPD were computed.

To illustrate the existence of sires with these characteristics consider the MEPD of four sires for WW direct additive (**WWAD**), nonadditive (**WWND**), and total (**WWTD**) genetic effects when mated to $\frac{1}{2}$ A $\frac{1}{2}$ B dams: 1) sire 17 (B) had an average MEPD for WWAD (.7 kg), a high MEPD for WWND (16.4 kg), and a high MEPD for WWTD (17.1 kg), 2) sire 74 ($\frac{3}{4}$ A $\frac{1}{4}$ B) had the same MEPD for WWAD (.7 kg) as B sire 17 but a low MEPD for WWND (10.8 kg),

Table 7. Correlations between additive, nonadditive, and total multibreed expected progeny differences of sires mated to 1/2A 1/2B dams for birth weight (BW) and weaning weight (WW)

Genetic effect ^a	Genetic effect ^a										
	WW	BW	WW	BW	WW	BW	WW	BW	WW	BW	WW
	AD	AM	AM	ND	ND	NM	NM	TD	TD	TM	TM
BWAD	.86	-.44	.41	.25	.03	.0	-.11	.98	.76	-.36	.35
WWAD		-.29	.43	.27	.20	.01	-.12	.86	.94	-.23	.36
BWAM			.22	-.12	.14	.40	.40	-.43	-.20	.96	.29
WWAM				-.07	-.03	-.04	.32	.38	.36	.17	.98
BWND					.50	.15	-.06	.42	.41	-.06	-.08
WWND						.27	.06	.12	.53	.21	-.01
BWNM							.31	.03	.10	.65	.03
WWNM								-.11	-.08	.43	.52
BWTD									.79	-.35	.32
WWTD										-.13	.31
BWTM											.25

^aAD(M) = additive direct (maternal); ND(M) = nonadditive direct (maternal); TD(M) = total direct (maternal).

which yielded a medium MEPD for WWTD (11.5 kg), 3) sire 124 (A) had a low MEPD for WWAD (-9.8 kg), a high MEPD for WWND (15.9 kg), and a rather low MEPD for WWTD (6.1 kg), and 4) sire 114 (B) had a high MEPD for WWAD (9.7 kg), a low MEPD for WWND (7.9 kg), and a high MEPD for WWTD (17.6 kg). However, when choosing sires for crossbreeding BW and WW need to be considered. Let the objective be to find a sire that has an MEPD for BW direct total (**BWTD**) close to zero, and a positive MEPD for WWTD genetic effects *when mated to dams of a particular breed composition*. Assume that the sire will be mated to 1/2A 1/2B dams. Three sires in the AB multibreed herd met these conditions: sire 66 (A) had a negative MEPD for BWTD (-8 kg) and a medium MEPD for WWTD (11.1 kg), sire 99 (1/2A 1/2B) had a low MEPD for WWTD (.3 kg) and also a medium size MEPD for WWTD (10.9 kg), and sire 151 (B) had a slightly negative MEPD for BWTD (-2 kg) and a high MEPD for WWTD (16.1 kg).

Use of additive, nonadditive, and total MEPD would be of great benefit to both purebred and commercial cattle producers. Purebred producers would benefit by marketing sires that combine well with dams of a specific breed composition. Commercial producers would be able to choose sires according to their specific combining ability when mated to dams of the breed groups available in their herds. Ideally, these additive, nonadditive, and total genetic predictions should come from national multibreed genetic evaluations.

Implementing national multibreed evaluations requires addressing issues such as 1) multibreed contemporary groups, 2) multibreed genetic base(s), 3) large number of base breeds and breed group combinations, 4) unbalanced structure of the breed-group-of-sire × breed-group-of-dam subclasses, 5) connectedness within and across sire × breed-group-of-dam subclasses, and 6) publication of additive, nonadditive, and total genetic predictions. Probably

connectedness is the most serious problem in the potential multibreed populations in the United States. Initially, multibreed experimental herds and multibreed commercial herds with individual mating records will probably be responsible for most of the connections among sire × breed-group-of-dam combinations. In the long run, however, commercial multibreed herds are likely to be the ones creating most of the connections among sire × breed-group-of-dam subclasses. A major step in this direction has already been taken. Cornell University has succeeded in developing a national multibreed evaluation program that accounts for multibreed additive and fixed nonadditive (heterosis) genetic effects using field data from the Simmental, Simbrah, and Canadian Simmental populations (Klei et al., 1996). Perhaps a future generation of this program will account for random nonadditive effects due to sire × breed-group-of-dam interactions.

Implications

Covariance estimates for birth and weaning weights in an Angus-Brahman multibreed herd suggest that additive and nonadditive genetic effects are important sources of variation for these traits. Thus, to find the most appropriate sires to mate specific breed groups of dams in a crossbreeding program, sires would need to have expected progeny differences for additive, nonadditive, and total genetic effects for these particular matings. A regression approach would allow the prediction of nonadditive genetic effects for sires and groups of dams of any fractions of breeds. However, this regression approach will quickly increase in complexity as the number of base breeds increases. Simplifying assumptions will need to be made (e.g., grouping breeds according to their interactive ability). Data from purebred breeders and from commercial

producers will be needed to carry out national multibreed sire evaluations.

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