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# DIRECT AND MATERNAL GENETIC EFFECTS DUE TO THE INTRODUCTION OF *BOS TAURUS* ALLELES INTO BRAHMAN CATTLE IN FLORIDA: I. REPRODUCTION AND CALF SURVIVAL[1]

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## ABSTRACT

Pregnancy rate, calf survival rate to weaning and calf age at weaning of several types of crossbred cows (2/3 or more Brahman) were compared to those of straightbred Brahman and Angus cows over a 12-yr period at Subtropical Agricultural Research Station near Brooksville, FL. The purpose of this study was to determine the relative importance of additive vs nonadditive genetic effects on reproductive and calf survival traits in a population of cattle whose foundation was selected on the basis of superior reproductive performance under harsh environmental conditions. Best linear unbiased estimates (BLUE) of direct additive effect (measured as the deviation of Brahman additive breed effect from Angus) for pregnancy rate and calf age, measured as traits of the dam, were 6 ± 3% and –7.2 ± 2.1 d, respectively. Thus, *Bos taurus* germ plasm did not increase pregnancy rate but resulted in an earlier calving date. The BLUE of nonadditive (intralocus) direct genetic effects measured as deviations from intralocus group genetic effects in the parental breeds on pregnancy rate and calf age at weaning were 25 ± 4% and –6.4 ± 2.5 d. Nonadditive effects on pregnancy rate were the primary cause of the superior reproductive rates observed in Brahman crossbred cows. Calf survival was considered to be a trait of the calf, and BLUE of direct additive, direct nonadditive, maternal additive and maternal nonadditive genetic effects were obtained. Only maternal nonadditive genetic effects were found to have a significant effect on survival rate (9 ± 4%).

(Key Words: Beef Cattle, Brahman Fertility, Survival, Heterozygosity, Crossbreeding.)

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## Introduction

Reproduction and calf survival traits long have been regarded as among the most economically important traits in commercial beef cattle operations. Weaning rate of Florida herds is low compared with that of average U.S. herds. Part of this problem may be related to the prevalence of Brahman crossbreeding in the commercial cowherd of Florida. Brahman females have lower reproductive rates than contemporary *Bos taurus* straightbred females (Franke, 1980; Turner, 1980). Survival rates of straightbred Brahman calves also are lower than those of contemporary *Bos taurus* calves (Koger et al., 1967).

Several studies have shown an advantage of crossbred cows over straightbred cows for fertility and calf survival traits (Turner et al., 1968; Cundiff et al., 1974; Spelbring et al., 1977; Crockett et al., 1978; Williams and Franke, 1988). Only a few studies have attempted to separate additive from nonadditive effects on fertility and calf survival traits (Peacock and Koger, 1980; Olson et al., 1985). None of these studies has included crossbred cows with levels of upgrading past backcrosses or *inter se* crossbred cows. Therefore, the objectives of this study

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TABLE 1. NUMBER OF RECORDS PER TRAIT BY BREED GROUP COMPOSITION OF SIRE AND DAM

| Breed group composition | | | No. of records[a] | | |
|---|---|---|---|---|---|
| Sire | Dam | Calf | PREG | SURV | CAGE |
| Brahman (B) | Brahman | Brahman | 496 | 364 | 332 |
| Brahman | 2/3B:1/3A | 5/6B:1/6A | 114 | 168 | 162 |
| Brahman | 5/6B:1/6A | 11/12B:1/12A | 109 | 78 | 75 |
| Brahman | 11/12B:1/12A | 23/24B:1/24A | 23 | 15 | 14 |
| Brahman | Angus | 1/2B:1/2A | 226 | 138 | 126 |
| 2/3B:1/3A | 2/3B:1/3A | 2/3B:1/3A | 423 | 317 | 301 |
| 2/3B:1/3A | Angus | 1/3B:2/3A | 92 | 67 | 61 |
| 5/6B:1/6A | 5/6B:1/6A | 5/6B:1/6A | 446 | 358 | 330 |
| 5/6B:1/6A | Angus | 5/12B:7/12A | 111 | 60 | 58 |
| Angus (A) | 2/3B:1/3A | 1/3B:2/3A | | 8 | 8 |

[a]PREG = dam pregnancy status, SURV = calf survival to weaning and CAGE = calf age at weaning.

were 1) to estimate additive group genetic differences between Brahman and Angus for pregnancy rate (**PREG**), survival rate (**SURV**) and calf age at weaning (**CAGE**) and 2) to estimate nonadditive group genetic effects due to Brahman × Angus heterozygosity for PREG, SURV and CAGE in a population containing upgraded and *inter se* crossbred Brahman cows and straightbred Angus and Brahman cows.

#### Materials and Methods

This study was conducted at the Subtropical Agricultural Research Station (STARS) located at Brooksville, Florida from 1970 through 1982. The study was initiated with the purchase of 85 Brahman (**B**) crossbred females during the fall of 1969 from a Florida commercial herd in which all open females had been culled systematically for a number of years. These crossbred cows, sired by B bulls and approximately two-thirds B, exhibited the general breed characteristics of B, had calved for the first time at 3 yr of age, had weaned a normal calf, and had become pregnant again during the subsequent breeding season while nursing this calf. The non-B proportion in these crossbred cows included Angus (**A**) as well as other *Bos taurus* breeds. Fifteen additional cows were selected from the same herd in a similar manner in the fall of 1971 to replace those females culled for reproductive failure or loss of a calf.

Purebred B cows to which crossbred cows (2/3B or more) were compared were from a herd that had been maintained at STARS for a period of 20 yr. This purebred herd had been selected for reproduction through culling of open females whenever possible and for growth rate through selection of the heavier bulls at 18 mo of age as herd sires. Brahman bulls from outside sources also were used in the purebred herd and these bulls were selected on growth rate as well as other characteristics.

Brahman crossbred bulls (2/3B:1/3A) were produced in a rotational crossbreeding program conducted at the Beef Research Unit of the University of Florida. Sires of these 2/3B:1/3A bulls were straightbred B bulls from the STARS herd and dams were approximately 1/3B:2/3A. Straightbred B and 2/3B:1/3A bulls also were mated to A cows. Angus cows were purebreds, most of which were from the STARS A herd that had been established about 15 yr before the initiation of the study; others originally were from the Front Royal Experiment Station in Virginia and had been transferred to the STARS herd several years before the beginning of this study.

The design of the mating system and numbers of records per trait are shown in Table 1. Foundation cows (assumed 2/3B:1/3A) were exposed to the same straightbred B bulls as the straightbred B cows during the 1970 and 1971 breeding seasons to produce 5/6B:1/6A calves. Natural mating in single-sire herds was utilized throughout the study. During the 1972 breeding season, a portion of the 2/3B:1/3A cows were bred to the same four straightbred B bulls as the straightbred B cows, whereas the remaining 2/3B:1/3A cows were mated to two 2/B:1/3A bulls. A total of 14 straightbred B bulls sired the 5/6B:1/6A calves. The 2/3B:1/3A bulls were mated to 2/3B:1/3A cows to produce first-generation *inter se* calves from the 1972 through the 1977 breeding seasons. A total of six 2/3B:1/3A bulls sired first-generation *inter se* 2/3B:1/3A calves. The

TABLE 2. NUMBER OF DAMS PER TRAIT BY BREED GROUP COMPOSITION OF THEIR SIRES AND DAMS

| Breed group composition[a] | | | No. of dams[b] | | |
|---|---|---|---|---|---|
| Sire of dam | Dam of dam | Dam | PREG | SURV | CAGE |
| Brahman | Brahman | Brahman | 183 | 156 | 144 |
| Brahman | 1/3B:2/3A | 2/3B:1/3A | 96 | 93 | 93 |
| Brahman | 2/3B:1/3A | 5/6B:1/6A | 72 | 69 | 66 |
| Brahman | 5/6B:1/6A | 11/12B:1/12A | 16 | 12 | 11 |
| 2/3B:1/3A | 2/3B:1/3A | 2/3B:1/3A | 96 | 76 | 72 |
| 5/6B:1/6A | 5/6B:1/6A | 5/6B:1/6A | 87 | 75 | 66 |
| Angus | Angus | Angus | 182 | 141 | 130 |

[a]1/3B:2/3A dams of bulls were produced in a long-term rotational crossbreeding experiment at the Beef Research Unit, Univ. of Florida. 1/3B:2/3A dams of dams were produced in a similar rotational crossbreeding program in a private herd.

[b]PREG = dam pregnancy status, SURV = calf survival to weaning and CAGE = calf age at weaning.

number of cows of each breed or crossbred type with records for each trait evaluated are shown in Table 2.

The 2/3B:1/3A and 5/6B:1/6A breed groups were mated *inter se* for the remainder of the study. A total of 7 *inter se* 2/3B:1/3A and 15 5/6B:1/6A bulls (10 of them *inter se* bred) sired calves. Beginning in 1977, a portion of the 5/6B:1/6A cows were mated to a straightbred B bull to produce calves with a second topcross to B (11/12B:1/12A). Straightbred B calves sired by at least three bulls were produced each year during which the various types of grade calves were produced with the exception of 1978, when only two straightbred B bulls sired calves.

Straightbred B and both 2/3B:1/3A and 5/6B:1/6A crossbred bulls were mated to A cows each year except the first and last 2 yr. Progeny of these matings were sold at weaning or used in other research projects.

All B × A crossbred sires other than the foundation 2/3B:1/3A bulls were produced at STARS, as were 16 of the 38 straightbred B bulls. All bull calves were grown postweaning on pasture and supplemented with 3 to 5 kg daily of a concentrate feed (70% corn, 20% molasses, 10% protein premix) per head until approximately 550 d of age. Bulls were selected for use in all breeding groups based on 550-d weight and freedom from structural defects. Attempts were made to utilize only bulls whose dams had not had a reproductive failure. Some effort also was made to avoid use of closely related sires. Only rarely was a bull used for more than 2 yr.

The mating plan for this study was designed to separate any observed superiority of B × A crossbred females over straightbred females into that due to additive differences between the B breed and the *Bos taurus* component, primarily A, of the grade females, and that due to nonadditive (intralocus) genetic effects. The level of intralocus heterozygosity relative to breed origin of alleles (B × A) in the foundation-grade females was assigned to be 66.6% of maximal $F_1$ *Bos induces Bos taurus* heterozygosity, because they were produced in a Brahman × *Bos taurus* rotational crossbreeding program. The foundation B crossbred bulls were known to be of about 2/3 B and 1/3 A breeding. Thus, *inter se* progeny of these parents would be expected to retain the additive effect of 1/3 *Bos taurus* germ plasm in their dams as well as 44.4% of maximal heterozygosity due to *Bos indicus-Bos taurus* intraallelic combinations. The level of expected nonadditive effects due to *Bos taurus-Bos taurus* interbreed intraallelic combinations was not possible to determine due to lack of complete knowledge of the proportions of *Bos taurus* breeds in foundation B crossbred cows. In any event, nonadditive effects attributable to *Bos taurus* × *Bos taurus* interbreed combinations have been small for reproductive performance in Florida (Peacock and Koger, 1980).

A 90-d breeding season was utilized, beginning approximately March 15 of each year. Heifers were first exposed to a bull at 2 yr of age. All females were palpated in late August for pregnancy diagnosis. Calf weaning weights also were recorded at this time. All nonpregnant B × A crossbreds and most nonpregnant purebreds were culled annually. Females whose calves were stillborn or died early in life usually were culled also.

Pastures, composed primarily of Bahiagrass (*Paspalum notatum*), were grazed most of the year. These pastures were fertilized annually, and a stocking rate of about 1.5 to 2 ha per cow/calf unit was utilized. The winter feeding program was approximately 9 kg of grass hay, 1.8 kg of molasses and 1.4 kg of range pellets (20% protein) per cow each day. The winter feeding program usually began in December and continued into March, depending on status of the pastures. This area is susceptible to drought during spring and, during droughts, supplemental feeding was continued. Salt and mineral supplements also were provided. Except during the breeding season, cows of all breeding groups were maintained in the same groups.

Traits examined were dam pregnancy status (PREG), calf survival to weaning (SURV) and calf age at weaning (CAGE). Two of these traits, PREG and SURV, are discrete, and CAGE is continuous. A dam was given a 1 if she calved, otherwise she received a 0. Similarly, for calves present at weaning SURV was coded a 1; stillborn calves and those that died before weaning were coded 0. The third trait, CAGE, gives an indication of the length of time from the initiation of the breeding season until the time of conception. This trait contains the effects of gestation length and survival, both from conception to birth and from birth until weaning, because calves that did not survive did not have a CAGE value.

Best linear unbiased estimates (BLUE) of additive and nonadditive genetic effects were estimated using regression procedures for group genetic effects as outlined by Elzo and Famula (1985). Group genetic effects account for average genetic values of groups of animals (e.g., 1/2B:1/2A) measured as deviations from the average genetic value of a reference group of animals (e.g., A) for specific genetic effects within traits (e.g., additive direct group genetic effects of 1/2B:1/2A for weaning weight). These regression procedures differ from those used by several authors (Koger et al., 1975; Dillard et al., 1980; Peacock et al., 1981; Robison et al., 1981) in that calf additive group genetic effects are explained in terms of their parental components. Because sire and dam group genetic effects are estimated separately, predictions of sire, dam and calf group genetic values are unbiased regardless of the value of the group genetic effects of the parental breeds. On the other hand, procedures that consider calf group effects yield biased results when the sire and dam additive direct group genetic values differ, which may happen due to nonrandom choices of breeding animals. The regression approach used here must assume equal additive direct group genetic effects in order to estimate direct and maternal genetic effects. Each trait was analyzed separately. The traits PREG and CAGE were analyzed as traits of the dam. Dams were assumed to be random samples of their breed groups. Thus, sire of dam and dam of dam additive direct group genetic effects were assumed to be equal. Consequently, the regression approach of Elzo and Famula (1985) reduced to that used by Koger et al. (1975) and Robison et al., (1981) for PREG and CAGE. Because maternal effects were assumed to be negligible, analyses of PREG and CAGE yielded estimates of direct additive and nonadditive group genetic effects only. The third trait, SURV, was considered to be a trait of the calf. Both direct and maternal, additive and nonadditive genetic effects were estimated for SURV. To obtain the BLUE of group genetic effects, a two-step procedure was followed. First, regression procedures were used to obtain the BLUE of dam (for PREG, SURV and CAGE) additive and nonadditive group genetic effects and sire additive and calf nonadditive (for SURV only) group genetic effects. Second, these BLUE were equated to their expected genetic composition and solved for direct and maternal additive and nonadditive components.

The statistical model for PREG and CAGE contained year, age of dam, B dam additive genetic group, B × A dam nonadditive (intralocus) genetic group and residual effects. All effects were considered as fixed, except residuals. Residual effects were assumed to be uncorrelated and to have a common variance. The model for SURV also included the effects of B sire additive genetic group and B × A calf nonadditive (intralocus) genetic group. Both effects were considered to be fixed. Additive group genetic effects were defined as deviations from A. Thus, the incidence matrix contained the probability of having B alleles in the dam (PREG, SURV, CAGE) and the sire (SURV).

Interbreed (B × A) nonadditive (intralocus) group genetic effects were defined as deviations from the nonadditive (intralocus) group genetic effects of the parental breeds (A and B). Hence, the incidence matrix for these effects contained the probabilities of having B and A alleles at one locus (over all loci) in the dam (PREG, SURV, CAGE) and in the calf (SURV).

The BLUE of the direct and maternal additive and nonadditive group genetic effects were determined using the following expressions: (i) Brahman additive direct group genetic effect = Brahman dam additive group genetic effect for

TABLE 3. *F*-VALUES AND SIGNIFICANCE LEVELS FROM THE LEAST SQUARES ANALYSES OF PREGNANCY STATUS, CALF SURVIVAL AND CALF AGE AT WEANING

| | Trait[a] | | | | | |
|---|---|---|---|---|---|---|
| | PREG | | SURV | | CAGE | |
| Source[b] | df | *F* | df | *F* | df | *F* |
| Year | 10 | 6.00** | 11 | 1.82* | 11 | 14.23** |
| Sex | | | 3 | 4.60** | 2 | 5.26** |
| Age of dam | 7 | 7.67** | 7 | 1.22 | 7 | 15.78** |
| Brahman dam additive[c] | 1 | 4.97** | 1 | 1.21 | 1 | 11.88** |
| B × A dam nonadditive[d] | 1 | 39.65** | 1 | 5.70 | 1 | 6.83** |
| Brahman sire additive[c] | | | 1 | .01 | | |
| B × A calf nonadditive[d] | | | 1 | 1.32 | | |
| Error mean square | | .16 | | .06 | | 470.34 |

[a]PREG = dam pregnancy status, SURV = calf survival at weaning and CAGE = calf age at weaning.

[b]A = Angus, B = Brahman.

[c]Brahman additive genetic group effects expressed as deviations from Angus.

[d]B × A intralocus nonadditive genetic group effects defined as deviations from those of the parental breeds.

*$P < .05$.

**$P < .01$.

PREG and CAGE = 2(Brahman sire group genetic effect) for SURV, (ii) B × A nonadditive (intralocus) direct group genetic effect = B × A dam nonadditive (intralocus) group genetic effect for PREG and CAGE = B × A calf nonadditive (intralocus) group genetic effect for SURV, (iii) Brahman additive maternal group genetic effect = Brahman dam additive group genetic effect − Brahman sire additive group genetic effect for SURV, and (iv) B × A dam nonadditive (intralocus) maternal group genetic effect = B × dam nonadditive (intralocus) group genetic effects for SURV.

Computations for this study were carried out using the generalized least squares program of SAS (1985).

### Results and Discussion

The *F*-values from the analyses of variance of PREG, SURV and CAGE are shown in Table 3. The environmental variables, year and age of dam, influenced ($P < .01$) PREG and CAGE, but only year affected ($P < .05$) SURV. Sex of calf also influenced SURV ($P < .01$) and CAGE ($P < .05$). The importance of the group genetic effects varied considerably across the three traits and will be discussed individually for each trait. The BLUE of the group genetic effects are shown in Table 4.

*Pregnancy Rate.* Pregnancy rate was analyzed as a trait of the dam. Thus, only direct additive (B and A) and B × A nonadditive (intralocus) group genetic effects were determined. The additive genetic difference of .06 ± .03 ($P < .05$) found between B and A dams indicates an advantage for B under these conditions. Although it may be surprising, this result is in general agreement with a previous study in Florida (Peacock and Koger, 1980) in which a nonsignificant additive genetic difference between B and A for calving rate and a slightly higher mean calving rate for B than for A cows were found. Turner et al. (1968) similarly found a slight advantage in percentage of cows calving for B over A under Gulf Coast conditions (Louisiana). In contrast, Crockett et al. (1978) reported the pregnancy rate of A cows to be 88%, as opposed to 72% for B cows, in southern Florida (Belle Glade), where nutritional conditions were superior to those at STARS. The lack of positive additive effect of *Bos taurus* (A) germ plasm in the B crossbred females indicates that any improvement in reproductive efficiency in a population of B cattle upgraded from a *Bos taurus* base would need to arise from residual nonadditive effects.

Nonadditive effects due to intralocus interactions of alleles of B and A origin were found to be very large (.25 ± .04, $P < .01$). Thus, the advantage of B × A crossbred cows over straight-

TABLE 4. BEST LINEAR UNBIASED ESTIMATES OF THE ADDITIVE AND NONADDITIVE GROUP GENETIC EFFECTS FROM THE LEAST SQUARES ANALYSES OF PREGNANCY STATUS, CALF SURVIVAL AND CALF AGE AT WEANING

| | Trait[a] | | |
|---|---|---|---|
| Group genetic effect[b] | PREG | SURV | CAGE, d |
| Brahman dam additive[c] | .06 ± .03* | −.10 ± .09 | −7.24 ± 2.10** |
| B × A dam nonadditive[d] | .25 ± .04** | .09 ± .04* | −6.41 ± 2.45** |
| Brahman sire additive[c] | | −.005 ± .06 | |
| B × A calf nonadditive[d] | | −.11 ± .10 | |

[a]PREG = dam pregnancy status, SURV = calf survival to weaning and CAGE = calf age at weaning.

[b]A = Angus, B = Brahman.

[c]Additive group genetic effects are expressed as deviations from Angus.

[d]B × A intralocus nonadditive group genetic effects are defined as deviations from those of the parntal breeds.

*$P < .05$.

**$P < .01$.

bred B cows reported in a preliminary analysis of these data (Olson et al., 1981) probably was due to nonadditive effects and not to an additive genetic superiority resulting from the selection procedure used to establish the foundation herd. Peacock and Koger (1980) also found a highly significant positive effect on calving rate due to B × A heterozygosity in the dams they evaluated. Large positive effects of B × A heterozygosity on reproductive performance also were found by Turner et al. (1968) and Crockett et al. (1978).

*Calf Age.* The direct additive effect of the B breed for age of calf at weaning was large (−7.24 ± 2.10 d), indicating a strong tendency for later calving of B cows. Calving date is influenced by both date of conception and length of gestation. Plasse et al. (1968) reported that the gestation length of straightbred B cattle is 292 d. This compares to an average gestation length of 282 d in A cattle (Bourdon and Brinks, 1982). Thus, this difference in gestation length could explain the observed difference in age of the calves from A vs B straightbred dams. Peacock et al. (1981) also reported that B cows calved later than A cows, with calf ages at weaning of 216 and 234 d.

The nonadditive direct effect of the B × A crossbred dams on calf age at weaning was negative (−6.41 ± 2.45 d; $P < .01$), indicating that nonadditive effects were responsible for later calving (Table 4). No clear explanation is readily apparent. One possible explanation is that open straightbred B cows occasionally were retained and were not lactating during the subsequent breeding season and thus conceived early. Peacock et al. (1981) found a nonsignificantly positive effect in CAGE due to B × A heterozygosity in B × A $F_1$ dams.

*Calf Survival.* Of the genetic effects, only the maternal B × A nonadditive group genetic effect increased ($P < .05$) calf survival (Table 4). These results agree with those of Peacock and Koger (1980), who observed an increase in SURV due to maternal B × A nonadditive group genetic effects and also failed to find any significant additive breed effects of calf nonadditive genetic group effects on SURV. On the other hand, Crockett et al. (1978) reported significant effects on SURV due to combined direct and maternal nonadditive group genetic effects in a B× A rotational crossbreeding system.

## Implications

Results indicate that reproductive performance and calf survival rates in the Brahman breed could be increased somewhat by increased heterozygosity resulting from introduction of small amounts of *Bos taurus* (Angus) breeding. This could be accomplished by allowing animals resulting from upgrading programs (perhaps 7/8 Brahman: 1/8 *Bos taurus*) to be registered as purebreds. Upgrading programs of this type are not currently approved by the American Brahman Breeders Association. It is permissible, however, to incorporate *Bos taurus* germ plasm from recently imported Brazilian Nellore, Guzerat, Gir and Indu-Brazil cattle. Although several of these breeds were part of the original base population that established the American Brahman breed, they have been bred as isolated populations from the Brahman for many years and importations from India have influenced Brazilian zebu breeds. Thus, incorporation of germ plasm from these breeds might be expected to have positive effects on reproductive traits similar to those observed in this study.

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