

# Additive and Nonadditive Genetic Variability for Growth Traits in the Turipaná Romosinuano-Zebu Multibreed Herd<sup>1</sup>

M. A. Elzo<sup>\*,2</sup>, C. Manrique<sup>†</sup>, G. Ossa<sup>‡</sup>, and O. Acosta<sup>‡</sup>

\*Animal Science Department, University of Florida, Gainesville 32611;

<sup>†</sup>Facultad de Veterinaria y Zootecnia, Universidad Nacional, Santa Fe de Bogotá, Colombia;

<sup>‡</sup>Centro de Investigación Turipaná, CORPOICA, and Instituto Colombiano Agropecuario, Montería, Córdoba, Colombia

**ABSTRACT:** Intrabreed additive genetic, environmental, and phenotypic variances and covariances for Romosinuano (R) and Zebu (Z), as well as interbreed nonadditive genetic variances and covariances (sire  $\times$  breed-group-of-dam interactions), for birth weight (BWT), weaning weight (WW), and postweaning gain (GW) were computed using a Romosinuano-Zebu multibreed data set from the Turipaná Experiment Station in Colombia. Covariances were estimated with a sire-maternal grandsire model, using a multibreed REML procedure. The computing algorithm was a generalized expectation-maximization (GEM) algorithm. This algorithm yields no asymptotic standard errors as part of its computations. Because of the small size of the data set (2,546 calves), these REML covariance estimates should be viewed with caution. Estimates of intrabreed heritabilities were similar to the ratios of interbreed nonadditive to phenotypic

variances (interactibilities) for direct and maternal effects of the growth traits evaluated in this study. Intrabreed heritability estimates for BWT, WW, and GW direct genetic effects were .16, .09, and .14, for R and .24, .10, and .14 for Z. Corresponding heritability values for maternal effects were .18, .09, and .23 for R and .14, .13, and .07 for Z. Interactibility estimates were .21, .05, and .12, for direct and .26, .04, and .11, for maternal BWT, WW, and GW. Negative correlations between additive maternal weaning weight and direct and maternal postweaning gain, as well as between environmental weaning weight and postweaning gain, suggested that there was compensatory postweaning gain in this herd. Estimates of genetic variation and predictions of expected progeny differences showed that Romosinuano animals competed well against Zebu and RZ crossbred animals under the tropical environmental conditions at Turipaná.

Key Words: Beef Cattle, Analysis of Covariance, Genetic Parameters, Growth, Populations

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## Introduction

Romosinuano (**R**) is a tropically adapted *Bos taurus* breed of beef cattle developed from cattle of Spanish origin in the Sinú Valley of Colombia (Rouse, 1977). This is one of seven Colombian Criollo breeds adapted to tropical and subtropical conditions (Bejarano et al., 1986). The R breed in Colombia is recognized for its fertility, heat tolerance, and good combining ability with Zebu (**Z**). Thus, interest in R has increased in recent years as a source of tropically

adapted *Bos taurus* germplasm throughout tropical and subtropical America. Currently there are R cattle in Brazil, Costa Rica, the United States, and Venezuela. Most R cattle in these countries can trace their pedigrees back to the R herd at Turipaná. Thus, the R herd at the Turipaná Experiment Station has become a genetic base for the R breed. Consequently, it is important to document the degree of genetic variability that exists in the R herd at Turipaná for traits of economic importance.

The R breed in Colombia is not only used in straightbred matings, but also in crossbred matings, primarily matings of R sires to Z and  $\frac{1}{2}$ R- $\frac{1}{2}$ Z ( $F_1$ ) dams. Thus, a multibreed RZ herd was developed in 1979 at the Turipaná Experiment Station to compare the additive and nonadditive genetic effects of R, Z, and their crosses. The objectives of this research were 1) to estimate additive direct and maternal genetic covariances for birth weight (**BWT**), weaning weight (**WW**), and postweaning gain (**GW**) in the R and Z

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<sup>2</sup>To whom correspondence should be addressed: phone: (352) 392-7564; fax: (352) 392-7652; E-mail: elzo@animal.ufl.edu

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breeds; 2) to estimate nonadditive covariances due to intralocus R/Z interactions in sire  $\times$  breed-group-of-dam subclasses; and 3) to compare additive, nonadditive, and total predicted genetic values of sires used in the RZ multibreed herd at Turipaná.

## Materials and Methods

### Mating Design and Records

The RZ multibreed herd was housed at the Turipaná Experiment Station, which is located in the Sinu Valley, Department of Córdoba, Colombia. Turipaná is 13 m above sea level, has a mean annual temperature of 27°C, an annual precipitation of 1,100 mm, and a mean annual relative humidity of 82%.

The mating system used to create the RZ multibreed herd was an incomplete diallel design. The Z animals were Brahman. Straightbred R and Z and crossbred RZ sires and dams used in the multibreed herd were produced within the herd. The initial set of sires and dams was obtained from purebred R and Z and crossbred RZ groups of cattle that existed at the Turipaná Experiment Station in 1979. One hundred sires of three breed groups (71 R, 11  $\frac{1}{2}$ R- $\frac{1}{2}$ Z, and 18 Z) were mated to 903 dams of five breed groups (464 R, 55  $\frac{3}{4}$ R- $\frac{1}{4}$ Z, 199  $\frac{1}{2}$ R- $\frac{1}{2}$ Z, 67  $\frac{1}{4}$ R- $\frac{3}{4}$ Z, and 118 Z) over a period of 17 yr (1979 to 1995) to produce 252,546 straightbred and crossbred calves (Table 1). Connectivity over time was maintained by the use of various sires (R,  $\frac{1}{2}$ R- $\frac{1}{2}$ Z, and Z) across years. The cattle were maintained on grass pastures (*Dichanthium aristatum*) and were provided ad libitum access to a complete mineral supplementation. Cows were bred from April to June, and calving occurred between January and March.

The original data file was checked and corrected for erroneous information. The total numbers of calf records in the data file for the three growth traits were 2,546 BWT, 1,961 WW, and 1,687 GW. Adjustments for WW (205 d) and GW (345 d) were computed using Beef Improvement Federation formulae (BIF, 1996).

### Estimation of Covariance Component and Genetic Prediction Procedures

The structure of the RZ data set permitted the use of multibreed covariance estimation procedures (MREMLEM, Elzo, 1994). The MREMLEM procedure estimated covariances by Restricted Maximum Likelihood (Harville, 1977) using a Generalized Expectation-Maximization (GEM) algorithm (Dempster et al., 1977). An in-house FORTRAN program, run on an IBM RS6000 workstation, model 580, was used to perform computations. Computations in the GEM algorithm do not include the information matrix; thus, the MREMLEM program did not compute asymptotic

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

Breed group of dam	Breed group of sire		
	Romosinuano	$\frac{1}{2}$ R- $\frac{1}{2}$ Z	Zebu
Romosinuano	64 <sup>a</sup>	4	8
	41 <sup>b</sup>	0	3
	426 <sup>c</sup>	16	26
	1,466 <sup>d</sup>	16	39
$\frac{3}{4}$ R- $\frac{1}{4}$ Z	16	0	7
	1	0	2
	31	0	24
	51	0	43
$\frac{1}{2}$ R- $\frac{1}{2}$ Z	16	11	15
	6	6	12
	37	102	60
	117	144	198
$\frac{1}{4}$ R- $\frac{3}{4}$ Z	25	0	1
	13	0	0
	67	0	0
	161	0	2
Zebu	26	3	13
	13	0	8
	55	5	58
	108	5	196

<sup>a</sup>Number of sires.

<sup>b</sup>Number of maternal grandsires.

<sup>c</sup>Number of dams.

<sup>d</sup>Number of calves.

standard errors of the REML covariance estimates. Covariance estimates were kept within their boundaries by first computing the Cholesky elements of each covariance matrix and then obtaining the covariance matrices by multiplication of the Cholesky matrices by their transposes (Elzo, 1996b).

The small unbalanced data set allowed the simultaneous estimation of direct and maternal covariances for at most two traits. Thus, three separate analyses were conducted: BWT and WW, BWT and GW, and WW and GW. These analyses yielded three values for each variance and a single value for each covariance. Repeated estimates of variances ( $n = 3$ ) were averaged to obtain a single estimate. These means of variance estimates and single covariance estimates produced the final set of estimates of additive and nonadditive covariance matrices.

Estimates of direct and maternal covariances from single trait analyses, and zero covariances between traits, were used as priors for the two-trait analyses. The convergence criterion was that CCONV was less than  $10^{-4}$ , where CCONV was the ratio of the sum of squares of the absolute difference between covariance estimates in GEM iterations  $i$  and  $i - 1$  to the sum of squares of the covariance estimates in GEM iteration  $i - 1$ .

**Multibreed Model.** The model used for the two-trait analyses (BWT and WW, BWT and GW, and WW and GW) was a sire-maternal grandsire model similar to

the one used by Elzo and Wakeman (1998). The sire-maternal grandsire model here contained no interbreed RZ additive direct and maternal genetic effects. Interbreed additive genetic effects occur only when the parents in the model (sires and maternal grandsires) are crossbred. However, the parents of all sires and maternal grandsires represented in the RZ multibreed herd (R, F<sub>1</sub> ½R-½Z, and Z) were straightbred. Thus, interbreed RZ additive genetic effects due to sires and maternal grandsires were not included in the model, and interbreed additive genetic covariances were not estimated.

The multibreed model for each trait contained fixed environmental effects, fixed regression genetic group effects, random genetic effects, and residual. The fixed environmental effects were 1) contemporary group (year × sex of calf) and 2) age of dam within sex-of-calf × breed-group-of-dam subclass, where breed group of dam was modeled as a function of the fraction of R alleles in the dam. The fixed regression genetic group effects were as follows: 1) intrabreed additive direct (as a function of the expected fraction of R alleles in all sires plus .5 the expected fraction of R alleles in all maternal grandsires), 2) intrabreed additive maternal (as a function of the expected fraction of R alleles in all maternal grandsires), 3) intralocus interbreed R/Z nonadditive direct (as a function of the probabilities of the R and Z alleles in one locus in the progeny of all sires), 4) intralocus interbreed R/Z nonadditive maternal (as a function of the probabilities of the R and Z alleles in one locus in the female progeny [i.e., dams of calves] of all maternal grandsires), and 5) maternal granddam genetic group effect (as a function of the expected fraction of R alleles in maternal grandams). Intrabreed additive regression genetic group effects estimated the difference between R and Z genetic group effects. Intralocus R/Z nonadditive regression group effects estimated the difference between interbreed R/Z and intrabreed R/R and Z/Z intralocus interaction effects, as a function of the probability of R and Z alleles from different parents received by the progeny of sires and maternal grandsires. Maternal granddam genetic group effects contained the direct and maternal additive genetic effects.

The random genetic effects 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 A/B intralocus interactions in the progeny of the sire), 5) maternal nonadditive maternal grandsire genetic effect (as a function of A/B intralocus interactions in the progeny of the maternal grandsire), and 6) residual.

The multibreed model for each two-trait analysis (BWT and WW, BW and GW, and WW and GW) had the same matrix representation as the one described in Elzo and Wakeman (1998). However, the vector of

additive regression group genetic effect and its corresponding matrix excluded interbreed additive genetic effects. Also, additive direct and maternal random genetic effects did not contain interbreed additive genetic effects. For completeness, the two-trait multibreed model used here, in matrix notation, is described below.

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

$$\begin{bmatrix} y \\ s_a \\ s_n \\ v \end{bmatrix} \sim MVN \left\{ \begin{bmatrix} Xb + Z_{ga}g_a + Z_{gn}g_n + Z_{mgd}g_{mgd} \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} Z_a G_a Z_a' + Z_n G_n Z_n' + R & Z_a G_a & Z_n G_n & R \\ & G_a & 0 & 0 \\ & G_n & G_n & 0 \\ & R & 0 & R \end{bmatrix} \right\} \quad [1]$$

where

- y** = vector of calf records ordered by traits (BWT and WW, BWT and WW, or WW and GW) within calves,
- b** = vector of contemporary groups (**b<sub>cg</sub>**) and age of dam within sex of calf (**b<sub>adx</sub>**) effects,
- g<sub>a</sub>** = vector of intrabreed additive A direct (**g<sub>AAd</sub>**), and maternal (**g<sub>AAm</sub>**) genetic group effects;
- g<sub>n</sub>** = vector of interbreed A/B nonadditive direct (**g<sub>A/Bnd</sub>**) and maternal (**g<sub>A/Bnm</sub>**) genetic group effects,
- g<sub>mgd</sub>** = vector of maternal granddam genetic group effects,
- s<sub>a</sub>** = vector of sire additive direct (**s<sub>ad</sub>**) and maternal (**s<sub>am</sub>**) genetic effects,
- s<sub>n</sub>** = vector of sire nonadditive direct (**s<sub>nd</sub>**) and maternal (**s<sub>nm</sub>**) genetic effects,
- v** = vector of residuals.
- X** = matrix that relates calf records to 1) to elements of **b<sub>cg</sub>** (1's and 0's), and 2) to elements of **b<sub>adx</sub>** through the expected fraction of A alleles in the dam of the calf,
- Z<sub>ga</sub>** = matrix that relates calf records to 1) elements of **g<sub>AAd</sub>** through the expected fraction of A alleles in the sire and the maternal grandsire of the calf (**p<sub>As</sub> + .5p<sub>Am</sub>**), 2) elements of **g<sub>AAm</sub>** through the expected fraction of A alleles in the maternal grandsire of the calf (**p<sub>Am</sub>**), where **p** = probability, and the subscripts A = Angus, B = Brahman, s = sire, and m = maternal grandsire,

$\mathbf{Z}_{gn}$  = matrix that relates calf records to 1) elements of  $\mathbf{g}_{nd}$  through the probability of intralocus A and B alleles in the calf ( $p_{As} p_{Bd} + p_{Bs} p_{Ad}$ ), and 2) elements of  $\mathbf{g}_{nm}$  through the probability of intralocus A and B alleles in the dam of the calf ( $p_{Asd} p_{Bdd} + p_{Bsd} p_{Add}$ ), where the subscripts d = dam, sd = sire of dam, and dd = dam of dam,

$\mathbf{Z}_a$  = matrix that relates calf records to 1) elements of  $\mathbf{s}_{ad}$  through the sire (1) and the maternal grandsire (.5), and 2) elements of  $\mathbf{s}_{am}$  through the maternal grandsire (1),

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

$\mathbf{Z}_{mgd}$  = matrix that relates calf records to elements of  $\mathbf{g}_{mgd}$  through the expected fraction of A alleles in the maternal grandam.

**Computational Strategy.** The multibreed mixed model equations (**MMME**) for Model [1] were constructed as indicated in Elzo and Wakeman (1998). The inverses of  $\mathbf{G}_a$  and  $\mathbf{G}_n$  were obtained by Hendersonian rules (Elzo, 1990a,b), and the multibreed covariances needed to apply these computational rules were obtained by formulas 3 to 6 in Elzo and Wakeman (1998). The inverse of the block-diagonal matrix  $\mathbf{R}$  was computed by direct inversion of its  $2 \times 2$  diagonal blocks. The MMME were solved by sparse matrix procedures (FSPAK, Perez-Enciso et al., 1994). Residual sire additive and nonadditive genetic predictions, and their corresponding error variances of predictions, were subsequently obtained (Elzo and Wakeman, 1998). Similarly, predictions of residuals for the multibreed model ( $\hat{v}$ ) and their error variances of prediction were computed as indicated in Elzo (1994). These predicted sire genetic residuals, and they predicted residuals for the multibreed model, and their variances of prediction errors were used by the MREMLEM procedure to estimate base genetic and environmental covariances.

**Multibreed Genetic Parameters.** The MREMLEM program yielded estimates of base additive genetic (intra-breed R, and Z), base nonadditive genetic (interbreed R/Z), and base environmental (intra-breed R and Z) covariances. For example, the BWT-WW analysis computed a total of 36 base covariances: 10 additive direct and maternal intra-breed R, 10 additive direct and maternal intra-breed Z, 10 nonadditive direct and maternal interbreed R/Z, 3 intra-breed environmental R, and 3 intra-breed environmental Z.

The 10 covariances in each base additive and nonadditive genetic covariance matrix were as follows: var(BWTD), cov(BWTD, WWD), cov(BWTD, BWM), cov(BWTD, WWM), var(WWD), cov(WWD, BWTM), cov(WWD, WWM), var(BWTM), cov(BWTM, WWM), and var(WWM), where **D** = direct and **M** = maternal. The three covariances in each base environmental covariance matrix were var(BWTE), cov(BWTE, WWE), and var(WWE), where **E** = environmental. Similar sets of covariances were estimated for the BWT-GW and WW-GW pairs of traits. Base covariance estimates were used to compute intrabreed ratios of additive genetic to phenotypic variances (heritabilities), ratios of interbreed nonadditive genetic to phenotypic variances (interactibilities; Elzo et al., 1996; Elzo and Wakeman, 1998), and intrabreed additive as well as interbreed nonadditive genetic correlations.

**Multibreed Genetic Predictions.** The same model used to compute covariances was used to obtain estimates of additive and nonadditive regression genetic groups and predictions of sire direct and maternal genetic effects. Three types of multibreed expected progeny differences (**MEPD**) were computed for direct and maternal BWT, WW, and GW sire genetic effects: additive, nonadditive, and total MEPD. Because additive and nonadditive group genetic effects were modeled separately from their corresponding random genetic effects, sire additive and nonadditive MEPD were computed as a weighted sum of a fixed group effect plus a random effect. Nonadditive and total MEPD were computed using the formulas given in Elzo and Wakeman (1998). However, regression genetic group solutions for the RZ multibreed data set involved only intrabreed genetic effects. Thus, additive direct (maternal) sire MEPD were computed here as the fraction of R in the sire times the solution for direct (maternal) R sire genetic group effect plus the sire direct (maternal) prediction.

Additive MEPD predict the mean additive genetic value of the progeny of a sire of any breed composition relative to a multibreed additive genetic base. A multibreed additive genetic base can be defined as a linear combination of intra-breed and interbreed genetic (or genetic group, for a multibreed model with genetic groups) effects. Because intra-breed regression additive genetic group effects were assumed to be fixed in multibreed Model [1], R and Z additive direct and maternal group genetic effects were not estimable—only their differences were estimable. Thus, for computational convenience, the multibreed additive genetic base here was defined to be Z (i.e., 0R-1Z). A consequence of using regression to estimate additive group genetic effects is that Z alleles from purebred Z and crossbred RZ sires contribute to their estimation. Consequently, the mean additive genetic value of the sample of Z alleles from Z sires only may, or may not, be the same as the mean of the sample of

Z alleles coming from Z and RZ crossbred sires. Thus, the prediction of the difference between the mean of the purebred Z sire additive MEPD and the mean of the sample of Z alleles in the RZ multibreed herd may, or may not, be zero.

Nonadditive sire MEPD predict the mean nonadditive genetic value of the progeny of a sire of any breed composition relative to a multibreed nonadditive genetic base. The same as for an additive multibreed genetic base, a multibreed nonadditive genetic base can be defined as a linear combination of intrabreed and interbreed nonadditive genetic effects. The multibreed model used here contained only intralocus interbreed R/Z genetic group effects. Because these nonadditive groups were assumed to be fixed, interbreed intralocus R/Z genetic group effects were not estimable, but the difference between interbreed (R/Z) and intrabreed (R/R and Z/Z) intralocus interactions was estimable. Thus, the nonadditive genetic base was defined to be the mean of the intralocus (R/R and Z/Z) interactions in the RZ multibreed herd.

Nonadditive direct and maternal sire MEPD differ depending on the breed composition of the dams mated to a sire. Thus, a sire will have as many nonadditive direct and maternal MEPD as breed groups of dams it was mated to. Because sire total

Table 2. Estimates of base additive and nonadditive genetic variances and covariances for birth weight (BWT), weaning weight (WW), and postweaning gain (GW)

Trait 1 <sup>a</sup>	Trait 2 <sup>a</sup>	Genetic variances and covariances, kg <sup>2</sup>		
		Additive intrabreed R	Additive intrabreed Z	Nonadditive interbreed R/Z
BWT	BWTD	2.04	3.68	3.65
	WWD	1.81	4.17	1.05
	GWD	.23	1.71	.70
	BWTM	-.42	-.51	.07
	WWM	.23	-2.46	-.05
	GWM	.52	.25	-.09
WWD	WWD	72.72	108.15	50.75
	GWD	-20.70	6.73	-8.24
	BWTM	.71	-.04	.33
	WWM	16.63	-63.41	-.36
	GWM	-21.15	11.00	.56
GWD	GWD	100.46	155.55	127.76
	BWTM	-.90	-1.21	.79
	WWM	-19.16	-21.64	.05
	GWM	10.57	-1.65	1.66
BWTM	BWTM	2.32	2.23	4.52
	WWM	.49	-1.59	.13
	GWM	-.82	-1.34	-.27
WWM	WWM	73.64	149.38	41.96
	GWM	-25.25	-13.99	-1.46
GWM	GWM	166.52	74.83	110.32

<sup>a</sup>D = direct; M = maternal.

Table 3. Estimates of base environmental variances and covariances for birth weight (BWT), weaning weight (WW), and postweaning gain (GW)

Trait 1	Trait 2	Environmental variances and covariances, kg <sup>2</sup>	
		Intrabreed R	Intrabreed Z
BWT	BWT	8.73	9.97
	WW	43.72	67.61
	GW	4.87	5.24
WW	WW	674.03	936.01
	GW	-164.25	-390.61
GW	GW	456.47	873.86

MEPD were defined as the sum of sire additive and nonadditive MEPD, there will be as many total MEPD as nonadditive MEPD.

Nonadditive and total MEPD can be used to compare sires of any R and Z breed fractions when mated to dams of any R and Z breed fractions. For example, a R sire mated to 1/4R-3/4Z dams could be compared with a 1/2R-1/2Z sire mated to Z dams. However, a more realistic situation would probably be the comparison of sires of various R and Z breed fractions when mated to dams of a single breed group (e.g., 1/2R-1/2Z, 1/4R-3/4Z, and Z). To illustrate sire nonadditive and total MEPD in this case, a single group of dams (1/2R-1/2Z) was used. Sires of all R and Z breed fractions were assumed to have been mated to 1/2R-1/2Z dams. This breed group of dams was chosen because the value of the probability of intralocus R/Z interactions in the progeny of all RZ breed compositions is 1/2, which simplifies comparisons across sires. It should be emphasized, however, that dams of any breed group could have been used to compare sires for nonadditive and total MEPD.

## Results and Discussion

### Covariance Components and Genetic Parameters

Table 2 contains estimates of intrabreed R and Z additive and nonadditive interbreed R/Z genetic variances of and covariances among direct (D) and maternal (M) genetic effects for BWT, WW, and GW. Table 3 shows the intrabreed R and Z environmental variances and covariances among these three growth traits. Covariance estimates in Tables 2 and 3 were obtained in three independent two-trait analyses: (BWT, WW), (BWT, GW), and (WW, GW). These analyses yielded two estimates for each direct and maternal genetic variance, and one estimate for each genetic covariance. Values of variances reported in Tables 2 and 3 are means of these pairs of estimates of direct and maternal variances for each trait. Table 4 shows R and Z heritabilities and R/Z interactibilities

Table 4. Estimates of additive intrabreed ratios and genetic correlations, and nonadditive interbreed ratios and genetic correlations, for birth weight (BWT), weaning weight (WW), and postweaning gain (GW)

Parameter <sup>a</sup>	Genetic effect		
	Additive intrabreed R	Additive intrabreed Z	Nonadditive interbreed R/Z
$v_X(\text{BWTD})/v_P(\text{BWT})$	.16	.24	.21
$r_X(\text{BWTD}, \text{WWD})$	.15	.21	.08
$r_X(\text{BWTD}, \text{GWD})$	.02	.07	.03
$r_X(\text{BWTD}, \text{BWTM})$	-.19	-.18	.02
$r_X(\text{BWTD}, \text{WWM})$	.02	-.11	.0
$r_X(\text{BWTD}, \text{GWM})$	.03	.02	.0
$v_X(\text{WWD})/v_P(\text{WW})$	.09	.10	.05
$r_X(\text{WWD}, \text{GWD})$	-.24	.05	-.10
$r_X(\text{WWD}, \text{BWTM})$	.05	.0	.02
$r_X(\text{WWD}, \text{WWM})$	.23	-.50	-.01
$r_X(\text{WWD}, \text{GWM})$	-.19	.12	.01
$v_X(\text{GWD})/v_P(\text{GW})$	.14	.14	.12
$r_X(\text{GWD}, \text{BWTM})$	-.06	-.07	.03
$r_X(\text{GWD}, \text{WWM})$	-.22	-.14	.0
$r_X(\text{GWD}, \text{GWM})$	.08	-.02	.01
$v_X(\text{BWTM})/v_P(\text{BWT})$	.18	.14	.26
$r_X(\text{BWTM}, \text{WWM})$	.04	-.09	.01
$r_X(\text{BWTM}, \text{GWM})$	-.04	-.10	-.01
$v_X(\text{WWM})/v_P(\text{WW})$	.09	.13	.04
$r_X(\text{WWM}, \text{GWM})$	-.23	-.13	-.02
$v_X(\text{GWM})/v_P(\text{GW})$	.23	.07	.11

<sup>a</sup> $v$  = variance;  $r$  = correlation; subscripts: X = genetic effect (i.e., additive intrabreed R, additive intrabreed Z, nonadditive interbreed R/Z), and P = phenotypic; D = direct; M = maternal.

for direct and maternal genetic effects of as well as additive intrabreed and nonadditive interbreed genetic correlations among BWT, WW, and GW. Table 5 contains environmental and phenotypic correlations among BWT, WW, and GW for R and Z. The estimates of covariances and genetic parameters presented in these tables should be viewed with caution. It should be emphasized that these correlations were computed using a small data set and that their asymptotic standard errors are expected to be large. Substantially different estimates might be obtained with another small data set from a single multibreed herd or with a large data set that incorporated data from many herds.

**Additive Genetic Variances and Heritabilities.** Estimates of intrabreed direct genetic variances were larger in Z than in R for BWT, WW, and GW (Table 4). Estimates of intrabreed maternal genetic variance showed no clear pattern; they were similar for BWTM, smaller in R than in Z for WWM, and larger in R than in Z for GWM. However, estimates of variances of intrabreed environmental effects for BWT, WW, and GW were also larger in Z than in R. Consequently, except for GWM, estimates of heritabilities for direct and maternal genetic effects of R were similar to those of Z. As indicated earlier, the MREMLEM procedure

did not compute standard errors of the REML covariance estimates. Given the small size of the RZ multibreed data set, and the large number of covariances estimated simultaneously in the analyses, asymptotic standard errors of covariance estimates are likely to be large.

Heritability estimates of BWT and WW direct and maternal and of GW direct for R and for Z were within the range of values reported in the literature for *Bos taurus* breeds (Garrick et al., 1989; Nuñez-Dominguez et al., 1993; Meyer, 1994; Rodríguez-Almeida et al., 1995; Elzo and Wakeman, 1998) and for *Bos indicus* breeds (Kriese et al., 1991; Eler et al., 1994, 1995; Van Vleck et al., 1996; Diop, 1997; Elzo and Wakeman, 1998). Estimates of heritabilities for direct genetic effects in the RZ multibreed herd tended to be smaller than literature values for all traits. No distinct pattern existed, however, for maternal heritabilities. Literature values of heritabilities for BWT maternal were mostly smaller than the estimates for R and Z obtained here; the opposite occurred for WW maternal.

Genetic and environmental factors may have contributed to the rather low values of heritabilities estimated in this RZ multibreed data set. On one hand, the number of R and Z straightbred and RZ crossbred sires used to estimate covariances was small. A different sample, or a substantially larger sample of sires than the one used here (e.g., 1,000 sires per breed group), might have produced larger estimates of direct and maternal genetic covariances. On the other hand, animals in the RZ multibreed herd were maintained on grass pastures throughout the year without any protein or energy supplementation. Because both breeds had low heritability estimates, this might be an indication that the nutritional environment was insufficient for animals to express their direct and maternal genetic potential. Had a protein-energy supplementation been provided during critical preweaning and postweaning periods we might have uncovered more genetic variation among sires. Nevertheless, the genetic parameters estimated in the

Table 5. Estimates of intrabreed environmental and phenotypic correlations among birth weight (BWT), weaning weight (WW), and postweaning gain (GW)

Correlation	Breed	
	Romosinuano	Zebu
Environmental		
$r_E(\text{BWT}, \text{WW})$	.57	.70
$r_E(\text{BWT}, \text{GW})$	.08	.06
$r_E(\text{WW}, \text{GW})$	-.30	-.43
Phenotypic		
$r_P(\text{BWT}, \text{WW})$	.46	.51
$r_P(\text{BWT}, \text{GW})$	.04	.04
$r_P(\text{WW}, \text{GW})$	-.32	-.37

RZ multibreed herd suggest that selection for growth traits will be feasible under the current feeding system.

The values of heritabilities for GWM in R (.23) and Z (.07) suggest that the preweaning maternal environment continued to affect calf growth after weaning and that this postweaning maternal effect was more important for the progeny of R than the progeny of Z dams. Most studies estimated maternal heritabilities for postweaning weights (yearling weights, 18-mo weights) rather than gains. The heritability of GWM for R was larger than most maternal yearling weight and maternal 18-mo weight heritabilities reported for *Bos taurus* breeds (Meyer et al., 1993; Nuñez-Dominguez et al., 1993; Meyer, 1994), whereas the one for Z was somewhat smaller than those estimated for *Bos indicus* breeds (Eler et al., 1995; Diop, 1997) but similar to that estimated for maternal 18-mo weight in *Bos taurus* × *Bos indicus* crossbreds by Mackinnon et al. (1991). It seems that the postweaning compensatory growth that occurs when animals are reared under pasture conditions without supplementation may be insufficient to offset preweaning maternal influences (Eler et al., 1995; Diop, 1997).

The final selection of beef animals for their own ability to grow (i.e., direct additive postweaning gain) is usually performed at 18 mo of age. Thus, under pasture production systems without supplementation, multibreed genetic evaluation models will probably need to include both direct and maternal postweaning growth effects to ensure proper separation of these effects.

**Additive Genetic Correlations.** Additive genetic correlations (Table 4) were mostly low for R (−.24 to .23) and Z (−.50 to .21). Correlations among additive direct genetic effects were small and positive, except for the correlation between WWD and GWD in R (−.24). However, correlations among additive maternal genetic effects were all negative, except for the correlation between BWTM and WWM in R which was close to zero (.04). Although most correlations between additive direct and maternal genetic effects in R and Z were of the same sign, there were a few differences, particularly between WWD and WWM. For example, the correlation between additive 1) BWTM and WWM was near zero for R (.02) and negative for Z (−.11), 2) WWD and WWM was positive for R (.23) and negative for Z (−.50), and 3) WWD and GWM was negative for R (−.19) and positive for Z (.12). Agreement in sign existed, for example, in the correlations between additive 1) BWTM and BWTM (−.19 for R and −.18 for Z), 2) GWD and maternal preweaning (BWTM and WWM) traits (−.06 and −.22 for R, −.07 and −.14 for Z), and 3) WWM and GWM (−.23 for R and −.13 for Z).

Correlation estimates for preweaning growth traits were within the range of values reported for *Bos*

*taurus* breeds (Garrick et al., 1989; Nuñez-Dominguez et al., 1993; Meyer, 1994; Rodríguez-Almeida et al., 1995; Elzo and Wakeman, 1998), *Bos indicus* breeds (Kriese et al., 1991; Eler et al., 1994, 1995; Van Vleck et al., 1996; Diop, 1997; Elzo and Wakeman, 1998), and *Bos taurus* × *Bos indicus* crosses (Mackinnon et al., 1991; Meyer et al., 1993; Meyer, 1994; Elzo and Wakeman, 1998). As indicated above, most studies analyzed postweaning growth in terms of weights rather than gains. Because of the part-whole relationship that exists between pre- and postweaning weights, correlations between pre- and postweaning weights in these studies are not comparable to the correlations involving preweaning weights and postweaning gains estimated here. The only study that explicitly separated postweaning gain (weaning to yearling) was the one in Simmental by Garrick et al. (1989). Correlation estimates for preweaning weight-postweaning gain traits in the RZ multibreed herd were consistent with those estimated in the Simmental population.

Perhaps the most interesting correlations estimated here were those between WWM and GWM (−.23 in R and −.13 in Z) and between WWM and GWD (−.22 in R and −.14 in Z). Maternal effects are genetic to the dam but environmental to the calf. Thus, these correlation estimates suggest that animals in the RZ multibreed herd exhibited compensatory growth; calves that received a poorer preweaning maternal environment (probably associated to lower maternal milk production, Garrick et al., 1989) tended to have larger postweaning weight gains than calves that received better preweaning maternal care. This situation may change if a protein-energy supplement and/or improved pastures are provided for pre- and postweaning. However, the values of the genetic correlations between WWD and WWM suggest that the effect of an improved preweaning environment will be different for R and Z. This direct-maternal correlation was positive (.23) for R and negative (−.50) for Z, which indicates that selection for direct preweaning growth would be advantageous in R, but not in Z.

**Nonadditive Genetic Variances, Interactibilities, and Nonadditive Correlations.** Estimates of R/Z nonadditive variances were comparable to intrabreed variances for direct and maternal genetic effects (Table 2). Consequently, estimates of interactibilities were similar to those of intrabreed heritabilities (Table 4). Interactibility estimates in the RZ multibreed herd were similar to those obtained in an Angus-Brahman multibreed herd in Florida (Elzo and Wakeman, 1998) for direct and maternal BWT traits, but smaller for direct and maternal WW traits. However, even though these interactibility estimates included only R/Z interbreed intralocus genetic effects in sire × breed-group-of-dam subclasses, they had comparable values to ratios of dominance (intrabreed and interbreed intralocus genetic effects) to phenotypic variances in

various synthetic lines of cattle (Rodríguez-Almeida et al., 1995). Nonadditive R/Z interbreed correlation estimates were low ( $-.10$  to  $.08$ ) and mostly (12 out of 15) zero or positive. These R/Z interbreed correlations were somewhat smaller than, but in the same direction as, those estimated in the Angus-Brahman multibreed herd in Florida (Elzo and Wakeman, 1998).

The values of interactibilities estimated for the RZ multibreed herd indicate that R/Z nonadditive genetic effects due to sire  $\times$  breed-group-of-dam R/Z interactions were as important as additive genetic effects, and they should be included in the genetic evaluation of R and Z sires in addition to additive genetic effects, when they are used in crossbred matings. Thus, sires will have three MEPD: additive, nonadditive, and total (additive plus nonadditive). Prediction of additive, nonadditive, and total MEPD for R sires should help increase their usage in crossbreeding programs that will contribute to the breed's conservation and to its spread by making the breed part of commercially active production systems. A similar argument can be made for Z sires used with R and RZ crossbred dams.

**Environmental and Phenotypic Correlations.** Environmental and phenotypic correlations had approximately the same magnitude and sign in R and Z. These correlations were of medium size and positive between BWT and WW (.46 to .70), small and positive between BWT and GW (.04 to .08), and medium size and negative between WW and GW ( $-.30$  to  $-.43$ ). Positive environmental (Kriese et al., 1991; Elzo and Wakeman, 1998), residual (Garrick et al.,

1989; Eler et al., 1994; Meyer, 1994), and phenotypic (Garrick et al., 1989; Kriese et al., 1991; Eler et al., 1994; Meyer, 1994; Elzo and Wakeman, 1998) correlations between BWT and WW have been found in various *Bos taurus* and *Bos indicus* breeds. Except for a low negative environmental correlation in Brahman cattle, literature estimates of environmental (Kriese et al., 1991), residual (Garrick et al., 1989), and phenotypic (Garrick et al., 1989; Kriese et al., 1991) correlations between BWT and GW were low and positive.

As with the negative genetic correlations between maternal weaning and postweaning traits, the negative environmental and phenotypic correlations between WW and GW in R and Z indicate that there was compensatory postweaning gain. Kriese et al. (1991) also found negative environmental correlations between environmental effects of WW and GW (weaning to yearling) in Brahman, Brangus, Beefmaster, and Santa Gertrudis. Similarly, negative residual correlations between WW and GW (weaning to yearling) were found in Simmental (Garrick et al., 1989) and in Africander and Africander-Brahman crossbreds (Mackinnon et al., 1991).

#### Multibreed Genetic Predictions

As previously indicated, additive, nonadditive, and total MEPD can be used to compare sires of any RZ breed composition when mated to dams of one or more R and Z breed fractions. However, to illustrate the

Table 6. Means and ranges of additive, nonadditive, and total expected progeny differences of sires mated to  $\frac{1}{2}$ R- $\frac{1}{2}$ Z dams for birth weight (BWT), weaning weight (WW), and postweaning gain (GW)

Genetic effect, kg <sup>a</sup>	Breed group of sire		
	Romosinuano	$\frac{1}{2}$ R- $\frac{1}{2}$ Z	Zebu
BWTAD	-2.1 (-3.0, -1.4) <sup>b</sup>	-1.1 (-2.2, -.3)	-.2 (-1.0, .4)
BWTND	.9 (.2, 1.7)	1.0 (.6, 1.9)	.8 (.2, 1.9)
BWTTD	-1.2 (-2.3, -.2)	-.1 (-1.3, 1.6)	.6 (-.8, 1.8)
WWAD	-4.8 (-9.5, 4.3)	-2.7 (-7.4, 2.9)	.0 (-3.5, 3.4)
WWND	7.7 (5.6, 10.2)	7.6 (5.1, 10.7)	7.8 (5.8, 9.7)
WWTD	2.9 (-2.9, 13.2)	4.8 (-2.3, 13.6)	7.8 (2.5, 12.1)
GWAD	.0 (-8.6, 8.5)	-.1 (-7.8, 5.6)	.0 (-4.8, 6.1)
GWND	15.8 (10.7, 19.8)	14.8 (6.7, 20.3)	15.6 (9.1, 22.2)
GWTD	6.5 (-6.5, 16.0)	9.5 (-6.7, 20.1)	16.0 (6.3, 24.2)
BWTAM	2.5 (1.7, 3.5)	1.4 (.7, 2.1)	-.1 (-.7, .7)
BWTNM	-.4 (-1.6, .7)	-.2 (-.7, .4)	-.4 (-1.1, .8)
BWTTM	2.1 (1.0, 3.2)	1.1 (.4, 2.0)	-.5 (-1.5, 1.5)
WWAM	.0 (-4.1, 5.0)	-.7 (-5.0, 2.5)	-.5 (-10.3, 4.2)
WWNM	4.1 (2.5, 5.6)	3.7 (1.9, 4.5)	4.0 (1.5, 4.8)
WWTM	4.1 (-.7, 8.4)	3.0 (-2.8, 6.3)	3.4 (-8.0, 8.9)
GWAM	10.5 (-5.6, 16.2)	5.5 (4.0, 9.6)	.2 (-1.9, 2.6)
GWNM	-10.3 (-13.2, -7.2)	-10.3 (-12.4, -7.5)	-10.4 (-16.0, -6.8)
GWTM	.2 (-16.1, 5.8)	-4.8 (-8.4, 2.0)	-10.3 (-17.9, -4.2)

<sup>a</sup>AD(M) = additive direct (maternal); ND(M) = nonadditive direct (maternal); TD(M) = total direct (maternal).

<sup>b</sup>Mean (smallest, largest) sire expected progeny difference.



Table 7. Correlations between additive, and nonadditive and total expected progeny differences of sires mated to 1/2R-1/2Z dams for birth weight (BWT), weaning weight (WW), and postweaning gain (GW)

Genetic effect	Genetic effect <sup>a</sup>											
	BWT ND	WW ND	GW ND	BWT NM	WW NM	GW NM	BWT TD	WW TD	GW TD	BWT TM	WW TM	GW TM
BWTAD	.04	.01	-.05	.09	-.14	-.13	.94	.49	.62	-.82	-.19	-.70
WWAD	.02	.45	-.10	.25	-.08	-.01	.54	.97	.25	-.47	.04	-.58
GWAD	-.04	-.13	.24	.0	-.13	.03	.72	.27	.91	-.78	-.26	-.53
BWTAM	-.03	.02	.0	-.09	.11	.10	-.82	-.47	-.64	.95	.0	.76
WWAM	.03	-.03	-.03	-.07	.32	-.08	-.16	.04	-.22	-.05	.98	-.02
GWAM	.10	-.07	.11	-.04	.05	.14	-.63	-.53	-.41	.75	.01	.97
BWTND		-.09	.36	.18	-.16	.04	.39	-.01	.13	.03	-.01	.11
WWND			-.27	.03	.05	.01	-.02	.66	-.22	.03	-.01	-.07
GWND				.25	-.04	.02	.08	-.16	.62	.09	-.04	.10
BWTNM					-.55	-.14	.15	.22	.11	.24	-.19	-.07
WWNM						-.06	-.18	-.06	-.12	-.07	.52	.03
GWNM							-.10	.0	.03	.05	-.09	.35

<sup>a</sup>AD(M) = additive direct (maternal); ND(M) = nonadditive direct (maternal); TD(M) = total direct (maternal).

comparison of sires for nonadditive and total MEPD, sires were assumed to be mated to 1/2R-1/2Z dams. This group of dams was chosen because the probability of R/Z intralocus interactions is the same (1/2) regardless of the breed composition of the sire, which simplifies explanations. Table 6 shows the means and ranges of sire MEPD values for additive, R/Z nonadditive, and total genetic effects for BWT, WW, and GW. Means in Table 6 were included to be able to compare breed groups of sires in terms of their mean additive, nonadditive, and total MEPD. Ranges in Table 6 were included to provide information on the extent that sires differed within a breed group and on the degree of overlapping that existed across breed groups of sires for additive, nonadditive, and total sire MEPD.

As expected, given the small size of the RZ multibreed data set, the standard errors of prediction (SEP) of additive (A), nonadditive (N), direct (D), and maternal (M) sire MEPD were large. The overall means and ranges of the SEP of sire MEPD were .7 (.5, .9) kg for BWTAD, 4.6 (3.1, 5.3) kg for WWAD, 5.3 (3.4, 6.2) kg for GWAD, .9 (.4, 1.0) kg for BWTAM, 5.9 (3.3, 6.7) kg for WWAM, 6.7 (2.6, 8.5) kg for GWAM, .7 (.3, .9) kg for BWTND, 2.4 (.4, 3.0) kg for WWND, 4.2 (1.8, 5.3) kg for GWND, .9 (.3, 1.1) kg for BWTNM, 2.0 (.0, 2.5) kg for WWNM, and 4.0 (1.4, 4.8) kg for GWNM.

**Multibreed Additive Genetic Predictions.** The R breed group of sires had the smallest mean MEPD for preweaning direct additive genetic effects (BWTAD and WWAD), whereas 1/2R-1/2Z sires had intermediate values, and Z sires had the largest values of the three breed groups. With the exception of WWAM for 1/2R-1/2Z, this trend was the opposite for preweaning maternal additive genetic effects (BWTAM and WWAM). Mean MEPD values for GWAD were close to zero for all breed groups of sires. For GWAM, R sires had the largest mean MEPD, followed by 1/2R-1/2Z sires, and lastly, by Z sires. The range of additive

MEPD overlapped for all traits and effects across breed groups of sires, except for the ranges of BWTAD and BWTAM in R and Z, which suggests that R and Z may be additively different for BWT direct and maternal additive genetic effects. These ranges were lower in R (-3.0 to -1.4 kg) than in Z (-1.0 to .4 kg) for BWTAD, but higher in R (1.7 to 3.5 kg) than in Z (-.7 to .7 kg) for BWTAM. Thus, all R sires ranked lower for BWTAD and higher for BWTAM than Z sires. However, as evidenced by the overlapping ranges, the ranking of sires across breed groups for all other growth traits and effects yielded a mixture of R, 1/2R-1/2Z, and Z sires.

**Nonadditive and Total Multibreed Genetic Predictions.** Mean MEPD for R/Z nonadditive genetic effects were similar across breed groups of sires for all traits, thus no clear advantage of one sire group over another was found in the RZ multibreed herd. However, the mean MEPD for total genetic effects (T) presented clear trends across breed groups of sires for direct and maternal total genetic effects. Because of the similarity of the mean nonadditive MEPD, the trends of the mean MEPD for total genetic effects across breed groups of sires were essentially the same as the trends of the mean MEPD for additive genetic effects. Thus, Z sires had the highest total MEPD means for all growth traits (BWTTD, WWTD, and GWTD), followed by 1/2R-1/2Z sires and R sires. The opposite trend existed with total maternal genetic effects (except for WWTM), where R had the largest total MEPD means (BWTTM, WWTM, and GWTM), 1/2R-1/2Z sires had intermediate values, and Z had the smallest total MEPD means. The ranges of nonadditive and total MEPD for all traits and effects overlapped across breed groups of sires. Thus, the ranking of sires across breed groups for nonadditive and total MEPD does contain representatives of the R, 1/2R-1/2Z, and Z breed groups in the top, medium, and bottom tiers.

**Relationship Between Additive, Nonadditive, and Total MEPD.** Table 7 contains correlations between

direct and maternal additive MEPD, and nonadditive and total MEPD, for BWT, WW, and GW. Correlations between additive and nonadditive MEPD within traits and effects ranged from low to medium, and they were somewhat larger for direct genetic effects (.04 to .55) than for maternal genetic effects (-.09 to .32). Correlations between additive and total MEPD within traits and effects were substantially larger (.91 to .98) than those between nonadditive and total MEPD (.24 to .66). Correlations between MEPD *across* traits and genetic effects were positive between additive direct and total direct (.25 to .72), mostly negative between additive direct and total maternal or between additive maternal and total direct (-.82 to .04), close to zero or positive between additive maternal and total maternal (-.05 to .76), and low (positive and negative) between nonadditive direct and maternal and total direct and maternal (-.22 to .15).

The low to medium correlations between additive and nonadditive MEPD indicate that superior sires for additive genetic effects will not necessarily be superior for nonadditive genetic effects, and vice versa. Also, the higher correlations between additive and total MEPD than between nonadditive and total MEPD indicated that a sire's additive MEPD was a better indicator of its total MEPD than its nonadditive MEPD. These correlations also point out the additional complexity introduced by nonadditive genetic predictions when trying to find a sire with desirable predictions for several traits and effects. From a commercial producer's perspective, total genetic predictions may be the best alternative. However, seedstock producers may want to consider additive, nonadditive, and total genetic predictions separately if they are providing sires for straightbred and crossbred breeding programs. No sire in the Turipaná RZ multibreed herd was superior for additive and nonadditive genetic effects across all traits. For example, the sire with the *highest* WWAD (a R sire) had the following MEPD: BWTAD (-2.2 kg), WWAD (4.3 kg), GWAD (-11.9 kg), BWTAM (2.7 kg), WWAM (5.0 kg), GWAM (9.1 kg), BWTND (1.2 kg), WWND (8.9 kg), GWND (16.4 kg), BWTNM (.4 kg), WWNM (3.3 kg), GWNM (-9.1 kg), and the MEPD for the sire with the *lowest* WWAD (another R sire) were BWTAD (-2.3 kg), WWAD (-9.5 kg), GWAD (-10.5 kg), BWTAM (2.9 kg), WWAM (.5 kg), GWAM (7.2 kg), BWTND (.7 kg), WWND (7.0 kg), GWND (19.1 kg), BWTNM (-2 kg), WWNM (3.7 kg), GWNM (-12.1 kg). Thus, the sire with the lowest MEPD for WWAD ranked higher than the best one for BWTAD, GWAD, GWND, and WWNM.

*Utilization of Additive, Nonadditive, and Total MEPD.* The primary goal of multibreed genetic evaluation procedures is the computation of expected progeny differences (additive, nonadditive, total) that allows the comparison of a variety of breed compositions (straightbred, crossbred). The cornerstone of

MEPD is the multibreed contemporary group in which animals of various breeds and(or) crossbred groups are reared under the same environmental conditions. Additive, nonadditive, and total MEPD are computed using all available information (straightbred, crossbred) from these multibreed contemporary groups. The emphasis given to additive, nonadditive, and total sire MEPD when choosing sires will depend on the specific breeding objectives of purebred breeders and commercial cattle producers.

Additive MEPD can be used independently of nonadditive MEPD, because they predict the expected value of the alleles that progeny received. In other words, additive MEPD can be used to compare straightbred and(or) crossbred sires in the same fashion as intrabreed additive EPD are used to compare sires within a breed. Comparison of sires of different breed compositions with additive MEPD is possible because these are deviations from a single *multibreed genetic base*, as opposed to the various *unibreed genetic bases* in intrabreed genetic evaluations (Elzo, 1996a).

It would be inadvisable, however, to use nonadditive MEPD in isolation, because they are predictions of intralocus interbreed interactions that are re-created each time male and female gametes unite. Thus, nonadditive MEPD should be used *in conjunction with* additive MEPD (i.e., as total MEPD) to take advantage of the information provided by nonadditive MEPD to predict the performance of future *crossbred* progeny of a straightbred or a crossbred sire.

Breeding objectives of purebred breeders and commercial producers are interdependent. Commercial producers buy sires that fit their breeding program from purebred breeders. If the predominant mating program to produce beef is crossbreeding, then sires should be genetically evaluated and be selected not only for their additive MEPD, but also for their nonadditive MEPD. Perhaps a two-step procedure could be used: 1) choose the best sires according to their additive MEPD, and 2) among the sires selected in step 1, select those that have the best total MEPD; "best" is defined by the breeder. The objective of this selection procedure would be to move the multibreed population in the desired direction additively and nonadditively.

The R and Z breeds are used in straightbred and crossbred matings in Colombia. However, even though the Z breed is the main beef breed in Colombia, only a few thousand R cattle remain (Bejarano et al., 1986). If the R breed is to survive, and perhaps increase its population, it must be competitive as a beef breed. To achieve this goal, R sires must compare favorably with Z and RZ crossbred sires. This study showed that there were some R sires whose MEPD for growth traits were as good as, or better than, those of some Z and RZ sires. However, this is only a single historical study. Multibreed genetic evaluation of R, Z, and RZ

crossbred sires should be regularly conducted with data from all available herds. This would permit selection of R, Z, and RZ sires using current MEPD. Hopefully, the availability of MEPD for R sires would stimulate their use in straightbred and crossbred matings, thus helping the conservation effort and the commercial use of R cattle not only in Colombia, but also in other countries.

### Implications

Estimates of intrabreed additive and interbreed nonadditive genetic parameters as well as the additive, nonadditive, and total expected progeny differences indicate that Romosinuano can favorably compete with Zebu and Romosinuano-Zebu crossbred animals under the environmental conditions at the Turipaná Experiment Station. The interbreed combining abilities predicted here suggest that it will be advantageous to use Romosinuano sires in crossbreeding programs with Zebu and(or) crossbred dams. This will increase the marketability of Romosinuano sires and help the conservation effort for this endangered Criollo breed. To fully characterize the Romosinuano breed, this research should be expanded to include reproduction, production, and carcass traits, and animals from multiple herds and production systems. Because of the small number of Romosinuano cattle in Colombia and in other countries, a multinational research effort may be needed to accomplish this goal.

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