DIRECT AND MATERNAL GENETIC EFFECTS DUE TO THE INTRODUCTION OF BOS TAURUS ALLELES INTO BRAHMAN CATTLE IN FLORIDA: III. POSTWEANING GROWTH TRAITS1

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ABSTRACT

Brahman (as a difference from Angus) additive and Brahman × Angus intralocus nonadditive (as a difference from the parental breeds) genetic effects of postweaning gain traits were estimated based on postweaning weights collected on 642 bulls and 641 heifers of Brahman (B), Angus (A) and B × A ancestry born at the Subtropical Agricultural Research Station, Brooksville, FL, between 1971 and 1982. The postweaning gain traits were 205-d to 365-d weight gain (WYGAIN), 365-d to 550-d weight gain (YHGAIN) and 205-d to 550-d weight gain (WHGAIN). Linear combinations of Best Linear Unbiased Estimates (BLUE) of Brahman sire and dam additive, B × A dam nonadditive and B × A individual nonadditive genetic effects were used to compute the BLUE of direct and maternal Brahman additive and B x A nonadditive genetic effects. Because bulls and heifers received different levels of nutrition, their data were analyzed separately. The BLUE of Brahman additive genetic effects for bulls and heifers were as follows: WYGAIN direct -29.8 \pm 15.5 and -14.5 \pm 13.2 kg, maternal 23.0 \pm 14.1 and 1.1 \pm 11.6 kg; YHGAIN direct -9.9 ± 19.4 and 32.4 ± 17.9 kg, maternal 13.0 ± 17.4 and -23.0 ± 15.7 kg; and WHGAIN direct -50.4 ± 23.9 and 16.4 ± 21.4 kg, maternal 53.8 ± 21.4 and -2.5 ± 18.7 kg. The BLUE of the B x A nonadditive group genetic effects for bulls and heifers were as follows: WYGAIN direct 25.7 \pm 12.0 and -.5 \pm 10.9 kg, maternal -2.9 \pm 4.9 and .7 \pm 3.7 kg; YHGAIN direct 25.1 \pm 14.4 and 9.5 \pm 16.2 kg, maternal -6.3 \pm 5.9 and -5.1 \pm 4.8 kg; and WHGAIN direct 61.9 \pm 17.8 and 26.4 \pm 19.3 kg, maternal -11.5 \pm 7.3 and -4.9 \pm 5.7 kg. The most important genetic factor affecting postweaning gain was the direct nonadditive genetic effect; it was greater with a higher plane of nutrition. (Key Words: Brahman, Angus, Growth Rate, Crossbreeding, Maternal Effects, Beef Cattle.)

J. Anim. Sci. 1990. 68:1588-1594

crossbreeding programs. Reproductive and preweaning growth traits in Brahman (B), Angus

(A) and $B \times A$ crossbreds have been studied

more extensively than postweaning growth

traits have. Few postweaning growth studies

involving A, B and A × B crossbred groups

have been reported. Data from previous studies

genetic effects for postweaning growth traits in

inter se Brahman × Bos taurus and upgraded

Brahman cattle. Thus, the objectives of this

Introduction

Crossbreeding Brahman with Bos taurus breeds of British and continental origin has been used widely in the Gulf Coast Region of the U.S., and particularly in Florida, as a means of increasing beef cattle productivity. Angus is used frequently with Brahman in

(Damon et al., 1959; Long et al., 1979a,b; Peacock et al., 1982) came from straightbreds, F₁ crossbreds and, in some cases, backcrosses. No experimental information was found on estimates of additive and nonadditive group

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Accepted October 16, 1989.

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¹Florida Agric, Exp. Sta. Journal Series No. 10052.

TABLE 1. NUMBER OF ANIMALS WITH RECORDS BY BREED COMPOSITION OF THEIR SIRES AND DAMS

		•	No. of animals					
	Breed composition		365 d		550 d			
Sire	Dam	Animal	Bulls	Heifers	Bulls	Heifers		
Brahman (B)	Brahman	Brahman	151	173	147	171		
Brahman	2/3B:1/3A	5/6B:1/6A	81	80	75	79		
Brahman	5/6B:1/6A	11/12B:1/12A	30	40	29	39		
Brahman	11/12B:1/12A	23/24B:1/24B	2	6	2	6		
Brahman	Angus (A)	1/2B:1/2A	29	45	28	40		
2/3B:1/3A	2/3B:1/3A	2/3B:1/3A	142	123	126	122		
2/3B:1/3A	Angus	1/3B:2/3A	36	13	33	8		
5/6B:1/6A	5/6B:1/6A	5/6B:1/6A	154	134	153	133		
5/6B:1/6A	Angus	5/12B:7/12A	17	27	17	22		

research were 1) to estimate additive direct and maternal genetic differences between Brahman and Angus bulls and heifers for weight gain between 205 d and 365 d of age (WYGAIN), weight gain between 365 d and 550 d of age (YHGAIN) and weight gain between 205 d and 550 d of age (WHGAIN) and 2) to estimate nonadditive direct and maternal genetic effects of bulls and heifers for WYGAIN, YHGAIN and WHGAIN, in a multibreed population composed of straightbred B and A, B × A mated *inter se*, and upgraded B cattle.

Meterials and Methods

Four postweaning weights (November, March, June and August) were collected on 642 bulls and 641 heifers of B and B \times A ancestry born between 1971 and 1982 at the Subtropical Agricultural Research Station near Brooksville, FL. Table 1 shows the distribution of these animals by breed of sire and dam. Approximately 46% of bulls and heifers were produced by straightbred B × B matings and by upgrading to B. Only two groups were mated inter se: 2/3B:1/3A and 5/6B:1/6A. A total of 66 sires and 527 dams had progeny with postweaning weights. The distribution of sires and dams by breed composition of their parents is presented in Table 2. Straightbred B composed 56% of all sires of calves and 27% of all dams of calves. Straightbred A dams accounted for 20% of all dams. Cows remained in the herd for an average of 3 yr and nearly 50% of the sires were used for 2 or more yr. This mating strategy created a wellconnected data set that allowed use of all records to estimate additive and nonadditive genetic parameters for WHGAIN, YHGAIN and WYGAIN. For a detailed explanation of the experimental design and origin of animals used in this research, refer to Olson et al. (1990).

Postweaning gain traits were defined as follows:

- (i) WHGAIN = WT365 WT205,
- (ii) YHGAIN = WT550 WT365,
- (iii) WHGAIN = WT550 WT205.

where WT205, WT365 and WT550 are weights adjusted to 205 d, 365 d and 550 d of age according to recommendations of the Beef Improvement Federation (BIF, 1986). The total postweaning period (i.e., 205 d to 550 d) was separated into two periods to obtain information regarding the point at which maternal effects ceased to be an important factor for postweaning weight gain. Also, climatic conditions in the two postweaning periods were different. The first postweaning period (September to February) was colder and less humid than the second (March to August), which was predominantly hot and humid. Thus, although stage of growth and climate were confounded. some information on growth rate of animals of different breed composition in two seasons was obtained.

After weaning, bulls and heifers were placed on different nutritional programs. Bulls were offered about 3.9 kg of a concentrate feed (70% corn, 20% molasses and 10% of a protein premix) daily throughout the postweaning period (from approximately September of one year to August of the following year) to supplement the nutrients obtained from pasture. When pasture (mostly Pensacola bahiagrass) was insufficient, animals had ad libitum access to grass hay. A complete mineral mix

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TABLE 2. NUMBER OF SIRES AND DAMS BY BREED COMPOSITION
OF THEIR RESPECTIVE SIRES AND DAMS

	No. of parents			
Sire of parent	Dam of parent	Parent	Sires	Dams ^a
Brahman (B)	Brahman	Brahman	37	140
Brahman	1/3B:2/3A	2/3B:1/3A	7	92
Brahman	2/3B:1/3A	5/6B:1/6A	5	64
Brahman	5/6B:1/6A	11/12B:1/12A		7
2/3B:1/3A	2/3B:1/3A	2/3B:1/3A	· 7	62
5/6B:1/6A	5/6B:1/6A	5/6B:1/6A	10	57
Angus (A)	Angus	Angus		105

^aNumbers of dams of 365-d progeny. Number of dams of 550-d progeny were slightly smaller in some breed groups.

was available at all times. Heifers were fed about 2 kg of the same concentrate diet until the following spring (i.e., until March to June, depending on rainfall and[or] late frosts). Grass hay was available free choice to heifers during periods of inadequate pasture.

Because bulls and heifers were subjected to different nutritional regimens during the postweaning period, statistical analyses were separated by gender. The statistical procedure, model and assumptions used in the analyses of WYGAIN, YHGAIN and WHGAIN were the same as those used by Elzo et al. (1990) for preweaning growth traits. The model for bulls and heifers included the effects of year and age of dam as environmental fixed effects. Brahman sire and Brahman dam additive genetic effects, $B \times A$ dam and $B \times A$ calf nonadditive (intralocus) genetic effects and residual effects. Residual effects were assumed to be random and uncorrelated and to have a common variance. Nonadditive genetic effects at two or more loci were assumed to be negligible. Additive and nonadditive genetic effects were expressed as continuous variables. The generalized least squares (GLM) program of the SAS computing package (SAS, 1985) was used to compute best linear unbiased estimates (BLUE) of the environmental fixed effects and the genetic effects in the model. Genetic expectations of solutions are as follows: i) Brahman sire additive genetic effect is the BLUE of .5 Brahman direct additive genetic effect, ii) Brahman dam additive genetic effect is the BLUE of .5 Brahman direct plus Brahman maternal additive genetic effect, iii) B × A dam nonadditive group genetic effect is the BLUE of $B \times A$ maternal nonadditive genetic effect, and iv) $B \times A$ calf nonadditive genetic effect is the BLUE of B × A direct nonadditive genetic effect. The GLM program also was used to compute the BLUE of direct and maternal Brahman additive and intralocus $B \times A$ nonadditive genetic effects as linear combinations of the appropriate effects in the model. Computations were carried out as follows: i) Brahman direct additive genetic effect = $2 \times B$ rahman sire additive genetic effects, ii) Brahman additive maternal genetic effect = Brahman dam additive genetic effect, iii) $B \times A$ maternal and direct nonadditive genetic effects were obtained directly from the BLUE of the $B \times A$ dam and $B \times A$ calf nonadditive genetic effects.

Results and Discussion

Values of F-tests and their probability levels for WYGAIN, YGGAIN and WHGAIN of bulls and heifers are presented in Table 3. The fixed environmental effects of year and age of dam were important (P < .04) for all postweaning growth traits in bulls and heifers, except for the effect of age of dam on WYGAIN of bulls (P < .17). Differences between younger (3 to 7 yr) and older (8 yr or more) cows were mostly positive for all traits regardless of calf gender. This might be an indication of compensatory growth for progeny of young cows. Genetic effects were generally nonsignificant. Calf (bull or heifer) B × A nonadditive and sire additive genetic effects were more important for WHGAIN, YGGAIN and WHGAIN than dam $B \times A$ nonadditive and dam additive genetic effects, especially for bulls (Table 4).

Weight Gain Between 205 Days and 365 Days of Age (WYGAIN). The only significant genetic effect for WYGAIN was $B \times A$ bull nonadditive genetic effect (25.7 \pm 12.0 kg, P < .05; Table 4). The Brahman sire additive genetic effects for bulls (-14.9 \pm 7.8 kg, Table

TABLE 3. F-VALUES AND PROBABILITY LEVELS FROM THE LEAST SQUARES ANALYSES OF POSTWEANING GROWTH TRAITS FOR BULLS AND HEIFERS

		Trait ^b						
	dſ	WYGAIN		YHGAIN		WHGAIN		
Source ^a		F	P > F	F	P > F	F	P > F	
Bulls				•				
Year	11	39.58	.01	48.09	.01	19.41	.01	
Age of dam	7	1.48	.17	2.26	.03	2.56	.01	
Brahman dam additive	1	.57	.45	.38	.54	3.18	.08	
B × A dam nonadditive	1	.35	.56	1.13	.29	2,51	.11	
Brahman sire additive	1	3.68	.06	.26	.61	4,45	.04	
B × A bull (calf) nonadditive	1	4.61	.03	3.03	.08	12.16	.01	
Heifers								
Year	11	24.42	.01	43.27	.01	3.98	.01	
Age of dam	7	2.79	.01	2.28	.03	2.16	.04	
Brahman dam additive	1	.37	.54	.20	.66	.10	.75	
B × A dam nonadditive	1	.04	.85	1.12	.29	.73	.39	
Brahman sire additive	1	1.20	.27	3.26	.07	.58	.45	
B × A heifer (calf) nonadditive	1	.00	.97	.35	.56	1.87	.17	

 $^{^{}a}A = Angus$, B = Brahman. Brahman additive genetic effects are expressed as deviations from Angus. $B \times A$ intralocus nonadditive genetic effects are defined as deviations from those of the parental breeds.

4) approached significance (P < .06). Corresponding effects for heifers were nonsignificant. It appears that the nutrition supplied to heifers was not sufficient for full expression of their growth potential during this age period

(205 d to 365 d of age). This was reflected in the inconsequential BLUE of the B \times A nonadditive genetic effect for heifers (-.5 \pm 10.9, Table 4) and in the higher value of the Brahman (as a deviation from Angus) sire

TABLE 4. BEST LINEAR UNBIASED ESTIMATES OF ADDITIVE AND NONADDITIVE GENETIC EFFECTS FROM LEAST SQUARES ANALYSES OF POST-WEANING GROWTH TRAITS FOR BULLS AND HEIFERS

	Trait ^b				
Genetic effect ^a	WYGAIN, kg	YHGAIN, kg	WHGAIN, kg		
Bulls					
Brahman dam additive	8.1 ± 10.7	8.0 ± 13.0	28.5 ± 16.0		
B × A dam nonadditive	-2.9 ± 4.9	-6.3 ± 5.9	-11.5 ± 7.3		
Brahman sire additive	-14.9 ± 7.8	-5.0 ± 9.7	$-25.2 \pm 12.0*$		
B × A bull nonadditive	25.7 ± 12.0*	25.1 ± 14.4	61.9 ± 17.8**		
Brahman direct additive	-29.8 ± 15.5	-9.9 ± 19.4	$-50.4 \pm 23.9*$		
Brahman maternal additive	23.0 ± 14.1	13.0 ± 17.4	53.8 ± 21.4*		
Heifers			33.31		
Brahman dam additive	-6.1 ± 10.1	-6.8 ± 15.2	5.7 ± 18.1		
B × A dam nonadditive	7 ± 3.7	-5.0 ± 4.8	-4.9 ± 5.7		
Brahman sire additive	-7.2 ± 6.6	16.2 ± 9.0	8.2 ± 10.7		
B × A heifer nonadditive	5 ± 10.9	9.5 ± 16.2	26.4 ± 19.3		
Brahman direct additive	-14.5 ± 13.2	32.4 ± 17.9	16.4 ± 21.4		
Brahman maternal additive	1.1 ± 11.6	-23.0 ± 15.7	-2.5 ± 18.7		

 $[^]aA$ = Angus, B = Brahman. Brahman additive genetic effects are expressed as deviations from Angus. B × A intralocus nonadditive genetic effects are defined as deviations from those of the parental breeds.

bWYGAIN = weight gain between 205 d and 365 d of age. YHGAIN = weight gain between 365 d and 550 d of age. WHGAIN = weight gain between 205 d and 550 d of age.

bWYGAIN = weight gain between 205 d and 365 d of age. YHGAIN = weight gain between 365 d and 550 d of age. WHGAIN = weight gain between 205 d and 550 d of age.

^{*}P < .05.

^{**}P < .01.

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additive genetic effect for heifers (-7.2 ± 6.6 , Table 4) than for bulls (-14.9 ± 7.8 , Table 4). Additive direct genetic effects for bulls and heifers were computed as twice these values (i.e., -14.5 ± 13.2 kg for heifers and -29.8 ± 15.5 for bulls). Thus, Angus alleles seemed to promote faster growth than Brahman alleles in both bulls and heifers between the ages of 205 d and 365 d.

Maternal genetic effects were found to be an important factor for preweaning growth in these animals (Elzo et al., 1990). Total maternal genetic effect (i.e., Brahman additive plus B \times A nonadditive genetic effects) for WYGAIN was higher for bulls (20.1 \pm 10.8 kg) than for heifers (.4 \pm 9.3 kg). Thus, bull progeny from dams with superior maternal ability maintained their rates of growth better than heifer progeny from similar dams. This may have been due to the higher plane of nutrition that bulls received from weaning to yearling.

Weight Gain Between 365 Days and 550 Days of Age (YHGAIN). Neither Brahman sire and dam additive genetic effects (as a difference from Angus) nor $B \times A$ dam and $B \times A$ individual nonadditive genetic effects (as a difference from parental breeds) were significant for bulls or heifers. Only $B \times A$ bull nonadditive genetic effects (25.1 \pm 14.4 kg, P < .08, Table 4) and Brahman sire additive genetic effects for heifers (16.2 \pm 9.0, P < .07, Table 4) approached significance.

The climate during this second period was predominantly hot and humid. These weather conditions are more favorable to Brahman than to Angus cattle. However, nutrition still may have played an important role. In heifers there was a reversal of the sign and value of the Brahman sire additive genetic effect between the first period (WYGAIN) and the second period (YHGAIN). The BLUE of these effects went from -7.2 ± 6.6 kg (WYGAIN) to $16.2 \pm$ 9.0 kg (YHGAIN). These BLUE are estimates of one-half of the Brahman direct additive group genetic effects. Thus, Brahman alleles for additive direct genetic effects seemed to be superior to Angus to stimulate growth postyearling under predominantly hot and humid climatic conditions. In contrast, the Brahman maternal additive genetic effect for heifers changed from slightly positive $(1.1 \pm 11.6 \text{ kg})$ to negative (-23.0 ± 15.7 kg). Hence, these environmental conditions failed to sustain high preweaning growth rates. The situation for bulls was opposite. Bulls had the same pattern of relationships between direct and maternal additive genetic effects for YHGAIN as the one previously shown for WYGAIN. However, Brahman (as a deviation from Angus) additive genetic effect for YHGAIN was smaller than the one for WYGAIN. The Brahman direct additive genetic effect decreased from -29.8 ± 15.5 kg (WYGAIN) to -9.9 ± 19.4 kg (YHGAIN) and the Brahman maternal additive genetic effect dropped from 23.0 ± 14.1 kg (WYGAIN) to 13.0 ± 17.4 kg (YHGAIN). Thus, the 4 kg of concentrate fed to bulls permitted Angus alleles to promote a faster rate of growth than Brahman alleles in spite of the hot and humid environmental conditions. Also, those bulls that had a fast rate of growth during the preweaning period, due in part to the maternal environment received, were able to maintain a faster rate of growth during the 365-d to 550-d period than bulls that received a poorer preweaning maternal environment.

The trend for nonadditive genetic effects was the same in bulls and heifers. The dam nonadditive genetic effect had very similar values in bulls (-6.3 ± 5.9 kg, Table 4) and in heifers (-5.0 ± 4.8 kg, Table 4). However, the B x A bull nonadditive genetic effect was substantially larger for bulls (25.1 \pm 14.4 kg, Table 4) than that for heifers $(9.5 \pm 16.2 \text{ kg})$ Table 4). Thus, in heifers, any advantage due to nonadditive direct genetic effects was essentially offset by nonadditive maternal genetic effects. Although the same antagonistic relationship existed in bulls, their higher plane of nutrition allowed expression of a much larger nonadditive direct group genetic effect than the one found in heifers. The BLUE of the sum of the direct and maternal nonadditive genetic effects was 18.8 ± 11.9 kg in bulls compared to 4.5 ± 14.6 kg in heifers. Specific gender effects also might be partly responsible for this difference between bulls and heifers. but their different nutrition prevented testing for this possibility.

Weight Gain Between 205 Days and 550 Days of Age (WHGAIN). The BLUE of the additive and nonadditive genetic effects for WHGAIN in heifers and bulls were not equal to the sum of the two component postweaning growth periods, WYGAIN and YHGAIN (Table 4). This discrepancy likely was due to lack of accuracy of the BLUE of the genetic effects, probably a consequence of the high degree of imbalance in the data set used.

Genetic effects for WHGAIN in bulls followed the same pattern as during the WYGAIN and YHGAIN periods. The Brahman dam and sire additive genetic effects of WHGAIN were 28.5 \pm 16.0 kg and -25.2 \pm 12.0 kg (Table 4). The corresponding Brahman (as a deviation from Angus) direct and maternal additive genetic effects were -50.4 ± 23.9 kg and 53.8 ± 21.4 kg, respectively. Thus, over the complete growth period (WHGAIN), Brahman (as a deviation from Angus) sire and dam (or direct and maternal) additive genetic effects essentially cancelled each other out. On the other hand, the B × A bull (or direct) nonadditive genetic effect was much larger $(61.9 \pm 17.8 \text{ kg})$. P < .01, Table 4) than that of the B \times A dam (or maternal) nonadditive genetic effect (-11.5 ± 7.3 kg, Table 4); thus, their sum was positive. Consequently, under the nutritional conditions of bulls, the B × A direct nonadditive genetic effects were the most important effects in determining the superiority of crossbred over straightbred animals. For heifers, this also was true. The B x A direct nonadditive genetic effect for heifers was 26.4 ± 19.3 kg (Table 4). In addition, Brahman additive genetic effect also might (its BLUE has a large SE) be important $(16.4 \pm 21.4 \text{ kg})$ for heifers. The Brahman additive maternal and B × A nonadditive maternal genetic effects for heifers were both negative and nonsignificant $(-2.5 \pm 18.7 \text{ kg})$ and $-4.9 \pm 5.7 \text{ kg}$, respectively). Thus, the pattern of values of additive and nonadditive genetic effects of heifers for WHGAIN mimicked that for YHGAIN. Brahman alleles were superior to Angus alleles for additive genetic effects: the interaction between Brahman and Angus alleles for direct effects promoted additional weight gain in heifers between 205 d and 550 d of age. Also, any advantage in growth rate in heifers due to preweaning maternal environment was lost under the restricted nutritional conditions available postweaning.

Findings of this research generally agree with those of previous reports from Texas (Long et al., 1979a,b) and Florida (Peacock et al., 1982), which found that Angus additive genetic effects for postweaning growth were superior to those of Brahman. Also, the greater advantage of Angus over Brahman additive genetic effects found here when animals were under a higher plane of nutrition agreed with results reported by Long et al. (1979b) for heifers reared under two nutritional regimens. However, the B × A nonadditive genetic

effects of bulls and heifers did not decrease with age. In fact, the $B \times A$ nonadditive genetic effect in heifers was higher for YHGAIN (9.5 \pm 16.2 kg) than for WYGAIN $(-.5 \pm 10.9)$. These results differed from those of Long et al. (1979a,b), who found that levels of heterosis decreased with age. Finally, Peacock et al. (1982), in a study conducted under a higher plane of nutrition than the ones used in this study and in rather close confinement conditions, found that Angus additive maternal genetic effects for average daily gain were superior to Brahman. Their results were the opposite of those obtained in this study for WYGAIN, which covered a comparable growth period. This discrepancy may be due in part to the sample of animals used in each study and in part to the nutritional conditions provided to the animals. However, the BLUE of Brahman additive genetic effects had large standard errors, especially in heifers. This prevents drawing any firm conclusions about additive maternal group genetic effects.

Implications

Angus germ plasm resulted in more rapid postweaning growth rate than Brahman germ plasm when climatic conditions were cool and plane of nutrition was higher. Brahman germ plasm, on the other hand, was responsible for superior growth rates under a lower nutritional regimen during hotter, more humid conditions. However, the effect of nonadditive (heterotic) genetic effects, resulting from crossbreeding Angus and Brahman, on postweaning growth was much greater than that due to breed differences; effects were most pronounced when a higher plane of nutrition allowed its fuller expression.

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