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CHANGES IN ADDITIVE AND NONADDITIVE GENETIC VARIANCES OF WEIGHTS AND MACROMINERALS DURING PREWEANING GROWTH[1]

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Introduction

Genetic evaluation programs for beef cattle employ mixed model methodology as described by Quaas and Pollak (1980) and Pollak and Quaas (1983). To apply this methodology, it is necessary to know the genetic variation of traits included in these evaluation programs. Furthermore, in crossbred populations it is necessary to know not only the additive genetic variation but also the nonadditive genetic variation, such as the interaction of sire by breed group of dam (Benyshek, 1979; Massey and Benyshek, 1981; Elzo, 1990). Traits involved in these evaluation programs are usually weight traits. However, traits linked to growth may need to be used to improve the accuracy of prediction of genetic values of weight traits, especially in small populations. A possible set of traits is macrominerals, especially calcium, phosphorus and magnesium, due to their known biochemical and physiological links to growth (Odenya et al., 1992a). Estimates of additive genetic effects for weight and serum macrominerals at weaning have been reported for an Angus-Brahman multibreed herd (Odenya et al., 1992a), for weaning weight in Angus (Kennedy and Henderson, 1975; Nelsen and Kress, 1979), Brahman (Malagon and Duran, 1985; Kriese et al., 1991), and Angus × Brahman crossbred (Bertrand and Benyshek, 1987; Kriese et al., 1991). Estimates of nonadditive genetic effects have been reported only for weight traits, e.g., weaning weight in Limousin (Benyshek, 1979; Massey and Benyshek, 1981).

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Genetic evaluation for growth traits traditionally occurs at weaning. However, in many instances, it may be desirable to carry out selection or culling decisions before weaning to avoid incurring in unnecessary costs. Hence, additive and nonadditive variance components for weight and macrominerals before weaning need to be known to carry out early evaluation of animals. Thus, the objectives of this study were: 1) to obtain estimates of additive and nonadditive variance and covariance components for weight and amount of serum macrominerals at various calf ages before weaning, and 2) to investigate how these variance components vary through these preweaning ages.

Materials and Methods

Description of data

During 1989 and 1990, weights and blood samples from 380 calves of the multibreed research herd formed by Angus (A), Brahman (B), and several A × B crosses at the Pine Acres Research station of the University of Florida, Citra, were collected. Samples were taken at intervals of approximately 5 weeks after birth up to weaning. The data included birth weight (BW), and weights (WT) and serum calcium (Ca), serum phosphorus (P), and serum magnesium (Mg).

The animals used in this study were produced by the mating of six sire breed groups consisting of A, .75A .25B, .5A .5B, .25A .75B, B and Brangus (.625A .375B) and five dam breed groups (.25A .75B were unavailable). A total of 28 sires and 243 dams were used (Table 1). The number of sires per breed group per year ranged from two (.75a .25B in 1989) to five (Brangus in 1990), and the number of dams per breed group per year ranged from 14 (.75A .25B in 1990) to 65 (A in 1989). To ensure connectedness over time in this data set, from one (.5A .5B) to three (A) sires per breed group were used in both 1989 and 1990. The number of calves produced by mating subclass in both years (Table 2) ranged from three (.5A .5B sires mated to .75A .25B dams) to forty (B sires mated to B dams).

Weights and macrominerals were adjusted to 120, 150 and 205 d based on the formula recommended by the Beef Improvement Federation (BIF, 1990) using records from the first sampling instead of those at birth because blood samples were not collected at birth. Age at first sampling ranged from 1 to 85 d. Most calves (97%) were sampled within 70 d of birth. Age at weaning ranged from 151 to 275 d of age. However, the majority of calves (91%) were weaned between 210 and 270 d of age. To obtain the amounts of macrominerals, the estimated serum volume for each calf was computed first and the result was then multiplied by concentration of each mineral (Odenya et al., 1992a).

Genetic Analysis

Variance components of additive and nonadditive genetic effects for weight and macrominerals at 30, 60, 90, 120, 150 and 205 d were estimated using the restricted maximum likelihood (REML) method (Patterson and Thompson, 1971; Corbeil and Searle, 1976). Computations were carried out using the single-trait variance component program of the Statistical Analysis System (PROC VARCOMP, SAS, 1985). The program VARCOMP computes variance component estimates using the W transformation applied to a Newton-Raphson algorithm (R. C. Littell, personal communication). Standard errors of these REML estimates were obtained by taking the square root of the large sample variances, which are computed by inverting the information matrix (R. C. Littell, personal communication). Estimates of the variance of the sum of two traits and the variances of the traits were used to compute the covariance between them using the formula suggested by Searle and Roundsaville (1974), i.e., .5 [estimate of variance of (trait 1 + trait 2) – estimate of variance of trait 1 – estimate of variance of trait 2].

Preliminary runs with SAS VARCOMP showed that additive and nonadditive maternal genetic effects could not be estimated in these data set. The estimate of the additive maternal grandsire variance component was zero. In addition, the known maternal grandsires were almost exclusively mated within their own breed group. Only three maternal grandsires were mated to cows of breed groups different from their own, and their number of progeny per breed group of maternal granddam was small. This prevented the estimation of nonadditive maternal genetic effects. Consequently, the effects of maternal grandsire and the interaction of maternal grandsire × breed group of maternal granddam were left out of the model used to estimate variance components. The variance due to these effects is contained in the residual term.

The mixed model used to obtain the variance component estimates included year, management group within year, calf age at first sampling and sex of calf × age of dam subclass as environmental effects, breed group of sire × breed group of dam subclass and breed group of maternal grandsire × breed group of maternal granddam subclass as fixed genetic effects, sire within breed group of sire and sire × breed group of dam interaction as random genetic effects, and residual. Management group accounts for differences in macromineral response due to the assignment of cows to six replicated forage supplementation and one control (13 herds). There were three sex categories (bulls, heifers and steers) and six age of dam categories (three, four, five, six, seven and eight or more years of age). Six calf age categories at first sampling were defined (1 = 1 to 10 d, 2 = 11 to 20 d, etc.). The group genetic effects contain both main effects and interactions between them. Environmental effects were assumed to be fixed. Sire, sire × breed group of dam and residual effects were assumed to be random, each with mean equal zero, common variance and uncorrelated. The sire variance represented .25 additive direct genetic variance. The sire × breed group of dam variance represented the nonadditive direct genetic variance. The residual variance contained .75 additive direct genetic variance, additive and nonadditive maternal genetic variance, covariances between direct and maternal genetic effects and variances due to random environmental effects. Because of the method used to estimate covariance among traits, all variance components for all the traits were estimated using the same model across ages.

Heritabilities were computed as four times the estimate of the sire variance divided by the phenotypic variance. Phenotypic variances were computed as the sum of the estimates of sire plus sire × breed group of dam plus residual variances. This heritability represents the proportion of variation observed in a trait that is due to additive direct genetic effects. Similarly, interactibility was defined to be the estimate of the sire × breed group of dam variance divided by the phenotypic variance. This interactibility represents the proportion of variation observed in a trait that is due to nonadditive direct genetic effects.

Additive and nonadditive genetic correlations among pairs of traits were computed using the usual formula, i.e., the ratio of the appropriate covariances to the product of the standard deviations.

Results and Discussion

REML estimates and asymptotic standard errors of sire, sire × breed group of dam, and residual variance components for weights and amounts of serum Ca, serum P, and serum Mg at 30, 60, 90, 120, 150 and 205 d are shown in Table 3. Among variance components, estimates of the residual variances had higher accuracies than the genetic variances for all the traits over all ages. Estimates of sire variance components decreased for weight from 31.39 ± 34.54 kg^2 at 30 d to 7.53 ± 6.71 kg^2 at 60 d but then increased to 24.00 ± 22.83 kg^2 at 205 d. For P and Mg, estimates of sire variance components decreased from 30 d (1773.29 ± 1989.18 mg^2 for P, 235.88 ± 196.72 mg^2 for Mg) to 90 d (521.63 ± 757.85 mg^2 for P, 40.69 ± 53.34 mg^2 for Mg), and then increased to 3446.33 ± 2767.22 mg^2 (for P) and 151.02 ± 170.53 mg^2 (for Mg) at 205 d. Ca decreased from 2716.84 ± 2772.86 mg^2 at 30 d to 1463.10 ± 1376.38 mg^2 at 120 d and increased to 3023.59 ± 2782.88 mg^2 at 205 d. Estimates of sire × breed group of dam variance components were zero for all traits at 30 d, and for weight, Ca and P at 60 d. This could be due to the small data set used to compute these estimates. For weight, the estimate of sire × breed group of dam variance component increased from 9.69 ± 11.66 kg^2 at 30 d to 30.13 ± 24.82 kg^2 at 150 d. Similar trends were found for serum Ca (427.68 ± 1512.37 mg^2 at 30 d to 1962.48 ± 2941.66 kg^2 at 150 d) and for P (1480.56 ± 1360.98 mg^2 at 30 d to 2471.54 ± 2606.73 mg^2 at 150 d). These estimates decreased at 205 d for these traits (19.14 ± 33.26 kg^2 for weight; 269.52 ± 3647.18 mg^2 for Ca; 1794.41 ± 3050.65 mg^2 for P). Mg was the only trait that had an increase from 6.62 ± 56.91 mg^2 at 60 d to 249.97 ± 216.67 mg^2 at 205 d. Additive direct variance components (expressed as four times the sire variance component) were more important than nonadditive direct variance components (expressed as sire × breed group of dam variance components) for weight and macrominerals across ages. These results indicate that changes for variance components occur across ages. This could be due to different sets of alleles that are activated at different ages. Thus, weights at different ages can be considered as different traits and it would be feasible to consider weights at an earlier age as traits for evaluation at breeding time, say, that is around 90 d of age.

Heritability and interactibility estimates for weight, serum Ca, P, and Mg at 120, 150 and 205 d are presented in Table 4. In general, heritabilities were in the low ($\leq$.25) and medium range ($\leq$.50). For weight, the estimate of heritability increased from .14 at 30 d to .24 at 205 d, with the highest value at 90 d (.26) indicating that the fraction of the variance due to additive genetic effects increases with age. Different heritability estimates have been reported at different calf ages. Kriese et al. (1991) reported heritability estimates at birth (.28) and at weaning (.21) for crossbred animals (Brangus) while Bertrand and Benyshek (1987) reported .25 at birth and .28 at weaning. In Brahman, Kriese et al. (1991) reported .37 at birth and .23 at weaning. In Angus, Nelsen and Kress (1979) reported .40 at birth and .35 at weaning.

For macrominerals, heritability estimates had trends similar to that found for weight. For Ca, the heritability estimate increased from .13 at 30 d to .21, with highest value at 60 d (.36). For P, this estimate increased from .15 at 30 d to .30 at 205, while for Mg increased from .20 to .22, with highest value at 60 d (.26). These results indicate that these macrominerals could be a possible set of traits to be used in multiple trait genetic evaluation procedures to increase the accuracy of evaluation of animals for growth traits at earlier ages. Odenya et al. (1992b), using a sire additive model, reported heritability estimates of .39 for Ca, .40 for P, and .36 for Mg at weaning for this Angus-Brahman multibreed herd. These values were higher than the ones found in this study because the sire variance component in Odenya et al. (1992b) must have contained at least part of the sire × breed group of dam variance component, which here was computed separately.

Interactibility estimates were in the low range (≤.25) for all the traits for all the periods, and were lower than heritabilities. Thus, the fraction of the variance due to additive effects was larger than the one due to nonadditive effects. At 30 d, interactibility estimates were zero for weight and macrominerals because of the zero value obtained for the sire × breed group of dam variance component for all the traits at this age. Similar results were observed at 60 d for weight, Ca and P. After 60 d, the interactibility estimate for weight increased from .07 at 90 d to .12 at 150 d, decreasing then to .05 at 205 d. For Ca, the trend was similar, increasing from .02 at 90 d to .06 at 150 d, but decreasing to .01 at 205 d. For P, this estimate decreased from .11 at 90 d to .04 at 205 d. For Mg, there was an increase from .01 at 60 d to .09 at 205 d, with the highest value being .12 at 90 d. Thus, these results indicate that the combining ability of sire with breed group of dam had different effects at different ages. For macrominerals, Ca was the only one that showed a pattern similar to weight for interactibility. Based on these results and those found for heritability, among these three macrominerals, Ca appeared to be most related to weight. This could be due to the more direct participation of Ca in bone formation and, thus, in weight.

Additive and nonadditive genetic correlations for weight, Ca, P, and Mg at 30, 60, 90, 120, 150 and 205 d are presented in Table 5. Additive genetic correlations were within the limits (−1,1), except for the correlation between P and Mg at 205 d (1.04). Nonadditive genetic correlations between macrominerals were zero prior to 90 d and out of boundaries at 90 d and 205 d. These zero values and values outside of the boundaries may have been largely due to the small data set used for these analyses.

Estimates of additive genetic correlations between macrominerals and weight were positive in all ages. Among these, the highest correlation occurred with Ca (.97 at 60 d, .92 at 90 d, .92 at 120 d, .90 at 150 d, and .98 at 205 d). Similar results were reported by Odenya et al. (1992b) at weaning in this Angus-Brahman multibreed herd. They found genetic correlations between Ca, P, and Mg with weight of 1.00, .78, and .86, respectively. Also, the correlations of Ca and weight were more consistent after 90 d than were the correlations of the other minerals with weight. This indicates that the degree of genetic association of amount of serum Ca and weight was consistent across ages.

Estimates of nonadditive genetic correlations between macrominerals and weight were positive within periods except for the correlation with P at 205 d which was slightly negative (−.01). The highest correlations were between weight and Mg (.92 at 90 d) and between weight and Ca (.86 at 120 d, .92 at 150 d, .70 at 205 d). The additive and nonadditive correlations between macrominerals and weight found in this study suggest that the relationship among these traits changed across ages. Because of its consistent high correlation in all ages, Ca would be the macromineral of choice to be used in animal evaluation procedures to improve the accuracy of prediction of genetic values for weight.

Implications

The estimates of variance components of additive and nonadditive genetic effects for growth traits (weight, macrominerals) showed important changes over time. This indicates that changes exist in the genetic variation during the growth and development of the animals. Thus, it is necessary to study the effect of these changes in the genetic evaluation of animals, especially at earlier ages, so better selection or culling decisions can be made. Also, the results found in this study indicate that these nutritional traits (macrominerals) are of potential use in multiple trait animal evaluation procedures so that the accuracy of prediction of genetic values for growth traits can be improved, especially in small populations.

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Table 1. DISTRIBUTION OF ANIMALS BY BREED GROUP COMPOSITION AND YEAR

Breed Group[a]	Sires				Dams			
	Total	1989	1990	1989 & 1990[b]	Total	1989	1990	1989 & 1990[c]
A	5	4	4	3	65	65	42	42
.75A.25B	3	2	3	2	18	18	14	14
.5A.5B	4	2	3	1	38	30	33	25
.25A.75B	4	4	3	3	0	0	0	0
B	5	3	4	2	76	52	59	35
BRANGUS	7	4	5	2	46	25	40	19
Total	28	19	22	13	243	190	188	135

[a]A = Angus, B = Brahman.
[b]Number of sires present in both 1989 and 1990.
[c]Number of dams present in both 1989 and 1990.

Table 2. DISTRIBUTION OF PROGENY BY MATING TYPE

Breed group of dam[a]	Breed group of sire[a]						
	A	.75A.25B	.5A.5B	.25A.75B	B	BRAN-GUS	TOTAL
A	26	13	7	17	20	24	107
.75A.25B	6	5	3	6	6	6	32
.5A.5B	12	9	5	9	16	12	63
B	14	18	11	15	39	14	111
BRANGUS	8	6	5	8	11	29	67
TOTAL	66	51	31	55	92	85	380

[a]A = Angus, B = Brahman.

Table 3. RESTRICTED MAXIMUM LIKELIHOOD ESTIMATES OF VARIANCE COMPONENTS FOR WEIGHT, SERUM Ca, SERUM P AND SERUM Mg AT SEVERAL CALF AGES

		Age of adjustment, d					
Trait[a]	Effect[b]	30	60	90	120	150	205
Wt	Sire	31.39 ±34.54	7.53 ± 6.71	8.40 ± 7.68	8.74 ± 10.15	8.91 ± 13.30	24.00 ± 22.83
	Sire × BGD	0	0	9.69 ± 11.66	18.59 ± 17.35	30.13 ± 24.82	19.14 ± 33.26
	Residual	892.64 ± 75.01	120.73 ± 10.25	113.30 ± 11.00	158.82 ± 15.43	219.12 ± 21.31	362.70 ± 34.76
Ca	Sire	2716.84 ± 2772.86	1640.14 ± 1106.02	1468.28 ± 1145.77	1463.10 ± 1376.38	1474.46 ± 1726.41	3023.59 ± 2782.88
	Sire × BGD	0	0	427.68 ± 1512.37	1085.12 ± 2112.10	1962.48 ± 2941.66	269.52 ± 3647.18
	Residual	77798.93 ± 6513.43	16415.23 ± 1394.52	18359.14 ± 1752.53	23917.03 ± 2295.16	31795.29 ± 3061.17	54252.63 ± 5020.65
P	Sire	1773.29 ± 1989.18	858.32 ± 676.74	521.63 ± 757.85	718.73 ± 1033.91	1353.89 ± 1520.24	3446.33 ± 2767.22
	Sire × BGD	0	0	1480.56 ± 1360.98	2034.22 ± 1889.51	2471.54 ± 2606.73	1794.41 ± 3050.65
	Residual	45970.97 ± 3881.39	11212.61 ± 952.93	11523.54 ± 1122.79	16552.24 ± 1606.59	24038.24 ± 2324.68	40569.75 ± 3718.51
Mg	Sire	235.88 ± 196.72	47.33 ± 43.12	40.69 ± 53.34	43.17 ± 70.42	48.02 ± 92.51	151.02 ± 170.53
	Sire × BGD	0	6.62 ± 56.91	99.58 ± 79.42	118.41 ± 106.88	135.14 ± 142.38	249.97 ± 216.67
	Residual	4467.69 ± 375.61	668.46 ± 63.24	675.18 ± 64.80	986.27 ± 94.03	1420.00 ± 134.51	2391.53 ± 222.47

[a] Wt = weight (expressed in kg^2); Ca = serum Ca (expressed in mg^2); P = serum phosphorus (expressed in mg^2); Mg = serum magnesium (expressed in mg^2)
[b] Sire × BGD = sire × breed group of dam

Table 4. ESTIMATES OF HERITABILITIES AND INTERACTIBILITIES OF WEIGHT AND AMOUNTS OF SERUM Ca, P AND Mg AT SEVERAL CALF AGES

	Trait							
	Weight		Ca		P		Mg	
Age, d	HER[a]	INT[b]	HER	INT	HER	INT	HER	INT
30	.14	0	.13	0	.15	0	.20	0
60	.23	0	.36	0	.28	0	.26	.01
90	.26	.07	.29	.02	.15	.11	.20	.12
120	.19	.10	.22	.04	.15	.11	.15	.10
150	.14	.12	.17	.06	.19	.09	.12	.08
205	.24	.05	.21	.01	.30	.04	.22	.09

[a] HER = Heritability estimates
[b] INT = Interactibility estimates

Table 5. ESTIMATES OF ADDITIVE AND NONADDITIVE GENETIC CORRELATIONS AMONG WEIGHT, SERUM Ca, P AND Mg AT SEVERAL CALF AGES[a]

		Trait			
Age, d	Trait	Wt	Ca	P	Mg
30	Wt		.90	.82	1.00
	Ca	0		.58	.80
	P	0	0		.89
	Mg	0	0	0	
60	Wt		.97	.84	.68
	Ca	0		.41	.35
	P	0	0		.79
	Mg	0	0	0	
90	Wt		.92	.82	.58
	Ca	.68		.33	.29
	P	.69	.37		.55
	Mg	.92	1.01	.86	
120	Wt		.92	.36	.47
	Ca	.86		-.04	.14
	P	.79	.62		.41
	Mg	.82	.78	.78	
150	Wt		.90	.25	.14
	Ca	.92		−.28	−.08
	P	.84	.75		.51
	Mg	.73	.63	.66	
205	Wt		.98	.79	.94
	Ca	.70		.69	.53
	P	−.01	−1.48		1.04
	Mg	.54	.87	−1.17	

[a] Additive genetic correlations above the diagonal; nonadditive genetic correlations below the diagonal