

JOURNAL OF ANIMAL SCIENCE

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J ANIM SCI 1998, 76:1810-1823.

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Genetic Variation and Prediction of Additive and Nonadditive Genetic Effects for Six Carcass Traits in an Angus-Brahman Multibreed Herd^{1,2}

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ABSTRACT: Estimates of covariances and sire expected progeny differences of additive and nonadditive genetic effects for six carcass traits were obtained using records from 486 straightbred and crossbred steers from 121 sires born between 1989 and 1995 in the Angus-Brahman multibreed herd of the University of Florida. Steers were slaughtered at a similar carcass composition end point. Covariances were estimated by REML procedures, using a generalized expectation-maximization algorithm applied to multibreed populations. Straightbred and crossbred estimates of heritabilities and additive genetic correlations were within ranges found in the literature for steers slaughtered on an age- or weight-constant basis for hot carcass weight, longissimus muscle area, and shear force but equal to or less than the lower bound of these ranges for fat-related traits. Maximum values of interactibilities (i.e., ratios of nonadditive variances to phenotypic variances in the F_1) and nonadditive genetic correlations were smaller than heritabilities

and additive genetic correlations in straightbreds and crossbred groups. Sire additive and total direct genetic predictions for longissimus muscle area, marbling, and shear force tended to decrease with the fraction of Brahman alleles, whereas those for hot carcass weight and fat thickness over the longissimus were higher, and those for kidney fat were lower in straightbreds and F_1 than in other crossbred groups. Nonadditive genetic predictions were similar across sire groups of all Angus and Brahman fractions. These results suggest that slaughtering steers on a similar carcass composition basis reduces variability of fat-related traits while retaining variability for non-fat-related traits comparable to slaughtering steers on a similar age or weight basis. Selection for carcass traits within desirable (narrow) ranges and slaughter of steers at similar compositional end point seems to be a good combination to help produce meat products of consistent quality.

Key Words: Beef Cattle, REML, Genetic Effects, Carcasses, Populations

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J. Anim. Sci. 1998. 76:1810-1823

Introduction

The beef cattle industry in the United States has faced serious competition from other sources of animal protein for a number of years. Consumers are demanding meat products that have specific characteristics, particularly in terms of meat quality traits. Thus, the beef industry faces the challenge of producing cattle that consistently yield meat products of desirable quality. This is a difficult goal to achieve because of

the large intrabreed and interbreed variability for carcass traits in beef cattle breeds.

The beef cattle industry has tried to minimize phenotypic variability among carcasses by constructing multibreed groups of cattle of similar weight and biological type before feeding them for a length of time determined by the expectation of obtaining a fraction of carcasses of a given category (e.g., 60% Choice). A way of achieving a higher degree of uniformity in meat products from animals of various breed compositions is to slaughter them at a similar carcass composition end point, if this can be done without increasing carcass weights beyond acceptability. Carcass traits measured under these conditions can be used for intrabreed and(or) multibreed genetic evaluation. Selection of cattle within specific ranges of predicted intrabreed and(or) multibreed genetic values for growth and carcass traits could further improve the degree of consistency of meat products.

The objectives of this study were 1) to estimate intrabreed and interbreed additive and interbreed

¹Florida Agric. Exp. Sta., Journal Series No. R-05980.

²We thank L. D. Van Vleck and R. L. Quaas for useful discussions and W. E. Kunkle, T. A. Olson, and C. Vargas for reviewing the manuscript. We gratefully acknowledge the personnel of the Beef Cattle Research Farms and the Meats Laboratory of the Univ. of Florida for their efforts in data collection and maintenance of the multibreed herd.

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Received October 6, 1997.

Accepted March 24, 1998.

Table 1. Numbers of sires, maternal grandsires, dams, and steer calves by breed-group-of-sire \times 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	12 ^a	2	3	6	6	9
	21 ^b	0	2	5	6	7
	24 ^c	5	4	12	14	12
	31 ^d	5	4	12	14	14
$\frac{3}{4}$ A $\frac{1}{4}$ B	8	5	3	4	6	6
	1	1	1	2	3	3
	11	7	5	8	6	7
	11	8	5	8	6	7
$\frac{1}{2}$ A $\frac{1}{2}$ B	10	6	7	7	13	12
	9	3	1	3	4	10
	15	15	15	16	20	22
	17	16	17	17	22	25
$\frac{1}{4}$ A $\frac{3}{4}$ B	5	2	4	3	6	6
	1	0	0	0	0	0
	7	3	7	4	11	9
	7	3	7	4	13	10
Brahman	10	5	6	6	16	11
	5	2	2	3	30	4
	18	15	10	10	32	19
	19	17	10	10	43	21
Brangus	6	4	6	5	9	14
	1	2	0	1	3	11
	7	5	9	8	12	29
	7	5	9	9	12	41
Total	14	6	8	10	18	15
	28	6	3	7	32	16
	82	50	50	58	95	98
	92	54	52	60	110	118

^aNumber of sires.^bNumber of maternal grandsires.^cNumber of dams.^dNumber of steers.

nonadditive direct genetic variances of and covariances among four carcass yield and two carcass quality traits and 2) to compare the means and ranges of predicted additive, nonadditive, and total genetic values of straightbred and crossbred sires in an Angus (**A**)- Brahman (**B**) multibreed cattle herd, using carcass data from steers evaluated at a similar carcass composition end point.

Materials and Methods

Animals, Mating Strategy, and Records

Data on four carcass yield and two carcass quality traits measured on 486 straightbred and crossbred steers representing 121 sires born between 1989 and 1995 in the AB multibreed cattle herd of the University of Florida were used in this research. Carcass yield traits were hot carcass weight (**CWT**, $n = 486$), area of the longissimus muscle at the 12th rib (**LMA**, $n = 485$), subcutaneous fat thickness over the 12th rib (**FAT**, $n = 482$), and kidney, pelvic, and heart

fat (**KPH**, $n = 481$). Carcass quality traits were marbling score (**MB**, $n = 485$) and Warner-Bratzler shear force (**WBS**, $n = 481$). Steers were the result of a diallel mating of 14 A, 6 $\frac{3}{4}$ A $\frac{1}{4}$ B, 8 $\frac{1}{2}$ A $\frac{1}{2}$ B, 10 $\frac{1}{4}$ A $\frac{3}{4}$ B, 18 B, and 15 Brangus ($\frac{3}{8}$ A $\frac{5}{8}$ B) sires to 58 A, 35 $\frac{3}{4}$ A $\frac{1}{4}$ B, 67 $\frac{1}{2}$ A $\frac{1}{2}$ B, 28 $\frac{1}{4}$ A $\frac{3}{4}$ B, 78 B, and 57 Brangus dams. The number of sires per breed group per year ranged from two to five. Sires were used for 2 yr to create connectedness across years. Of the total of 121 sires represented in the carcass data set, 50 were maternal grandsires only, 31 were sires only, and 40 were sires and maternal grandsires. Table 1 shows the numbers of sires, maternal grandsires, dams, and steers per breed-group-of-sire \times breed-group-of-dam combination.

Management

Preweaning Cow-Calf Management. Calves stayed with their dams from birth (December to March) to weaning in September (calves from A and crossbred AB dams) and October (calves from B dams). Although the long breeding season in the AB mul-

tibreed herd produced a continuous calving season in which the calving of dams of all breed groups overlapped, most calves from B dams were born in the latter part of the calving season. This occurred because B dams were bred about 1 mo later than A and AB dams due to concerns with calf mortality of straightbred B calves. Thus, to keep calves from B dams with their mothers for approximately the same length of time as calves from A and AB dams, they were weaned in October. Cows and calves were maintained on pastures of bahiagrass (*Paspalum notatum*) with mineral supplementation. In winter, diets were supplemented with bermudagrass (*Cynodon dactylon*) hay, urea, and molasses (Odenya et al., 1992; Elzo and Wakeman, 1998).

Postweaning Calf Management. Steers were allocated to a winter nutrition study (October to March) involving frosted bahiagrass (*Paspalum notatum*) pastures, bermudagrass (*Cynodon dactylon*) hay or silage, and molasses-based supplements. At the end of March, steers were transported to a contract feeder where they were fed a corn-protein diet fortified with minerals and vitamins until they reached a specified subcutaneous fat thickness of either 9 or 14 mm assigned at random within sire \times breed-group-of-dam subclasses at the beginning of the feeding period.

Slaughter and Carcass Processing

Steers were slaughtered at an approximate backfat end point of either 9 or 14 mm, estimated using real-time ultrasound (Aloka 500-V, Corometrics Medical systems, Wallingford, CT) operated by a certified ultrasound technician. On a monthly, and then a biweekly, basis when individual steers reached their assigned backfat end point, they were transported to Central Packing Company, Center Hill, Florida for processing.

Carcasses were chilled for 24 h, and USDA carcass yield and quality grade factors (USDA, 1989) were measured or evaluated by trained personnel from the University of Florida. The 13th rib section of the shortloin was removed and transported to the University of Florida Meat Processing Lab, where it was vacuum-packaged and held for 5 d at 2°C before freezing. Marbling scores were based on a scale wherein traces = 200 to 299, slight = 300 to 399, small = 400 to 499, and modest = 500 to 599. A 2.54-cm steak was cut for shear force determination.

Steaks for Warner-Bratzler shear force determination were thawed overnight at 4°C and broiled (Farberware "Open-Hearth" broiler, Model 450N, Bronx, NY) to an internal end point of 70°C (AMSA, 1995). Internal temperature was monitored by copper-constantan thermocouples (Omega Engineering Inc, Stamford, CT) placed in the approximate geometric center of each steak. Steaks were cooled to room temperature and 6 to 8 cores (1.27 cm) were removed parallel to the longitudinal orientation of the fiber and

sheared on a Warner-Bratzler shear device (G-R Electric Mfg. Co., Manhattan, KS).

Multibreed Covariance Component Estimation and Genetic Prediction Procedures

Restricted maximum likelihood procedures (Harville, 1977) using a generalized expectation-maximization (**GEM**) algorithm (Dempster et al., 1977) for multibreed populations (**MREMLEM**; Elzo, 1994) were used to estimate covariance components. Expectation-maximization algorithms do not provide the information matrix; thus, the MREMLEM program did not compute asymptotic standard errors of the REML covariance estimates. However, large standard errors of estimation of covariance components should be expected due to the small size of the multibreed data set used here. The MREMLEM algorithm ensured positive definiteness of the estimated covariance matrices by first computing the Cholesky elements of each covariance matrix, and then the covariance matrices themselves by multiplication of the Cholesky matrices by their transposes (Elzo, 1996b). A computer program written in FORTRAN (compiled using XL FORTRAN for AIX), run in an IBM RS6000 workstation, model 580, was used to perform computations.

The small size of the data set prevented the estimation of covariance components for more than two traits simultaneously. Thus, all possible pairwise combinations of the six carcass traits (15 combinations in all) were run separately. Multiple estimates of variances were subsequently averaged to produce a single estimate. To preserve positive definiteness, covariances between pairs of traits were reestimated as the square root of the product of the means of the variances of the two traits times the correlation between these two traits from the two-trait analyses. Starting values for the two-trait MREMLEM analyses were the variance estimates (additive, nonadditive, and environmental) from single-trait MREMLEM analyses and zeros for covariances between traits. The convergence criterion was that the square root of CCONV was less than 10^{-4} in two consecutive GEM iterations, where CCONV = ratio of the sum of squares of the differences between covariance estimates in GEM iterations i and $i + 1$ divided by the sum of squares of the covariances in GEM iteration i .

Multibreed Model. A multibreed sire-maternal grandsire model was used for all MREMLEM analyses. All carcass traits were assumed to be affected only by direct (D) genetic effects.

To account for differences in carcass traits due to finishing steers at the two assigned ultrasonic end points, carcass contemporary groups were defined as steers slaughtered in the same year and at the same assigned ultrasonic fat thickness end point. Had all steers been slaughtered at exactly the same fat thickness, no genetic evaluation or estimation of

variance components for FAT would have been possible. This was not the case here, so the frequency of slaughter and inaccuracies of the ultrasonic procedure left enough genetic and environmental variation to yield nonzero estimates of genetic predictions and estimates of variance components for FAT and other fat-related traits (KPH and MB). Genetic predictions and estimates of variance components for FAT, KPH, and MB were computed to document the amount of variability that was left for these traits given the slaughter timing procedure used, because the industry also uses the concept of slaughtering animals at a similar carcass composition end point. However, because the industry does not currently use ultrasound to determine the time of slaughter, larger amounts of variability for carcass traits probably exist in field AB multibreed data sets. Thus, estimates of genetic parameters in this experimental AB multibreed herd for carcass traits in general, and for fat-related traits in particular, are likely to be underestimates of those that exist in field AB multibreed data sets.

The multibreed model for carcass traits used here closely resembled (except for the absence of maternal effects) the one used to analyze preweaning growth traits in this same AB multibreed herd. Thus, a succinct description of the multibreed model and its assumptions is given here, and the reader is referred to Elzo and Wakeman (1998) for a detailed description of the multibreed model and methodology for prediction and covariance component estimation.

Fixed environmental effects in the model were contemporary group (year \times assigned ultrasonic backfat thickness end point subclass). Fixed regression genetic group effects were 1) intrabreed additive direct due to intrabreed A (deviated from B, as a function of the expected fraction of A alleles in sires plus .5 the expected fraction of A alleles in maternal grandsires), 2) interbreed AB additive direct (deviated from intrabreed AA and BB, as a function of the probability of A and B alleles in the parents of sires plus .5 the probability of A and B alleles in the parents of maternal grandsires), 3) intralocus interbreed A/B nonadditive direct (deviated from intrabreed A/A and B/B, as a function of the probability of A and B alleles in the progeny of sires), and 4) additive direct due to maternal granddams (as a function of the expected fraction of A alleles in maternal granddams). Random effects in the model were additive direct (due to sire and maternal grandsire) genetic effects, intralocus interbreed sire \times breed-group-of-dam direct regression effects (as a function of intralocus interbreed A/B interactions in the progeny of a sire), and residual. Covariances among additive genetic effects and among nonadditive genetic effects as well as heterogeneity of additive and nonadditive genetic and environmental covariances across breed-group-of-sire \times breed-group-of-dam combinations were accounted for in the multibreed model.

Computational Strategy. The computational strategy used to construct and to solve the multibreed mixed-model equations (**MMME**) was the same as the one used in Elzo and Wakeman (1998). Inverses of the additive and nonadditive multibreed covariance matrices were obtained directly by computational rules (Elzo, 1990a,b), and the inverse of the residual multibreed covariance matrix was computed by direct inversion of its diagonal blocks. Sparse matrix procedures (FSPAK, Perez-Enciso et al., 1994) were used to solve the MMME. Finally, residual sire additive and nonadditive genetic predictions and their error variances of prediction and predictions of residuals for the multibreed model and their error variances of prediction were computed and subsequently used as input by the MREMLEM program to estimate multibreed covariances (Elzo, 1994; Elzo and Wakeman, 1998).

Genetic, Environmental, and Phenotypic Covariances. Three additive genetic (intrabreed A, intrabreed B, interbreed AB), one nonadditive genetic (intralocus interbreed A/B), and three environmental (intrabreed A, intrabreed B, interbreed AB) covariance matrices were estimated for all carcass traits. These are *base* covariance matrices. They are used to construct multibreed additive genetic, nonadditive genetic, and environmental covariance matrices for animals of any combination of A and B fractions (Elzo, 1994; Elzo and Wakeman, 1998).

Intrabreed additive genetic and environmental covariances participate in the computation of *all* multibreed covariances. However, interbreed additive genetic covariances contribute to the covariance matrix of a crossbred group *only if one or both parents are crossbred*. To show the effect of interbreed additive genetic covariances on multibreed covariances, additive genetic and environmental multibreed covariance matrices were computed for the cases of crossbred progeny from 1) straightbred parents (A \times B), 2) one crossbred and one straightbred parent ($\frac{1}{2}$ A $\frac{1}{2}$ B sires \times A dams), and 3) two crossbred parents ($\frac{1}{2}$ A $\frac{1}{2}$ B sires \times $\frac{3}{4}$ A $\frac{1}{4}$ B dams).

Intralocus interbreed nonadditive covariances were defined as deviations from intralocus intrabreed nonadditive covariances. Thus, only crossbred progeny groups have nonzero interbreed nonadditive covariance matrices. Consequently, interbreed nonadditive covariance matrices were computed for the progeny of A sires \times B dams, $\frac{1}{2}$ A $\frac{1}{2}$ B sires \times A dams, and $\frac{1}{2}$ A $\frac{1}{2}$ B sires \times $\frac{3}{4}$ A $\frac{1}{4}$ B dams.

Multibreed Genetic Parameters. Heritabilities, interactivities (ratios of interbreed nonadditive genetic variances to phenotypic variances), and correlations (additive genetic, nonadditive genetic, environmental, and phenotypic) were computed for the two straightbred (A \times A, and B \times B) and three crossbred parental breed group combinations (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 three crossbred parental breed group combinations were chosen to

illustrate the effect of interbreed additive and nonadditive genetic variances and covariances (absent in both parents, $A \times B$; present in one of the parents, $\frac{1}{2}A \frac{1}{2}B \times A$ parents; and present in both parents, $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$) on multibreed genetic parameters of crossbred groups.

Multibreed Genetic Predictions. Additive, nonadditive, and total multibreed expected progeny differences (**MEPD**) were computed for all carcass traits as described in Elzo and Wakeman (1998). Sires of one or more A and B breed fractions mated to dams of any A and B breed composition can be compared for additive, nonadditive, and total MEPD. Comparison of sires for additive MEPD is independent of the breed composition of their mates. However, comparison of sires for nonadditive MEPD and total MEPD depends on the breed composition of their mates. Two factors affect the value of the predicted difference between two sires for nonadditive MEPD: 1) the probability of AB intralocus interbreed interactions in the progeny of each sire (which depends on the A and B fractions of the breed groups of dams), and 2) their nonadditive MEPD. These two factors also affect predicted differences between sires for total MEPD.

When sires of various A and B breed fractions are mated to dams of one or more breed groups, the probability of A/B intralocus interaction effects in their progeny will usually differ for sires of different breed composition, except when sires are mated to $\frac{1}{2}A \frac{1}{2}B$ dams. If sires are mated to $\frac{1}{2}A \frac{1}{2}B$ dams, the probability of intralocus interbreed A/B interactions in the progeny of any sire is the same (.5) regardless of their AB breed composition. Thus, to simplify the comparison of sires of different A and B breed fractions for nonadditive and total MEPD, sires were assumed to be mated to $\frac{1}{2}A \frac{1}{2}B$ dams. Consequently, 1) comparison of sires of any A and B fractions were made at the same probability value of A/B interbreed nonadditive interactions in their progeny and 2) predicted nonadditive differences between sires reflected only differences in their interbreed interactive ability.

Sire additive and nonadditive MEPD were computed as weighted sums of their estimated group effects and predicted random components obtained from the MMME (Elzo and Wakeman, 1998). Sire additive MEPD were predicted as (sire's A fraction) \times (solution for additive intrabreed group regression) + (probability of AB in the parents of a sire) \times (solution for additive interbreed group regression) + (sire's predicted additive intragroup deviation). Sire nonadditive MEPD were obtained as (probability of A/B allelic combination in the progeny of a sire) \times (solution for nonadditive intralocus interbreed group regression + sire's predicted nonadditive intralocus interbreed deviation). Sire total MEPD were computed as the sum of their additive and nonadditive MEPD.

Results and Discussion

Covariance Components and Genetic Parameters

Estimates of base intrabreed additive genetic, interbreed additive genetic, and interbreed nonadditive genetic covariances are shown in Table 2 for all carcass yield (CWT, LMA, FAT, and KPH) and carcass quality (MB and WBS) traits. Table 3 contains the base intrabreed and interbreed environmental covariances for these same traits. The number of GEM iterations needed to achieve convergence in the two-trait computer analyses ranged from 4 to 20, and the time to convergence was between 1.8 and 10.4 min.

To facilitate the comparison of estimates of intrabreed and multibreed genetic parameters and to illustrate the effect of interbreed additive genetic covariances on multibreed genetic parameters, Table 4 (heritabilities and additive genetic correlations), Table 6 (environmental correlations), and Table 7 (phenotypic correlations) include parameter estimates for straightbred and crossbred mating combinations. Thus, sets of parameter estimates for progeny groups from parental breed group combinations without ($A \times A$, $B \times B$, $A \times B$) and with ($\frac{1}{2}A \frac{1}{2}B \times A$, and $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$) interbreed additive genetic variability are presented in Tables 4, 6, and 7. Table 5 (interactibilities and nonadditive genetic correlations) contains nonadditive genetic parameters only for parental breed group combinations whose progeny show interbreed nonadditive genetic variation in crossbred matings without ($A \times B$) and with ($\frac{1}{2}A \frac{1}{2}B \times A$, and $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$) interbreed additive genetic variability.

A direct consequence of evaluating animals and estimating covariance components based on slaughtering steers at a similar fat thickness end point is that the amount of variability left for FAT, and probably to some extent for KPH and MB, will be drastically reduced. It should be emphasized that if all animals had been slaughtered at *exactly* the same fat thickness end point, genetic and environmental variances for FAT, and covariances between FAT and other traits, would have been zero, and those for KPH and MB probably would have been close to zero. However, because of the frequency of slaughter and the use of ultrasound to measure FAT, small amounts of genetic and environmental variability for FAT, KPH, and MB were determined. Thus, caution should be exercised when interpreting the *nonzero* heritability and interactibility estimates for FAT, KPH, and MB in Tables 4 and 5. It should be kept in mind that these two parameters were ratios of small genetic to small phenotypic variances that were the remnants of variation left for FAT (and to a lesser extent, for KPH and MB) due to the inaccuracy of the slaughter timing procedure.

The beef cattle industry determines the time of slaughter of a group of animals in the feedlot based on

Table 2. Estimates of base additive and nonadditive genetic covariances for carcass traits^a

Trait pair ^c	Genetic covariances ^b			
	Additive intrabreed A	Additive intrabreed B	Additive interbreed AB	Nonadditive interbreed A/B
CWT, CWT (kg ²)	294.1034	426.3208	365.0220	327.6854
CWT, LMA (kg × cm ²)	37.0337	40.2964	79.1413	33.5481
CWT, FAT (kg × cm)	.1127	-.0237	-1.0134	.0026
CWT, KPH (kg × %)	-.0414	.1391	-.5490	.0588
CWT, MB (kg × units)	-71.4794	63.5748	111.4501	14.7238
CWT, WBS (kg × kg)	.4678	1.0010	-7.1367	-.4358
LMA, LMA (cm ⁴)	22.8126	23.9393	21.1549	19.2247
LMA, FAT (cm ² × cm)	.0081	-.0172	-.1987	-.0002
LMA, KPH (cm ² × %)	-.0075	.0188	-.0414	.0056
LMA, MB (cm ² × units)	-14.4867	-1.1087	-12.1335	.7933
LMA, WBS (cm ² × cm)	.0549	.1488	-.6049	-.0873
FAT, FAT (cm ²)	.0116	.0168	.0088	.0018
FAT, KPH (cm × %)	-.0002	.0005	.0069	.0001
FAT, MB (cm × units)	.1544	.1057	-.6219	-.0171
FAT, WBS (cm × kg)	.0038	-.0047	-.0716	-.0002
KPH, KPH (% ²)	.0067	.0204	.0094	.0098
KPH, MB (% × units)	.1588	.1115	-.1213	.0061
KPH, WBS (% × kg)	-.0072	.0067	-.0445	-.0010
MB, MB (units ²)	745.5806	754.7334	1,617.2538	675.0798
MB, WBS (units × kg)	-1.5691	-1.3809	-22.0271	-.3811
WBS, WBS (kg ²)	.8664	.7292	1.5515	.2204

^aSimilar carcass composition basis.

^bA = Angus; B = Brahman.

^cCWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

Table 3. Estimates of base environmental covariances for carcass traits^a

Trait pair ^c	Environmental covariances ^b		
	Intrabreed A	Intrabreed B	Interbreed AB
CWT, CWT (kg ²)	348.7530	661.6228	490.6856
CWT, LMA (kg × cm ²)	52.6261	98.8281	95.1530
CWT, FAT (kg × cm)	2.3572	.5123	7.3013
CWT, KPH (kg × %)	1.9353	.2909	-18.6486
CWT, MB (kg × units)	384.1340	830.5558	-694.0326
CWT, WBS (kg × kg)	.1570	-9.4783	4.0046
LMA, LMA (cm ⁴)	32.0120	21.2716	74.7606
LMA, FAT (cm ² × cm)	-.1559	-.3169	-.2292
LMA, KPH (cm ² × %)	-.4014	.4067	.7809
LMA, MB (cm ² × units)	-122.3256	102.4701	-270.6806
LMA, WBS (cm ² × cm)	1.5050	-1.3530	-4.2914
FAT, FAT (cm ²)	.0739	.0526	1.4244
FAT, KPH (cm × %)	-.0018	-.0105	1.0084
FAT, MB (cm × units)	5.3098	4.9084	32.1996
FAT, WBS (cm × kg)	-.0270	-.0846	.2817
KPH, KPH (% ²)	.2368	.1306	1.9344
KPH, MB (% × units)	.9851	-2.7464	-40.7001
KPH, WBS (% × kg)	.1674	-.1796	-.8174
MB, MB (units ²)	4,417.3910	3,947.5029	981.7810
MB, WBS (units × kg)	2.4506	24.3988	-.6654
WBS, WBS (kg ²)	.6313	3.6651	.4027

^aSimilar carcass composition basis.

^bA = Angus; B = Brahman.

^cCWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

Table 4. Estimates of heritabilities and additive genetic correlations for carcass traits^a

Parameter ^c	Breed group combination ^b					
	A × A	B × B	A × B	½A	½B × A	½A ½B × ¾A ¼B
h ² (CWT)	.46	.39	.30	.37	.37	.37
r _A (CWT, LMA)	.45	.40	.42	.53	.53	.57
r _A (CWT, FAT)	.06	-.01	.02	-.07	-.07	-.13
r _A (CWT, KPH)	-.03	.05	.02	-.06	-.06	-.08
r _A (CWT, MB)	-.15	.11	-.01	-.01	-.01	.03
r _A (CWT, WBS)	.03	.06	.04	-.05	-.05	-.09
h ² (LMA)	.42	.53	.34	.33	.33	.32
r _A (LMA, FAT)	.02	-.03	-.01	-.07	-.07	-.12
r _A (LMA, KPH)	-.02	.03	.01	-.02	-.02	-.02
r _A (LMA, MB)	-.11	-.01	-.06	-.08	-.08	-.07
r _A (LMA, WBS)	.01	.04	.02	-.01	-.01	-.03
h ² (FAT)	.14	.24	.18	.03	.03	.02
r _A (FAT, KPH)	-.02	.03	.01	.12	.12	.18
r _A (FAT, MB)	.05	.03	.04	.00	.00	-.03
r _A (FAT, WBS)	.04	-.04	.00	-.12	-.12	-.19
h ² (KPH)	.03	.14	.07	.02	.02	.01
r _A (KPH, MB)	.07	.03	.04	.03	.03	.02
r _A (KPH, WBS)	-.09	.05	.00	-.12	-.12	-.14
h ² (MB)	.14	.16	.13	.19	.19	.23
r _A (MB, WBS)	-.06	-.06	-.06	-.19	-.19	-.24
h ² (WBS)	.58	.17	.25	.43	.43	.42

^aSimilar carcass composition basis.

^bA = Angus; B = Brahman.

^ch² = heritability; r_A = additive genetic correlation; CWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

the expectation of a percentage of carcasses of a certain category. Thus, the industry is using the concept of slaughtering animals at a similar carcass composition end point. However, the industry makes the decision that animals in a pen have reached the desired degree of fatness based on length of time in feedlot, feeding pattern, and visual observation. Thus, substantially larger amounts of variability (genetic and environmental) probably remain among animals for fat-related traits compared to the ones obtained in this study, thus higher values of heritabilities, intercorrelations, and additive and nonadditive correlations for these traits should be expected in field data sets. Consequently, estimates of genetic parameters for fat-related traits here (FAT, KPH, and MB; Tables 4 and 5) could also be viewed as underestimates of parameter values that would exist for these traits in the complete AB multibreed population.

Heritabilities. Estimates of base intrabreed additive genetic variances (Table 2) tended to be smaller in A than in B for all carcass traits, but, intrabreed environmental variances (Table 3) tended to be larger in A than in B across traits. Thus, intrabreed heritabilities were smaller in A than in B for four (LMA, FAT, KPH, and MB) out of six carcass traits. Estimates of additive genetic variances for REA were almost the same in A and B, but the estimate of the environmental variance was 50% larger in A than in

B, hence the difference in heritability estimates between A and B for this trait. The two carcass traits with higher heritability in A than in B were CWT and WBS. The larger estimate of heritability for CWT in A than in B was the result of a proportionally smaller estimate of environmental variance in A than in B; the estimate of the additive genetic variance for CWT was smaller in A than in B. Also, the disparity in the heritability values for WBS in the two straightbred groups was due to the large difference in the estimates of environmental variances for WBS in A and B; their estimates of additive genetic variances were similar.

Heritabilities of carcass traits for progeny of the A × B (F₁) breed group combination (Table 2) were below the smallest heritability of the two parental breeds for CWT, LMA, and MB, because of large values of A/B nonadditive variances contributing to phenotypic variances, and intermediate between the heritability of the two parental breeds for FAT, KPH, and WBS (due to small estimates of A/B nonadditive variances added to phenotypic variances).

Heritability estimates for carcass traits in the progeny groups of the last two parental breed combinations of Table 4 (½A ½B × A and ½A ½B × ¾A ¼B) differ from those of the straightbred and the A × B parental combinations in that their values depend not only on intrabreed genetic and environmental covariances (as A × A, B × B and A × B) and

Table 5. Estimates of interactibilities and nonadditive genetic correlations for carcass traits^a

Parameter ^c	Breed group combination ^b			
	A × B	½A	½B × A	½A ½B × ¾A ¼B
i ² (CWT)	.27	.14		.12
r _N (CWT, LMA)	.42	.42		.42
r _N (CWT, FAT)	.00	.00		.00
r _N (CWT, KPH)	.03	.03		.03
r _N (CWT, MB)	.03	.03		.03
r _N (CWT, WBS)	-.05	-.05		-.05
i ² (LMA)	.28	.11		.09
r _N (LMA, FAT)	.00	.00		.00
r _N (LMA, KPH)	.01	.01		.01
r _N (LMA, MB)	.01	.01		.01
r _N (LMA, WBS)	-.04	-.04		-.04
i ₂ (FAT)	.02	.00		.00
r _N (FAT, KPH)	.02	.02		.02
r _N (FAT, MB)	-.02	-.02		-.02
r _N (FAT, WBS)	-.01	-.01		-.01
i ² (KPH)	.05	.01		.00
r _N (KPH, MB)	.00	.00		.00
r _N (KPH, WBS)	-.02	-.02		-.02
i ² (MB)	.12	.06		.05
r _N (MB, WBS)	-.03	-.03		-.03
i ² (WBS)	.07	.04		.03

^aSimilar carcass composition basis.

^bA = Angus; B = Brahman.

^ci² = interactibility (ratio of intralocus interbreed genetic variance to phenotypic variance); r_N = nonadditive genetic correlation; CWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

interbreed nonadditive genetic variances (as A × B), but also on interbreed additive genetic and interbreed environmental variances. Estimates of base interbreed additive genetic variances for carcass yield traits

(Table 2) tended to be smaller than, or have intermediate values between, base intrabreed additive genetic variances; the opposite occurred with carcass quality traits. Conversely, base interbreed environ-

Table 6. Estimates of environmental correlations for carcass traits^a

Parameter ^c	Breed group combination ^b					
	A × A	B × B	A × B	½A	½B × A	½A ½B × ¾A ¼B
r _E (CWT, LMA)	.50	.83	.65	.54		.55
r _E (CWT, FAT)	.46	.09	.25	.24		.22
r _E (CWT, KPH)	.21	.03	.12	-.16		-.26
r _E (CWT, MB)	.31	.51	.42	.20		.14
r _E (CWT, WBS)	.01	-.19	-.14	-.04		-.05
r _E (LMA, FAT)	-.10	-.30	-.18	-.06		-.05
r _E (LMA, KPH)	-.15	.24	.00	.00		.03
r _E (LMA, MB)	-.33	.35	-.03	-.29		-.29
r _E (LMA, WBS)	.33	-.15	.01	-.03		-.13
r _E (FAT, KPH)	-.01	-.13	-.06	.46		.51
r _E (FAT, MB)	.29	.34	.31	.30		.34
r _E (FAT, WBS)	-.13	-.19	-.15	.04		.06
r _E (KPH, MB)	.03	-.12	-.03	-.18		-.26
r _E (KPH, WBS)	.43	-.26	-.01	-.12		-.22
r _E (MB, WBS)	.05	.20	.14	.09		.11

^aSimilar carcass composition basis.

^bA = Angus; B = Brahman.

^cr_E = environmental correlation; CWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

Table 7. Estimates of phenotypic correlations for carcass traits^a

Parameter ^c	Breed group combination ^b					
	A × A	B × B	A × B	½A ½A	½B × A	½A × ¾A ¼B
r _p (CWT, LMA)	.48	.63	.51	.52	.54	.54
r _p (CWT, FAT)	.33	.06	.15	.16	.15	.15
r _p (CWT, KPH)	.15	.03	.08	-.11	-.19	-.19
r _p (CWT, MB)	.17	.40	.24	.12	.10	.10
r _p (CWT, WBS)	.02	-.12	-.07	-.05	-.06	-.06
r _p (LMA, FAT)	-.07	-.19	-.10	-.05	-.05	-.05
r _p (LMA, KPH)	-.11	.16	.00	.00	.02	.02
r _p (LMA, MB)	-.26	.22	-.03	-.20	-.21	-.21
r _p (LMA, WBS)	.17	-.09	.01	-.03	-.09	-.09
r _p (FAT, KPH)	-.01	-.10	-.05	.45	.51	.51
r _p (FAT, MB)	.26	.28	.25	.26	.28	.28
r _p (FAT, WBS)	-.06	-.16	-.11	.01	.03	.03
r _p (KPH, MB)	.03	-.10	-.02	-.15	-.22	-.22
r _p (KPH, WBS)	.27	-.21	-.01	-.10	-.18	-.18
r _p (MB, WBS)	.01	.16	.09	.00	-.01	-.01

^aSimilar carcass composition basis.

^bA = Angus; B = Brahman.

^cr_p = phenotypic correlation; CWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

mental variances for carcass yield traits were mostly larger than both intrabreed environmental variances, whereas the one for MB was smaller than, and that of WBS had an intermediate value between, the corresponding intrabreed environmental variances (Table 3). Because estimates of interbreed environmental variances were substantially larger than their interbreed additive genetic counterparts within traits, multibreed heritabilities for progeny groups of ½A ½B × A and ½A ½B × ¾A ¼B parental breed group combinations reflected their relationships with intrabreed environmental variances. Thus, multibreed heritability estimates in the progeny of ½A ½B × A and ½A ½B × ¾A ¼B were smaller than the lowest intrabreed heritability for carcass yield traits (CWT, LMA, FAT, and KPH), higher than the heritability of both straightbred groups for MB, and intermediate between the heritability estimates of the straightbred groups for WBS.

The mostly lower heritability values in crossbred matings with and without interbreed additive genetic variation indicate that selection of straightbred and crossbred sires for additive MEPD using crossbred matings would require larger numbers of relatives to offset the additional variances (A/B nonadditive, AB environmental) that increased the phenotypic variance (and lowered the heritability) of crossbred groups and achieve a degree of accuracy similar to the one in intrabreed selection. It should be kept in mind, however, that this multibreed carcass data set was very small, thus substantially different estimates of interbreed genetic variability might be obtained with another multibreed data set or with the complete AB multibreed population in the country.

Estimates of heritabilities for carcass traits found in the literature were computed on an age-constant or a weight-constant basis. The ranges of estimates of heritability by paternal half-sibs analyses of several data sets involving various *Bos taurus* breeds, Brahman, and crossbred groups were .31 to .68 for CWT, .28 to .60 for LMA, .24 to .68 for FAT, .72 to .83 for KPH, .23 to .47 for MB, and .02 to .71 for WBS (Koch et al., 1982; Arnold et al., 1991; Van Vleck et al., 1992; Wilson et al., 1993; Marshall, 1994; Barkhouse et al., 1996). The values of heritabilities estimated here for A, B, and the three crossbred groups (Table 4) were 1) within the range of the age or weight base values for CWT, REA, and WBS, 2) equal to or less than their lower range for FAT and MB, and 3) less than the lower range for KPH. Thus, the main effect of slaughtering animals at a given fat thickness end point was to decrease the genetic and environmental variability of those carcass traits related to fat content (FAT, KPH, and MB) in straightbred and crossbred animals.

Interactibilities. Estimates of nonadditive interbreed genetic covariances were somewhat lower than additive intrabreed and interbreed genetic covariances (Table 2), which resulted in estimates of interactibilities that were primarily lower than either intrabreed or multibreed heritability estimates (Table 5). Estimates of interactibilities for carcass traits in the literature were unavailable for comparison. Interactibilities estimated here averaged 60% of the values of the heritabilities of the six carcass traits in the A × B breed group combination. It should be emphasized that this A/B nonadditive genetic variability among straightbred and crossbred sires for carcass traits

existed *in addition* to the additive genetic variation found in this multibreed herd. This implies that, as with growth traits (Elzo and Wakeman, 1998; Elzo et al., 1998), straightbred and crossbred sires could also be selected for their A/B combining ability in addition to selection for additive genetic ability.

The interactibility values obtained in this small AB multibreed data set suggest that even larger values would probably be obtained in the complete AB multibreed population in the country. If so, this would justify the inclusion of interbreed nonadditive genetic effects in a national AB multibreed genetic evaluation and the consideration of additive and A/B nonadditive sire MEPD in their selection process.

Genetic Correlations. Estimates of additive intrabreed and interbreed (Table 2) as well as interbreed nonadditive (Table 3) genetic covariances were small for all pairwise combinations of carcass traits, with the exception of those between CWT and LMA, CWT and MB, and LMA and MB. Consequently, all intrabreed additive ($A \times A$, and $B \times B$) and all multibreed additive and nonadditive ($A \times B$, $\frac{1}{2}A \frac{1}{2}B \times A$ and $\frac{1}{2}A \frac{1}{2}B \times \frac{3}{4}A \frac{1}{4}B$) genetic correlations (Tables 4 and 5) were low, except for those between CWT and LMA, which had positive medium size values.

The sign of the additive genetic correlations was the same for only 4 of the 15 pairwise combinations of the six carcass traits across the five breed parental breed group combinations (Table 4), suggesting that the additive relationships between some of these six carcass traits might be different in A, B, and (or) their crossbreds when slaughtered at the fat thickness end points used here. The four sets of additive correlations that showed consistency in sign across straightbred and crossbred groups were those between CWT and LMA (positive), LMA and MB (negative), KPH and MB (positive), and MB and WBS (negative). Except for the medium size of the additive genetic correlation estimates between CWT and LMA (which indicates that larger carcass weights tended to be accompanied by larger areas of the longissimus dorsi muscle), all other additive genetic correlation estimates were low or close to zero. Thus, interpretation of these additive genetic correlations should be made with caution because these correlation estimates are likely to have large asymptotic standard errors.

The majority of additive genetic correlations among the six carcass traits estimated here were smaller than those found in the literature for straightbred (Arnold et al., 1991; Wilson et al., 1993; Marshall, 1994) and multibreed (Koch et al., 1982; Van Vleck et al., 1992; Marshall, 1994; Barkhouse et al., 1996) data sets adjusted to a constant age or weight. This was particularly true of additive genetic correlations involving fat-related traits (FAT, KPH, and MB).

Nonadditive interbreed correlations (Table 5) were all close to zero, with the exception of the medium positive one between CWT and LMA, indicating an

almost complete lack of A/B nonadditive association among carcass traits. Literature values of nonadditive interbreed correlations were unavailable for comparison.

Environmental and Phenotypic Correlations. Intrabreed and interbreed environmental covariances (Table 3) and correlations (Table 6) were generally larger and tended to be of the same sign as additive genetic covariances (Table 2) and correlations (Table 5). Because environmental covariances were substantially larger than genetic covariances, phenotypic correlations tended to be of the same sign and to have values similar to those of environmental correlations (Table 7). Positive environmental and phenotypic correlations existed across the five parental breed group combinations between CWT and LMA, CWT and FAT, CWT and MB, and FAT and MB. These correlations indicate that steers fed for heavier carcasses had larger areas of the longissimus muscle and also had more fat over the longissimus and had more marbling regardless of their breed composition.

Negative environmental and phenotypic correlations existed across the five parental breed group combinations only between LMA and FAT, suggesting that within the range of fat thicknesses allowed by the slaughter timing procedure, straightbred and crossbred animals that finished with more fat over the longissimus muscle tended to have smaller longissimus muscle areas.

All the other combinations of carcass traits had a mixture of low positive, near zero, and low negative environmental correlations. In particular, the environmental and phenotypic correlations in the A, B, and crossbred groups for 1) CWT and WBS, and KPH and MB were near zero for A, and negative for B and for crossbred groups and 2) LMA and WBS, and KPH and WBS were positive for A, negative for B, and near zero to negative for crossbreds. These correlations might be an indication that 1) feeding animals to heavier carcass weights would have no effect on tenderness in A, but that heavier carcasses would be more tender than lighter ones in B and crossbred steers, 2) larger areas of longissimus muscle could be associated with tougher meat in A, but not in B or crossbred carcasses, and 3) higher KPH would tend to be related to lower MB and higher tenderness in carcasses of B and crossbred animals, but not in A carcasses.

The signs and magnitudes of environmental and phenotypic correlations estimated here resembled those reported in the literature for straightbred (Arnold et al., 1991; Wilson et al., 1993; Marshall, 1994) and multibreed (Koch et al., 1982; Van Vleck et al., 1992; Marshall, 1994; Barkhouse et al., 1996) data sets.

Multibreed Genetic Predictions

Three types of MEPD were computed for all sires: additive, nonadditive, and total. Expected fractions of

A/B combinations of alleles in the progeny of straightbred and crossbred sires vary according to the breed composition of their mates. This variability in A/B fractions prevents a fair comparison of sires of different breed group composition for nonadditive and total MEPD. Thus, nonadditive and total MEPD were computed assuming that sires were mated to $\frac{1}{2}$ A $\frac{1}{2}$ B dams, because this is the only breed group of dams whose progeny yield the same probability of occurrence of interbreed intralocus nonadditive effects regardless of sire's A and B fractions.

Table 8 shows the means and ranges of additive, nonadditive, and total direct MEPD for carcass yield (CWT, LMA, FAT, and KPH), and carcass quality (MB and WBS) traits, for sires assumed to be mated

to $\frac{1}{2}$ A $\frac{1}{2}$ B dams. The accuracies of additive and nonadditive direct MEPD were low, as expected, given the small size of the data set. The standard error of prediction of additive and nonadditive direct sire MEPD ranged from 6.2 to 12.2 kg for CWT, 1.49 to 3.14 cm² for LMA, .0334 to .0944 cm for FAT, .0516 to .1115 % for KPH, 10.01 to 21.86 units for MB, and .225 to .484 kg for WBS. Despite these low MEPD accuracies, various patterns emerged for the additive, nonadditive, and total sire MEPD means for the six carcass traits when compared across breed groups of sires.

Additive Multibreed Genetic Predictions. The mean additive MEPD of A, $\frac{1}{2}$ A $\frac{1}{2}$ B, and B sires was lower for CWT and FAT, and higher for KPH, than those of

Table 8. Means and ranges of additive, nonadditive, and total expected progeny differences of sires mated to $\frac{1}{2}$ A $\frac{1}{2}$ B dams for carcass traits^a

Genetic effect ^b	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
CWTA, kg	-.4 ^c (-8.6, 10.0) ^d	7.1 (1.3, 12.0)	-.5 (-9.1, 3.6)	5.7 (-3.1, 16.2)	.7 (-11.2, 14.4)	9.3 (-1.3, 17.7)
CWTN, kg	8.4 (-1.9, 21.7)	8.5 (3.1, 15.1)	8.1 (1.7, 11.9)	7.6 (.9, 12.3)	8.7 (-3.1, 17.7)	7.6 (-1.4, 14.9)
CWTT, kg	8.0 (-10.5, 31.7)	15.6 (4.4, 15.5)	7.6 (-7.4, 15.5)	13.3 (.0, 24.5)	9.4 (-9, 28.5)	16.9 (-9, 32.6)
LMAA, cm ²	3.45 (.58, 6.03)	2.57 (-.71, 4.21)	2.19 (-1.28, 4.48)	.75 (-2.10, 3.30)	.01 (-2.88, 3.10)	2.21 (-.15, 4.79)
LMAN, cm ²	1.49 (-.47, 2.97)	1.38 (-.85, 1.99)	1.98 (-.72, 3.30)	1.65 (.70, 3.11)	1.65 (-.38, 4.46)	1.48 (.12, 3.01)
LMAT, cm ²	4.94 (.11, 8.67)	3.96 (-1.55, 6.19)	4.17 (-2.00, 7.49)	2.40 (-.51, 6.42)	1.66 (-3.03, 7.55)	3.68 (-.03, 7.41)
FATA, cm	.0174 (-.0049, .0539)	.0603 (.0509, .0696)	.0155 (.0004, .0831)	.0525 (.0083, .0682)	.0006 (-.0580, .0462)	.0828 (.0689, .0939)
FATN, cm	.0043 (.0011, .0080)	.0043 (.0034, .0057)	.0040 (.0825, .0907)	.0044 (.0775, .1003)	.0041 (-.0008, .0058)	.0040 (.0022, .0055)
FATT, cm	.0217 (-.0034, .0584)	.0646 (.0550, .0753)	.0195 (.0040, .0873)	.0568 (.0125, .0736)	.0047 (-.0538, .0510)	.0869 (.0711, .0994)
KPHA, %	-.0358 (-.0831, -.0265)	-.0976 (-.1206, -.0939)	-.0292 (-.1244, -.0118)	-.0721 (-.0903, -.0176)	-.0012 (-.0588, .0192)	-.1273 (-.1357, -.1178)
KPHN, %	.0867 (.0571, .1028)	.0843 (.0685, .0893)	.0869 (.0825, .0907)	.0876 (.0775, .1003)	.0877 (.0789, .1050)	.0874 (.0805, .0933)
KPHT, %	.0508 (.0021, .0747)	-.0134 (-.0548, -.0053)	.0577 (.0040, .0873)	.0155 (-.0128, .0694)	.0865 (.0271, .1173)	-.0399 (-.0531, -.0245)
MBA, units	53.17 (36.68, 61.01)	27.91 (12.75, 37.70)	25.63 (3.89, 39.08)	2.68 (-15.17, 26.73)	-.01 (-7.93, 15.27)	24.40 (13.57, 43.68)
MBN, units	-4.83 (-10.78, 2.13)	-4.35 (-8.15, -.04)	-4.25 (-7.97, 3.06)	-5.64 (-18.90, 4.45)	-4.79 (-13.41, 5.52)	-4.84 (-11.36, 3.40)
MBT, units	48.35 (30.53, 57.70)	23.57 (10.20, 37.66)	21.38 (-4.08, 42.15)	-2.96 (-34.07, 31.00)	-4.80 (-21.13, 14.01)	19.55 (2.92, 47.08)
WBSA, kg	-1.017 (-1.341, -.630)	-.638 (-1.172, .920)	-.535 (-.726, -.345)	-.303 (-.809, .190)	.009 (-.262, .411)	-.834 (-1.419, -.160)
WBSN, kg	-.179 (-.260, -.106)	-.160 (-.226, -.004)	-.183 (-.222, -.133)	-.184 (-.263, -.102)	-.175 (-.240, .002)	-.182 (-.257, -.107)
WBST, kg	-1.196 (-1.525, -.796)	-.798 (-1.395, .916)	-.718 (-.942, -.478)	-.486 (-1.045, .088)	-.166 (-.446, .413)	-1.015 (-1.676, -.267)

^aSimilar carcass composition basis.

^bCWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force; A = additive; N = nonadditive; T = total.

^cMean of sire expected progeny differences.

^d(smallest, largest) sire expected progeny difference.

$\frac{3}{4}$ A $\frac{1}{4}$ B, $\frac{1}{4}$ A $\frac{3}{4}$ B, and Brangus sires. These differences were caused by the values of the estimates of AB interbreed group genetic effects (i.e., large and positive for CWT and FAT, and large and negative for KPH), which are part of the group component of the additive MEPD of sires with at least one crossbred parent ($\frac{3}{4}$ A $\frac{1}{4}$ B, $\frac{1}{4}$ A $\frac{3}{4}$ B, and Brangus). Most ranges for sire additive MEPD overlapped (only the ranges for $\frac{3}{4}$ A $\frac{1}{4}$ B and Brangus sires and those for A and B sires did not overlap), indicating that sires of high and low additive MEPD were present in all breed groups of sires for CWT, LMA, and KPH. Brangus sires were most similar to $\frac{3}{4}$ A $\frac{1}{4}$ B sires for these three carcass yield traits.

A completely different pattern existed for LMA and the two carcass quality traits (MB and WBS). The mean of the sire additive MEPD for LMA and MB showed a clear decreasing trend from A to B. Contrarily, the mean of the sire additive MEPD for FAT had an increasing trend from A to B. Crossbreeding studies using least squares analyses (Crouse et al., 1989; Huffman et al., 1990) have also found similar trends for MB and WBS. The mean and the range of additive MEPD of Brangus sires were similar to those of $\frac{1}{2}$ A $\frac{1}{2}$ B sires for LMA and MB, whereas for WBS they were more similar to A sires. The range of additive MEPD for Brangus sires, however, was similar to those of $\frac{3}{4}$ A $\frac{1}{4}$ B sires for LMA. Additive MEPD ranges overlapped across all six breed groups of sires only for LMA, indicating the existence of sires of similar additive MEPD for LMA in all breed groups. Additive MEPD ranges for MB and WBS for A and B did not overlap; thus, all A sires produced steers whose beef had more marbling and was more tender than that of steers from any of the B sires used in this multibreed herd. A similar situation existed between $\frac{1}{2}$ A $\frac{1}{2}$ B and B sires for WBS; thus, all $\frac{1}{2}$ A $\frac{1}{2}$ B sires produced steers that had beef that was more tender than that of steers from B sires. All other additive MEPD ranges overlapped, indicating that one or more sires across breed groups had comparable additive MEPD.

Nonadditive Multibreed Genetic Predictions. Mean sire nonadditive MEPD were very similar, and ranges of sire nonadditive MEPD overlapped across all breed groups of sires for all carcass traits. No trend across breed groups of sires was found for any of the six carcass traits. This indicated that all breed groups of sires in this AB multibreed herd had similar interbreed combining abilities regardless of their A and B breed composition.

Total Multibreed Genetic Predictions. The sum of the additive and nonadditive MEPD yield the total MEPD for each sire. Thus, because of the small differences among mean nonadditive MEPD for all carcass traits across breed groups of sires, the patterns of means and the overlapping of ranges for total direct MEPD across breed groups of sires was the same as the one observed for additive MEPD.

Table 9. Correlations between additive, nonadditive, and total expected progeny differences of sires mated to $\frac{1}{2}$ A $\frac{1}{2}$ B dams for carcass traits^a

Trait ^c	Genetic effect ^b		
	(A, N)	(A, T)	(N, T)
CWT	.41	.93	.72
LMA	.29	.94	.59
FAT	.04	1.00	.06
KPH	.16	1.00	.24
MB	.22	.99	.33
WBS	.33	1.00	.39

^aSimilar carcass composition basis.

^bA = additive; N = nonadditive; T = total.

^cCWT = hot carcass weight; LMA = area of the longissimus muscle at the 12th rib; FAT = fat thickness over the 12th rib; KPH = kidney, heart, and pelvic fat; MB = marbling score; WBS = Warner-Bratzler shear force.

Relationship Between Additive, Nonadditive, and Total MEPD. There was little association between sire additive and nonadditive direct MEPD within carcass traits (Table 9) in this multibreed herd (correlations ranged from near zero to medium). On the other hand, correlations between sire additive and total direct MEPD within carcass traits were very high, indicating that sire additive MEPD largely offset their corresponding A/B nonadditive MEPD. Finally, correlations between nonadditive and total direct MEPD, within carcass traits, had intermediate values between those of additive and nonadditive MEPD and those of additive and total MEPD. As implied by these correlations, the ranking of sires according to additive and total direct MEPD was either equal or very similar for all carcass traits in this AB multibreed herd. Thus, had nonadditive MEPD been unavailable, ranking sires by additive carcass trait MEPD would have given a close approximation to their ranking by total carcass trait MEPD.

The data set used here, as indicated earlier, was not a random sample of the A, B, Brangus, and other AB crossbred groups in the country. Estimates of covariances and patterns of additive, nonadditive, and total MEPD for carcass traits found here are only an *indication* of what might exist in a much larger AB multibreed population. Considering the large size of the AB multibreed population in the United States and the industry's use of a carcass composition end point procedure that is likely to allow more variability for carcass traits than the one used here, it seems reasonable to expect higher values of additive and nonadditive genetic parameters for carcass traits in the complete AB multibreed population. A genetic analysis that included data from A, B, Brangus, and other AB crossbred groups in the United States would be needed to make an accurate assessment of the actual additive and nonadditive genetic variability in the complete AB multibreed population. If the additive and nonadditive genetic parameters in the complete

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AB multibreed population were similar or higher than the ones estimated here, a multibreed AB national sire evaluation would seem justified. Such national multibreed sire evaluation would yield additive, A/B nonadditive, and total MEPD. A conservative sire selection strategy could be the following (Elzo et al., 1998): first select sires by their additive MEPD and then by total MEPD within those sires previously chosen by their additive MEPD. This selection strategy should increase the interbreed combining ability of sires in the AB multibreed population without affecting additive genetic progress.

National multibreed analyses that include combinations of other base breeds present in commercial beef cattle operations (e.g., Simmental, Simbrah, and Brahman; Hereford, Braford, and Brahman) would also need to be conducted. Sire evaluation in these overlapping multibreed populations could be a precursor to the ideal situation: a single national multibreed genetic evaluation involving all the beef breeds in the country (Elzo, 1996a). Close cooperation between universities and the various segments of the beef industry is, needless to say, essential to the realization of large-scale multibreed evaluations. Purebred and commercial producers, feedlot operators, and slaughter facilities will need to be involved. One of the first steps in a collaboration of this kind would be to identify the type of crossbred matings that the beef industry is, *or will be*, interested in supporting. Existing multibreed data sets can provide material to develop appropriate models and computing strategies for the resulting large unbalanced multibreed data sets. Researchers at Cornell University have already taken steps in this direction using field data from the Simmental-Simbrah-Canadian Simmental population (Klei and Quaas, 1995; Klei et al., 1996; Pollak and Quaas, 1998).

Implications

Appreciable additive intrabreed and interbreed, and nonadditive interbreed genetic variability existed among sires in an Angus-Brahman multibreed herd for carcass weight, longissimus muscle area, marbling, and shear force, and only small amounts of variation of fat thickness and kidney, heart, and pelvic fat remained when steers were slaughtered at similar carcass composition end points. Sire additive and nonadditive expected progeny differences overlapped, suggesting that sires with desirable carcass characteristics existed in straightbred and crossbred groups. Correlations between additive and total expected progeny differences were high, suggesting that, in the absence of nonadditive expected progeny differences, the ranking of sires by additive expected progeny differences might be a good approximation to their ranking by total expected progeny differences.

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