HETEROSIS AND HETEROSIS RETENTION FOR REPRODUCTIVE AND MATERNAL TRAITS IN NELLORE-ANGUS CROSSBRED COWS

A Dissertation

by

MOHAMMAD DIYA TALAL HAMED OBEIDAT

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Chair of Committee,	David G. Riley
Committee Members,	James O. Sanders
	Andy D. Herring
	Jason E. Sawyer
Head of Department,	H. Russell Cross

August 2013

Major Subject: Animal Breeding

ABSTRACT

Calving rate, weaning rate, birth weight, weaning weight, and ADG from 1997 to 2011 were investigated in Angus, Nellore, F_1 Nellore-Angus, first generation 3/8 Nellore 5/8 Angus produced as following: (1/2 Nellore 1/2 Angus sires and 3/4 Angus 1/4 Nellore dams, 3/4 Angus 1/4 Nellore sires and 1/2 Angus 1/2 Nellore dams, and 3/4 Nellore 1/4 Angus sires and Angus dams), and second generation 3/8 Nellore 5/8 Angus cows. The objectives were to estimate heterosis in Nellore-Angus crosses for cow reproductive traits and maternal effects on traits of their calves. The F_1 cows expressed 0.20 ± 0.02 heterosis for calving rate, while both first and second generation 3/8 Nellore 5/8 Angus expressed 0.13 ± 0.02. the first generation 3/8 Nellore 5/8 Angus produced out of 3/4 Angus 1/4 Nellore sires and 1/2 Nellore 1/2 Angus dams expressed 0.14 ± 0.03 heterosis for calving rate. The F_1 Nellore-Angus expressed 0.23 ± 0.03 heterosis for weaning rate and the 3/8 Nellore 5/8 Angus produced out of 3/4 Angus 1/4 Nellore sires × 1/2 Nellore 1/2 Angus dams and the second generation 3/8 Nellore 5/8 Angus expressed 0.14 ± 0.07 and 0.15 ± 0.05, respectively. No heterosis was expressed for birth weight in any breedtype group. Multiple attempts to analyze weaning weight and ADG and estimate heterosis resulted in excessive adjustments to least squares means. Young and oldest cows weaned lighter calves than others. F_1 cows weaned heavier calves at most ages. Nellore-sired F_1 calves were heavier at weaning than the reciprocal cross. Calves out of cows of intermediate ages had larger preweaning ADG than calves born to 2- and 3-yr-old and to aged cows. Generally, calves out of F_1 Nellore-Angus cows had

larger ADG than those out of cows of other breedtypes. Nellore-sired F_1 heifers had lower ADG than Angus-sired F_1 heifers. In general, bull calves had larger ADG than heifers. Non-F_1 crossbred cows expressed slightly larger heterosis than what would be expected by the dominance model. Heterosis expressed by second generation 3/8 Nellore 5/8 Angus for calving and weaning rate did not appear to differ from the first generation.

DEDICATION

This dissertation is dedicated to my wife Amal, my sons Talal and Omar, and my daughter. Thank you Amal for making my life great and for supporting me all the time.

ACKNOWLEDGEMENTS

I would like to thank the chair of my advisory committee Dr. David Riley for his guidance and help during the period of the graduate program, I learned so much from him and he was always there when I needed his assistance. I would also like to thank the members of my advisory committee Dr. James Sanders, Dr. Andy Herring, and Dr. Jason Sawyer for their help and willing to share their knowledge. Many thanks also for the professors in the department of animal science who taught me during the program period especially Dr. Clare Gill who gave me the chance to help her in the lab and learn new things.

I am blessed to have a great family here and in Jordan who supported me in every endeavor. Special thanks for my parents, my aunt, my brother Sofian, and my sisters for their emotional support and encouragement. I would also like to thank my family in-law for making my residency in the States easier and enjoyable. Special thanks also for Mr. Farouk Shami for his help and support during this program years. And finally, I would like to thank Jordan University of Science and Technology for supporting me financially during my program years.

Thank you all!!

TABLE OF CONTENTS

Page

LIST OF TABLES

Page

INTRODUCTION

The aim of a cow-calf operation is to enhance traits of economic importance, while at the same time controlling the cost of production. Of the most important traits are the reproduction efficiency and maternal ability traits. Several measurements are used to evaluate cow reproduction efficiency; the most well-known are pregnancy rate, calving rate and (or) weaning rate as a proportion of cows exposed to bulls in the breeding season. Maternal ability is usually evaluated as calf weaning weight and preweaning average daily gain. Many technologies are used to improve both reproduction and maternal ability, but the oldest and easiest is crossbreeding.

Crossbreeding has two primary advantages over straightbreeding including heterosis (hybrid vigor), and breed complementarity which “refers to the advantage of a cross over another cross or a purebred resulting from the manner in which two or more characters combine or complement each other.” (Cartwright, 1970). Heterosis is defined as the superiority of the crossbred animal performance compared to the average of the straightbred parental breeds. Often, traits that are lowly heritable are quite responsive to heterosis, for example, reproductive traits. First generation crossbred animals express the highest levels of heterosis; however, many operations in the Gulf Coast region of the United States are using cows that are not first generation crosses such as second generation crosses, composite breed cows, or other types that were produced by various crossbreeding systems. Usually non-F_1 cows are used because F_1 females are expensive to purchase, and it is expensive to maintain straightbred animals to produce F_1 replacements. Cartwright et al. (1964) reported high performance in Brahman x Hereford crossbred cows for reproductive and maternal traits. If heterosis expression is proportional to breed heterozygosity, heterosis expressed in F_1 cows will be reduced in subsequent generations. Australian research suggested total loss of heterosis for calving rate in second generation (F_2) *Bos indicus-Bos taurus* cows (Seifert and Kennedy, 1972; Seebeck 1973). Those results needed to be assessed under United States conditions.

LITERATURE REVIEW

Breeds

Nellore (Ongole) is a *Bos indicus* breed that is originally from India. It is distinguished by a long narrow head with short horns and small ears, and was used for both milk production and heavy draft in India. However, in Brazil, from where the most recent importations of Nellore cattle were made to the United States, this breed was selected as a beef breed. The Nellore breed was the predominant breed of the Zebu cattle in the United States until the middle of the 1920s; this resulted in grade Nellore females making a large contribution to the American Brahman breed (Sanders, 1980).

Angus is the most popular beef breed in the United States. It is a *Bos taurus* breed that is originally from Aberdeen and Angus counties of northeast Scotland. Angus cattle are naturally polled and can be black or red in color. Angus cattle are known for their adaptability and resistance to harsh cold weather, and early age at maturity. Females calve easily and perform very well maternally, indicated by high milk production and heavy calf weaning weight. In addition, Angus cattle have superior marbling ability which is considered as a key component of improvement of tenderness and other palatability traits (Oklahoma State University, 2011).

Heterosis

Heterosis is "the superiority of the outbred animals over the average of their parents in individual merit" for a given trait (Lush, 1945). Shull (1952) claimed that he first used the term heterosis to describe the phenomenon in 1911 when studying the effect of self and cross fertilization in maize. Shull (1952) also defined heterosis as the “interpretation of increased vigor, size, fruitfulness, and speed of development, resistance to disease and to insect pests, or to climatic rigors of any kind manifested by crossbred organisms as compared with corresponding inbred.” Heterosis appears to be is important for traits in cattle that are not easily improved through selection, such as reproductive traits, calf survival, and longevity traits (Riley and Crockett, 2006).

The quantitative explanation for heterosis has focused on two concepts: dominance (intralocus interactions of alleles) (Jones, 1917), or overdominance (Shull, 1908; Crow, 1948). Semel et al. (2006) reported significant contributions of overdominance to fitness traits but not performance traits in tomato. Epistasis may also be an alternative cause of heterosis. Springer and Stupar (2007) defined epistasis as the interactions between genes at two (or more) loci affecting the phenotypic expression of a trait. Moreover, Dickerson (1952) said that epistasis is “universal;” that is, gene expression depends on and (or) could be modified by gene effects in other sets of alleles within an organism. Hill (1982) studied dominance and epistasis as components of heterosis. The author wrote “… if heterosis is due to alleles’ interaction within locus (dominance), then the heterosis is proportional to heterozygosity;” this is the basis of what is commonly known among animal breeders as the “dominance model.”

Heterosis in Cow Reproductive Efficiency Traits

Crossbreeding is considered the fastest and easiest approach to improve reproductive traits, as they are known to be very lowly heritable. Mackinnon et al. (1990) reported that heritability estimates for cow fertility traits were (0.11). In addition, Meyer et al. (1990) reported that heritability estimates for calving rate have ranged from

0.07 in Hereford to 0.11 in Angus cattle. Cartwright et al. (1964) reported high levels of heterosis in the reproductive efficiency traits in Brahman-Hereford cross cows. Various authors (Cartwright et al., 1964; Koger, 1973; Koger et al., 1975; Gregory et al., 1978; Gregory and Cundiff, 1980) have reported that F_1 *Bos indicus* × *Bos taurus* cows had higher levels of heterosis for their reproductive traits compared to *Bos taurus* × *Bos taurus* cows.

Cartwright et al. (1964) investigated heterosis in Brahman-Hereford crosses; they reported a 9.5% estimate of heterosis for calving rate in the crossbred females. Cundiff et al. (1974a) investigated heterosis for reproductive traits in straightbred Hereford, Angus, and Shorthorn heifers and their reciprocal-cross heifers. They found that the level of heterosis for conception rate to natural service breeding for a 65-d season was 6.6% for first service conception. Estimates of heterosis for pregnancy rates (pregnant cows as a percentage of cows exposed to bulls for breeding) in British crosses have ranged from 3 to 8.9% (Cundiff et al., 1974a, 1992; Spelbring et al., 1977b; Koch et al., 1985). However, in British × Continental crosses estimates were higher and have ranged from 5 to 21.3% (Olson et al., 1985, 1993; Newman et al., 1993). In *Bos indicus* × *Bos taurus* crosses (Olson et al., 1990, 1993) estimates of heterosis have ranged from 7.6 to 25%. Morris et al. (1993) reported 12.2% heterosis for pregnancy rate in Angus-Hereford crosses. In a comparison of Brahman-Angus and Brahman-Hereford crossbreds and straightbreds, F_1 Brahman-Angus cows expressed high levels of heterosis for pregnancy rate (35%), and Brahman-Hereford crossbreds expressed 25% heterosis for this trait as 2 yr-old (Riley, 2000).

Spelbring et al. (1977b) evaluated reproduction and longevity in crossbred Angus × Milking Shorthorn cows, and reported that crossbred females were superior to straightbreds for all traits. Heterosis estimates for calving rates in this study were 12.3, 7.0, and 15.2 %, respectively, for their first three calf crops. In a review, Long (1980) reported 2.4% heterosis for calving rate in British crosses. Tawonezvi et al. (1988) evaluated the productivity of crossbred cows and reported 16.9% heterosis for calving rate in Africander x Sussex cross cows. Mackinnon et al. (1989) reported 19% calving rate heterosis in F_1 Africander (¼ Shorthorn ¼ Hereford) cows and 16% in the F_1 Brahman (¼ Shorthorn ¼ Hereford) cows. Estimates of heterosis for calving rate in Angus, Charolais, Brahman, and Hereford crossbred cows have ranged from 9.6 to 18.8% in crossbred females (Williams et al, 1991). Sanders et al. (2005) reported results of experiments evaluating *Bos indicus* × *Bos taurus* cross cows, including estimates of heterosis for calving rate of 9.5% and 15% in F_1 Brahman-Angus and F_1 Brahman-Hereford females, respectively. Neufeld-Arce (2006) reported 18% heterosis for calving rate in F_1 Nellore-Angus (F_1 NA) crossbred females and 14% for 3/8 Nellore 5/8 Angus cows. Estimates of heterosis ranged from 8.0 to 8.7% for caving rate in British × Continental crossbred cows (Peacock and Koger, 1980; Kress et al., 1992; Newman et al., 1993). Higher levels of heterosis for calving rate have been reported for *Bos indicus* × *Bos taurus* crossbred cows and ranged from 8.7 to 25% (Cartwright et al., 1964; Turner et al., 1968; Peacock and Koger, 1980; Neville et al., 1984a; Olson et al., 1990).

Weaning rate is defined as the proportion of cows exposed to bulls in the most recent breeding season that successfully weaned a calf. Tawonezvi et al. (1988) reported

10.4% mean heterosis for weaning rate of crossbred cows that were reciprocal crosses of Charolais, Africander, Mashona, Nkone, Brahman and Sussex. African *Bos indicus* and Sanga crossbreds had heterosis estimates of 3.0% to 6.8% (Gregory et al., 1985). Morris et al. (1993) reported 12.2% heterosis for weaning rate in Angus × Hereford crossbred cows. Heterosis for this trait in Angus × Criollo (Chaqueño) crosses was 10.1% (Corva et al., 1995). Key (2004) reported estimates of heterosis for weaning rate of 11% and 16% for Brahman-Angus and Brahman-Hereford cows, respectively. Estimates of heterosis were 20% and 19% for F_1 Nellore-Angus and ⅜Nellore ⅝ Angus crosses, respectively (Meuchel, 2005). In a later analysis of cattle from the same study, Neufeld-Arce (2006) reported estimates of heterosis for this trait to be 24% in the F_1 Nellore-Angus and 14% in the ⅜ Nellore ⅝ Angus crossbred females. Generally, in *Bos indicus* × *Bos taurus* crossbreds cows, heterosis estimates for weaning rate have ranged from 6.9% to 20% (Cartwright et al., 1964; Koger et al., 1975; Peacock and Koger, 1980; Neville et al., 1984a; Olson et al., 1990; Winder et al., 1992). Weaning rate heterosis estimates in British × Continental crosses have ranged from -3.0% to 13.0% (Gregory et al., 1978; Peacock and Koger, 1980; Olson et al., 1985; Dearborn et al., 1987; Kress et al., 1990, 1992; Newman et al., 1993). In British crosses heterosis estimates have ranged from 4.6% to 11.5% (Cundiff et al., 1974a, 1992; Spelbring et al., 1977b; Neville et al., 1984a).

Maternal Heterosis for Birth Weight

Maternal heterosis (that heterosis expressed by crossbred dams) effects on calf birth weight have been reported as low (Cartwright et al., 1964; McDonald and Turner, 1972; Cundiff et al., 1974b, 1992; Alenda et al., 1980; Dillard et al., 1980; Olson et al., 1985, 1990, 1993; Kress et al., 1990, 1992). Gaines et al. (1966) wrote that "…maternal heterosis on birth weight is very small or nonexistent." Low maternal heterosis (2.5%) for calf birth weight was observed by Spelbring et al. (1977a). McElhenney et al. (1986) suggested that the effect of maternal heterosis on birth weight is either zero or very little. MacNeil et al. (1989) reported 1.7 kg maternal heterosis for calf birth weight out of line-crossed Hereford cows. Maternal heterosis estimates were 1.5 kg for calves from Angus × Hereford and Angus × Red Poll cows (Oxford et al., 2009). Maternal heterosis estimates for Brahman-Angus and Romosinuano-Angus cows (first calves only sired by calving-ease bulls) were 8.6 and 12%, respectively (Riley et al., 2010).

Maternal Heterosis for Weaning Weight

Weaning weight is strongly affected by the dam's milking ability. Dearborn et al. (1987) reported that heterosis for 200 day weight/female exposed in British crosses was 7.7%; the data for this study were collected for cows from 3 through 7 years of age, and cows were mated to bulls that were ¾ or more Simmental. Heterosis in Africander × Simmental and Africander × Hereford cross cows for weaning weight per cow exposed as an evaluation of total cow efficiency was 13.4 kg in South Africa (Schoenan et al., 1993). Neufeld-Arce (2006) reported 34.8 kg and 7.3 kg maternal heterosis for weaning weight in F_1 Nellore Angus and ⅜ Nellore ⅝ Angus crossbred cows, respectively. F_1 Nellore Angus cows were bred to Angus and ¾ Angus ¼ Nellore bulls, while the ⅜ Nellore ⅝ Angus cows were bred to ½ Nellore ½ Angus, ⅜ Nellore ⅝ Angus, Angus, and ¾ Angus ¼ Nellore bulls. Maternal heterosis for weaning weight of calves from

British cross cows ranged from 3.2 to 8.4 kg (Cundiff et al., 1974b, 1992; Spelbring et al., 1977a; Alenda et al., 1980; Neville et al., 1984a; Dearborn et al., 1987). Hohenboken and Weber (1989) reported large maternal heterosis estimates (28.7 kg) in F_1 Angus-Hereford heifers. Estimates of maternal heterosis in British × Continental crosses have ranged from 6.8 to 16 kg (Alenda et al., 1980; Dillard et al., 1980; Knapp et al., 1980; Olson et al., 1985; Kress et al., 1990). Maternal heterosis for weaning weight has been greater than 18.0 kg in *Bos indicus* × *Bos taurus* crossbred females (McDonald and Turner, 1972; Roberson et al., 1986; Wyatt and Franke, 1986; Olson et al., 1993; Arthur et al., 1994).

Maternal Heterosis for Preweaning Average Daily Gain

Arthur et al. (1994) reported that direct heterosis for ADG was significant for Brahman × Hereford crosses, but maternal heterosis was not detected. In Charolais-Nellore crossbred cows, Trematore et al. (1998) reported that maternal heterosis for ADG (average daily gain) was 14.3%. No significant maternal heterosis effect in ADG was detected among Zebu breed crosses (Magaña and Segura, 2003). Preweaning daily gain was larger for calves out of Brahman- or Boran-sired females compared to calves out of Tuli or Angus/Hereford sired females (Jenkins and Ferrell, 2004). Teixeira and Albuquerque (2005) reported 11.2% maternal heterosis for ADG in crossbred Nellore, Hereford, and Angus cows. In addition, Vostrý et al. (2008) analyzed heterosis in Czech Fleckvieh, Beef Simmental cattle and their rotational crosses; 75% Czech Fleckvieh, 50% Czech Fleckvieh, and 25% Czech Fleckvieh. They reported that maternal heterosis was generally negative for all traits including ADG. Haile et al. (2011) reported that maternal heterosis was not significant for ADG in Boran-Holstein Friesian crosses; in that study, calves were separated from their dams 24 hours after birth, and cows were hand milked twice a day and milk was then given to their calves.

Heterosis Retention

For a certain trait, full heterosis is expressed in the F_1 individuals; however, in crossbred animals that are not F_1, only a proportion of the F_1 heterosis is expressed. This proportion is often called retained heterosis. If heterosis is adequately explained by the dominance model, then crossbred animals are expected to express a fraction of the F_1 heterosis that is proportional to their heterozygous loci. This is also expected in animals that are composites (*inter se* mated crossbreds) when n breeds contribute equally to the foundation of them (Dickerson, 1969, 1973); in those cases, if the levels of heterosis between the different pairs of breeds are the same, the proportion of heterosis expected to be retained is $\frac{(n-1)}{n}$. However, when breeds do not contribute equally, then the percentage of retained heterosis is proportional to $1 - \sum \pi^2$, where π represents the fractions of the breeds used in the foundation (Dickerson, 1973; Gregory et al., 1999). According to the dominance model, additional loss of heterosis is not expected to occur in later generations, that is, after loss between the first and second generation. Heterozygosity and consequently, heterosis, are expected to stabilize at 50% in the F_2 and later generations of a two-breed composite of equal proportions (Wright, 1922; Dickerson, 1969, 1973).

Epistasis may be responsible in part for heterosis expression and the amount of heterosis maintained in various kinds of crosses in advanced generations of *inter se* mating (Dickerson, 1969, 1973; Kinghorn, 1980; Sheridan, 1981; Hill, 1982). Dickerson (1973) concluded that for traits where epistasis contributes to the superiority of the crossbred, rotational crossbreeding is favored over composite breeds, while the opposite is true when epistasis does not contribute significantly to the crossbred superiority. Shrestha (2010) wrote, “When heterosis results from epistatic combinations fixed in their respective purebred parental breeds, especially with multiple loci, performance based on F_1 crosses may not be reliable for predicting heterosis retention in multiple breed crosses and in advanced generations of the newly developed composite breeds”.

Kinghorn (1980) suggested that epistasic loss could be estimated if a model containing additive effects, dominance effects (as related to heterozygosity), additive × additive, additive × dominance, and dominance × dominance interactions was used. Parental and F_1 epistasis were described as two potential sources of heterosis by Sheridan (1981). In that study, parental epistasis was described to result from “different homozygous epistatic gene combinations present in the parental lines being passed across to the crossbred in a manner analogous to the dominance model”. However, F_1 epistasis was characterized as a favorable combination of genes from the different breeds that were brought together in the F_1 crossbred. Sheridan (1981) also suggested that heterosis retention that resulted from F_1 epistasis involving pairs of unlinked loci can be almost proportional to heterozygosity of the crossbred individual. The parental model described by Sheridan (1981) involving two or three loci predicted much lower F_2 performance than expected by the dominance model (Cunningham, 1982). Hill (1982) suggested that the deviation in the F_2 performance from the expected by the dominance model could be a result of the additive × additive and dominance × dominance interactions.

These different models with either parental or F_1 episatic effects were evaluated by Koch et al. (1985) and Kinghorn and Vercoe (1989). Koch et al. (1985) reported that these models resulted in identical analyses of variance. Kinghorn and Vercoe (1989) suggested that models that use dominance effects as the only non-additive effect or models with both dominance and epistatic effects may be satisfactory to predict the merit of crossbred genotypes. Models containing dominance should be investigated first (before attempts to include epistatic effects) to evaluate crossbreeding studies (Kress et al., 1986). The authors supported their suggestions by the fact that the dominance model easily predicts animals' performance in multiple crossbreeding systems. However, Schmitt and Distl (1992) studied heterosis and recombination effects for calving and fertility traits in German Fleckvieh x Gelbvieh crosses, and concluded that dominance and epistasis were both important contributors to heterosis for pregnancy rate.

Heterosis Retention in Reproductive and Maternally Influenced Traits

Heterosis retention research involving crossbred *Bos taurus* cows produced from *inter se* matings was conducted at the Roman L. Hruska U. S. Meat Animal Research Center (MARC) in Nebraska. Composites at MARC were of three populations, MARC I (¼ Braunvieh ¼ Charolais ¼ Limousin ⅛ Angus ⅛ Hereford), MARC II (¼ Gelbvieh ¼ Simmental ¼ Angus ¼ Hereford), and MARC III (¼ Red Poll ¼ Pinzgauer ¼ Angus ¼ Hereford). Gregory et al. (1991a, 1991b, 1999) reported that combined (direct and maternal) retained heterosis for birth weight, weaning weight, and preweaning average daily gain was not less than what is expected by the dominance model. Heterosis retention for calving rate, weaning rate, and 200 day weight per female exposed was less than predicted by dominance model in MARC III cows, while their pregnancy rate did not differ from what was expected by the dominance model. Heterosis retained for reproductive traits in MARC I and MARC II cows did not differ from the dominance model expectations (Gregory et al., 1999).

Heterosis for calving and weaning rates did not differ from that expected by the dominance model in Hereford, F_1 Hereford × Simmental, ¾ Simmental ¼ Hereford and ¾ Hereford ¼ Simmental cows (Kress et al., 1990; 1992). Newman et al. (1993) investigated heterosis in ¼ Charolais ¼ Tarentaise ½ Red Angus cows; these cows were produced from crossing F_1 Charolais-Red Angus with F_1 Tarentaise-Red Angus, the resulting second generation cows were then *inter se* mated to produce third and fourth generation cows. The authors reported that pregnancy rate, calving rate, and weaning rate were greater in second generation crossbred cows than in the first generation cows. Morris et al. (1993) evaluated reproductive traits in the first generation cows produced from three breed crosses; ¼ Simmental ¼ Friesian ½ Angus, ¼ Maine Anjou ¼ Jersey ½ Angus, and ¼ Blonde d'Aquitaine ¼ Jersey ½ Angus, each cross was then interbred to produce second and third generations. The authors reported that weaning rate for the three F_1 generation crosses exceeded the straightbred Angus females. However, F_2 means were similar or below that of Angus, implying loss of heterosis for these traits depending on the average of purebred means relative to Angus.

High levels of heterosis for weaning rate in *Bos indicus* × *Bos taurus* cows were confirmed by Koger et al. (1975). Weaning rate of F_1 Brahman × Shorthorn cows was found to be less than that reported for the ¾ Shorthorn ¼ Brahman and ¾ Brahman ¼ Shorthorn. They concluded that heterosis for this trait was not linear with breed heterozygosity.

Williams et al. (1990) studied reproductive traits in two-, three-, and four-breed rotational crosses. Crossbreds in this study were three two-breed (Angus-Brahman, Charolais-Brahman and Hereford-Brahman), three three-breed (Angus-Brahman-Charolais, Angus-Brahman-Hereford and Charolais-Hereford-Brahman) and one four-breed (Angus-Brahman-Charolais-Hereford). No differences in calving rates were detected for cows in the three-breed (86.9%) and the four-breed rotations (85%). Hereford-Brahman crosses had significantly higher calving and weaning rates (87%and 81.4%, respectively) than either of the other two-breed crosses. Weaning rates were similar in the three- and four-breed rotations and they were both higher than the two-breed rotation group and the straightbred.

Australian researchers have reported heterosis retention in reproductive traits of *Bos indicus-Bos taurus* cows that were not consistent with dominance model expectation. Seebeck (1973) studied heterosis and heterosis retention in F_1, F_2, and F_3 generations for a 14 year period. The F_1 were produced from (Hereford × Shorthorn, Shorthorn × Hereford, Brahman × Hereford, Brahman × Shorthorn, Africander × Hereford and Africander × Shorthorn). The F_2 and F_3 generations were mated within Africander crosses, Brahman crosses, and Shorthorn-Hereford lines. The F_2 and F_3

Brahman crossbred cows had only 60.7% calving rate compared to 81.2% in the F_1 cows which represented a large loss of heterosis. No loss of heterosis was observed in the F_2 and F_3 Africander crossbred females (calving rate of 76.8% as compared to 76.4% of the F_1). After accumulation of more records from cows and their descendants in this population, Rendel (1980) reported that calving rate for the F_2 Brahman crossbred cows was as low as the straightbred calving rate. Mackinnon et al. (1989) evaluated reproductive traits in F_1, F_2, and F_n (F_3 and greater) crossbred females in the same population over a 28 year period, and the breed groups used in that study were (½ Africander ¼ Hereford ¼ Shorthorn, ½ Brahman ¼ Hereford ¼ Shorthorn, ¼ Africander ¼ Brahman ¼ Hereford ¼ Shorthorn). The authors reported higher heterosis for calving rate in the half blood Africander crosses than the half Brahman crosses for the three generations. Mackinnon et al. (1989) reported heterosis estimates of 19.1%, 13.3% and 11.2% in the F_1, F_2, and F_n generations, respectively, of the Africander crosses. Corresponding estimates in the Brahman crossbreds were 16.4%, -5.2% and 1.6% in the F_1, F_2, and F_n generations, respectively. In the four breed quarter blood composite the level of heterosis was 5% in the F_1 and 4.8% in F_2 and F_n combined. Mackinnon et al. (1996) investigated reproductive traits in Sahiwal (S), Brown Swiss (B), and Ayrshire (A) crosses in sub-humid coastal Kenya. Cows in that study were either ⅔ S ⅓ A mated to S bulls, or ⅔ A ⅓ S mated to A bulls, in a two-breed rotational breeding system. Later B bulls were introduced to the system and mated to the ⅔ S ⅓ A ⅔ A ⅓ cows to produce ½ B $^1/_6$ A ⅓ S, or ½ B $^1/_6$ S ⅓ A which were mated to A and S bulls, respectively. The authors concluded that dominance effects were the main cause of the heterosis between

Zebu and European breeds, because they failed to detect epistatic contribution. Epistatic contribution in that study was tested by regressing performance data on the expected average recombination of parental gene pairs.

Some U.S. work had similar results to the Australian studies. Hargrove et al. (1991) investigated reproductive traits in F_1 and F_2 Brahman Angus dams and ⅜ Brahman ⅝ Angus dams. The authors reported that F_1 dams had significantly higher calving and weaning rates compared to F_2 and ⅜ Brahman ⅝ Angus dams. In this study, calving rate was 96.7%, 81%, and 77.3%, weaning rate was 90.7%, 67.1%, and 80.8% for F_1, F_2, and ⅜ Brahman ⅝ Angus, respectively. Less heterosis was retained in the F_2 than expected. Olson et al. (1993) investigated reproductive and maternal performance in F_1, F_2, backcross, and three breed cross dams of Angus, Charolais, and Brahman breeds. The authors reported that heterosis for pregnancy rate was 0.071, 0.030, 0.063, and 0.072 for F_1, F_2, backcross, and three breed cross dams, respectively. In this study, the only bulls used to produce the F_2 Brahman-Angus cows were only Brahman sired F_1 bulls, while for the Brahman-Charolais F_2 cows the bulls were used form a group that contained either Brahman sired or Charolais sired F_1 bulls (T. A. Olson, Dept. Anim. Sci., Univ. Florida; personal communication with J. O. Sanders).

A research population of Brahman, Hereford, and Angus, and F_1 and F_2 crosses of Brahman with Angus and Brahman with Hereford has been characterized for heterosis expression in reproductive traits by the F_1 and F_2 groups. In her analyses of records of mostly young cows, Key (2004) reported that for calving rate the heterosis in F_1 Brahman-Angus cows was 10%, while it was -6% for F_2 Brahman-Angus cows. This drastic loss was not observed in Brahman-Hereford crosses; heterosis estimates in F_1 and F_2 were 15% and 13%, respectively, for this trait. Sanders et al. (2005) reported that for calving rate and weaning rate the lost heterosis in F_2 Brahman × Angus cows was greater than that expected by the dominance model, while in Brahman × Hereford cows less heterosis was lost than that expected by the dominance model. The most recent analyses of some of that data and later records of Brahman-Hereford cows by Boenig (2011) reported that heterosis retained in F_2 Brahman-Hereford crossbred cows was 39% for calving rate and 50% for weaning rate. The F_2 cows in this study were produced from all possible reciprocal matings with Brahman-Hereford and Hereford-Brahman sires (sire breed of the F_1 bull listed first, followed by dam breed of the bull), although the intent at the time was not to compare cows in different groups produced by those matings. When considered as a distinct group, those F_2 cows produced by Brahman-sired F_1 bulls had lower unadjusted means for these traits than the average of purebred Brahman and Hereford cows, which could indicate negative levels of heterosis. However, F_2 cows produced by Hereford-sired F_1 bulls had means as high as the F_1 group. This is an extremely important result as it could represent a cause of the tremendous loss of heterosis expressed for reproduction traits reported by others, as the evaluated cows in those studies were either entirely or primarily produced by Brahman-sired F_1 bulls (Seebeck, 1973; Seifert and Kennedy, 1972, Olson et al., 1993).

Koch et al. (1985) investigated heterosis retention in advanced generations of Angus-Hereford crosses. They found that heterosis for calf birth weight and preweaning daily gain were in agreement with the dominance model. Sacco et al. (1989) evaluated maternal heterosis retention in Angus, Hereford, Brahman, Holstein, and Jersey crosses. They reported that for birth weight 60% of the maternal heterosis was retained in the F_2 crossbred cows. In addition, the author reported that maternal heterosis for weaning weight was 17.0 kg in the first generation dams, while it was negligible for the second generation dams (-0.8 kg). Olson et al. (1993) reported that maternal heterosis for calf birth weight was 1.0, -1.4, 1.9, and 3.7 for F_1, F_2, backcross, and three breed cross dams, respectively.

Models

Linear models and multiple regression models have been the most widely used models to evaluate heterosis and heterosis retention in generations other than the F_1 generation. Breed was used in the linear model as the main effect of interest; other discrete and continuous variables were also included as appropriate. Heterosis and estimates of retained heterosis were calculated from contrasts of least squares means for breed groups (Knapp et al., 1980; Gregory et al., 1985, 1991a, 1991b, 1992a, 1992b, 1992c; Trail et al., 1985; Dearborn et al., 1987; Winder et al., 1992; Newman et al., 1993). The multiple regression model was applied to estimate heterosis for reproductive traits (Koger et al., 1975; Alenda et al., 1980; Dillard et al., 1980; Robison et al., 1981; Koch et al., 1985; Kinghorn and Vercoe, 1989; Olson et al., 1990; Kress et al., 1992; Schmitt and Distl, 1992). Several studies have used the two models in heterosis and heterosis retention estimation (Neville et al., 1984a, 1984b; Roberson et al., 1986; Madalena et al., 1990; Williams et al., 1991; Olson et al., 1993; Arthur et al., 1994; Perotto et al., 1994).

In summary, high levels of heterosis for reproductive traits in the F_1 *Bos indicus* × *Bos taurus* cows compared to *Bos taurus* × *Bos taurus* cows was reported by various authors (Cartwright et al., 1964; Koger, 1973; Koger et al., 1975; Gregory et al., 1978; Gregory and Cundiff, 1980). Researchers have reported that heterosis retention in reproductive traits of *Bos indicus*-*Bos taurus* cows was not consistent with dominance model expectation (Seebeck, 1973; Rendel, 1980; Mackinnon et al., 1989; Hargrove et al., 1991).

OBJECTIVES

The objectives of this study were to:

1. Estimate heterosis in Nellore-Angus crosses for cow reproductive traits and maternal effects on traits of their calves.
2. Estimate heterosis expressed for each trait in crosses other than the F_1 and compare to the heterosis expressed by F_1 cows, and evaluate the adequacy of the dominance model to estimate heterosis retained in the non-F_1 crossbred cows for reproductive traits.

Hypothesis: Heterosis levels for reproductive traits do not differ from the dominance model expectations for each type of cross.

MATERIALS AND METHODS

Description of Data

Data in this study were collected as a part of Texas Agricultural Experiment Station Project H6883 at the McGregor Research Center in Central Texas. Cows in this study were produced at the Texas A&M AgriLife Research Center at McGregor, TX. They were born from 1997 and through 2006. Table 1 shows the breedtypes and matings used. Table 2 shows the numbers of cows within each breedtype and their birth years. Table 3 shows the breeds of bulls bred to dams within each group.

Females in this study were exposed to bulls at one year of age and annually thereafter. Bulls were with the females in the pasture for approximately two months during the breeding season. Females were palpated for pregnancy during the fall. At that time cow weight, body condition score, and pregnancy status were recorded. The majority of calving occurred between February and May of each year. Calves were weaned when they were approximately seven months of age. Birth weight and weaning weight were recorded. Two failures to wean a calf resulted in cows being culled from the project.

Table 1. Breedtypes and how they were produced

Breedtype	Mating[1]	% Expected heterosis[2]
Angus (A)	A × A	0
Nellore (N)	N × N	0
Nellore x Angus (F_1 NA)	N × A	100
$^3/_8$ Nellore $^5/_8$ Angus ($^3/_8$ N $^5/_8$ A(a))	½ N ½ A × ¾ A ¼ N	50
$^3/_8$ Nellore $^5/_8$ Angus ($^3/_8$ N $^5/_8$ A(b))	¾ A ¼ N × ½ N ½ A	50
$^3/_8$ Nellore $^5/_8$ Angus ($^3/_8$ N $^5/_8$ A(c))	¾ N ¼ A × A	75
$^3/_8$ Nellore $^5/_8$ Angus-2 ($^3/_8$ N $^5/_8$ A-2)	$^3/_8$ N $^5/_8$ A × $^3/_8$ N $^5/_8$ A	47

[1] Sire breed presented first.
[2] Heterosis expected as a fraction of the F_1 heterosis according to the dominance model.

Table 2. Numbers and birth years for cows within each breedtype[1].

Breedtype	Numbers	Birth Years
A	51	1997, 1998, 1999
N	51	1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004
F_1 NA	50	1997, 1998, 1999
$^3/_8$ N $^5/_8$ A(a)[2]	8	1999, 2000, 2001
$^3/_8$ N $^5/_8$ A(b)[3]	47	2000, 2001, 2002, 2003, 2004, 2005
$^3/_8$ N $^5/_8$ A(c)[4]	8	1997, 1998, 2000
$^3/_8$ N $^5/_8$ A-2	52	2002, 2003, 2004, 2005, 2006
Total	267	

[1] A = Angus, N = Nellore
[2] $^3/_8$ N $^5/_8$ A (a) produced out of ½ N ½ A sire and ¾ A ¼ N dam,
[3] $^3/_8$ N $^5/_8$ A (b) produced out of ¾ N ¼ A sire and ½ A ½ N dam,
[4] $^3/_8$ N $^5/_8$ A (c) produced out of ¾ N ¼ A sire and A dam.

Table 3. Breeds of bulls mated to breedtype group[1]

Cow breed group	**Breeds of Bulls**
A	A, N, CH[3]
N	N, A
F_1 NA	A, ¾ A ¼ N, CH, F_1 NA
$^3/_8$ N $^5/_8$ A[2]	A, $^3/_8$ N $^5/_8$ A, CH, F_1 NA
$^3/_8$ N $^5/_8$ A-2	A, CH, $^3/_8$ N $^5/_8$ A

[1] A = Angus, N = Nellore
[2] includes $^3/_8$ N $^5/_8$ A(a) , $^3/_8$ N $^5/_8$ A(b), and $^3/_8$ N $^5/_8$ A(c).
[3] CH = Charolais.

Nellore cows were culled from the study if they failed three times to wean a calf, because, as is usual for the breed, very few calved at two years of age and none calved at both two and three years of age.

Traits Analyzed

Cow reproductive traits in this study included calving and weaning rates. Calving rate is the proportion of cows exposed to bulls in the most recent breeding season that successfully gave birth to a calf from those matings. Weaning rate is the proportion of cows exposed to bulls in the most recent breeding season that successfully weaned a calf produced from those matings. Numbers of records for each trait are shown in Table 4. Calving and weaning rates were analyzed as binary traits: values of zero were assigned to cows that did not calve or wean a calf, and values of one were assigned to those cows that gave birth to a calf and weaned a calf. Weight traits for calves in this study included birth weight, weaning weight, and preweaning average daily gain. Preweaning average daily gain was calculated as the difference between birth weight and weaning weight divided by weaning age in days.

Table 4. Numbers of observations for the traits within each breedtype.

Breedtype	**Calf crop Born**	**Calf crop weaned**	**Birth weight**	**Weaning weight**	**ADG**
A	301	301	258	233	233
N	357	357	245	211	211
F_1 NA	517	517	487	454	454
$^3/_8$ N $^5/_8$ A[2]	424	424	386	347	347
$^3/_8$ N $^5/_8$ A-2	256	256	226	215	215
Total	1855	1855	1602	1460	1460

[1] A = Angus, N = Nellore
[2] includes $^3/_8$ N $^5/_8$ A(a) , $^3/_8$ N $^5/_8$ A(b), and $^3/_8$ N $^5/_8$ A(c).

Statistical Analysis

Data were analyzed using the MIXED procedures of SAS (SAS Inst., Inc., Cary, NC). Cows were divided into four age groups (2, 3, 4, and older than 4 years of age). Data of first generation ⅜ Nellore ⅝ Angus cows were analyzed both by combining records of cows produced in the three different ways because there were insufficient numbers of the two of the three types, and separately (for the three groups). Effects that were not significant were excluded from the final model.

Reproductive Traits

Calving and weaning rates were analyzed as dependent variables using mixed linear models. Investigated fixed effects included breed and cow age within breed, while cow and year were considered random effects. Heterosis expressed in the crossbred cows was estimated by linear contrasts of the adjusted crossbred means from the weighted mean of the breeds that comprise the crossbred female. Comparison to dominance expectation was done using contrasts of non-F1 heterosis with F1 heterosis multiplied by the expectation (as a proportion).

Weight Traits

Calf birth and weaning weights, and preweaning average daily gain were analyzed using mixed linear models. Fixed effects investigated included cow age, sire breed of calf, cow breed group, and calf sex and possible interactions of these. Cow and year were modeled as random effects. Calf weaning age was included in weaning weight models as a continuous variable. Heterosis expressed and heterosis retained for the weight traits were estimated by linear contrasts of adjusted means as described previously.

RESULTS AND DISCUSSION

Calving Rate

The final model used contained sire breed of the cow, dam breed of the cow, cow age, and the three-way interaction of these ($P < 0.05$). Unadjusted means and SD for calving rate of cow's breedtype within age categories are presented in Table 5, and the corresponding adjusted means are presented in Table 6. Nellore cows had the lowest calving rate at 2 yr of age (0.04 ± 0.05). This low mean reflects late age at puberty like many *Bos indicus* breeds (Franke, 1980). The ⅜ Nellore ⅝ Angus produced out of ¾ Nellore ¼ Angus sire and Angus dam (this group contained only 8 animals) had 0.99 ± 0.12 calving rate as heifers; however, it did not differ ($P > 0.05$) from means for the other crossbred groups at 2 yr of age. The calving rate mean of the second generation ⅜ Nellore ⅝ Angus was as (0.94 ± 0.04) high as the F_1 Nellore-Angus (0.94 ± 0.04) at 2 yr of age. Calving rate of Nellore cows improved at 3 yr of age and their calving rate was 0.87 ± 0.04, while calving rate for the crossbred cows was lower than means at 2 yr of age and ranged from 0.74 to 0.86 with no significant differences between them. Most Nellore females were open at 2 yr of age, and likely better able to meet their maintanance requirements as they were not eating to provide energy for lactation and growth at the same time. On the contrary, the crossbred cows had higher nutritional requirements because they were lactating, which may be in part responsible for the lower means for calving rate at 3 yr of age. At 4 yr of age F_1 Nellore-Angus had the higest calving rate (0.99 ± 0.05) and it differed ($P < 0.05$) from both Nellore and first generation ⅜ Nellore ⅝ Angus. As mature cows (5 yr and older) Nellore cows had the

Table 5. Unadjusted means (SD) and number of records for calving rate by breedtype and age group[1]

	Age Category[7]			
Breedtype	**2**	**3**	**4**	**≥ 5**
A	0.78 (0.42)	0.86 (0.35)	0.85 (0.37)	0.91 (0.29)
	51	42	39	169
N	0.05 (0.21)	0.86 (0.35)	0.72 (0.45)	0.79 (0.41)
	44	50	50	213
F_1 NA	0.94 (0.24)	0.84 (0.37)	0.98 (0.14)	0.95 (0.21)
	50	50	50	367
⅜ N ⅝ A[2]	0.88 (0.35)	0.86 (0.38)	0.67 (0.52)	0.97 (0.18)
	8	7	6	30
⅜ N ⅝ A[3]	0.91 (0.28)	0.87 (0.38)	0.84 (0.37)	0.96 (0.20)
	47	47	45	170
⅜ N ⅝ A[4]	1.00 (0.00)	0.75 (0.46)	0.86 (0.38)	0.93 (0.26)
	8	8	7	41
⅜ N ⅝ A[5]	0.92 (0.27)	0.85 (0.36)	0.83 (0.38)	0.95 (0.21)
	63	62	58	241
⅜ N ⅝ A-2[6]	0.90 (0.30)	0.85 (0.36)	0.90 (0.31)	0.90 (0.30)
	52	52	49	104

[1] A = Angus, N = Nellore,

[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams

[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams

[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.

[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.

[6] Second generation ⅜ Nellore ⅝ Angus cows.

[7] Age category 2 = 2 yr-old-cows, 3 = 3 yr-old-cows, 4 = 4 yr-old-cows, ≥ 5 = cows 5 yr of age and older.

Table 6. Least squares means and SE for calving rate by breedtype and age category[1]

	Age Category[7]			
Breedtype	**2**	**3**	**4**	**≥ 5**
A	0.79 ± 0.05[b, y]	0.85 ± 0.05[xy]	0.86 ± 0.05[ab, xy]	0.91 ± 0.03[a, x]
N	0.04 ± 0.05[c, z]	0.87 ± 0.04[x]	0.72 ± 0.04[c, y]	0.79 ± 0.02[b, xy]
F_1 NA	0.94 ± 0.05[a, xy]	0.85 ± 0.05[y]	0.99 ± 0.05[a, x]	0.95 ± 0.02[a, x]
⅜ N ⅝ A[2]	0.87 ± 0.12[ab, xy]	0.84 ± 0.12[xy]	0.65 ± 0.12[bc, y]	0.97 ± 0.06[a, x]
⅜ N ⅝ A[3]	0.92 ± 0.05[a, xy]	0.86 ± 0.05[xy]	0.84 ± 0.05[b, y]	0.96 ± 0.03[a, x]
⅜ N ⅝ A[4]	0.99 ± 0.12[ab]	0.74 ± 0.12	0.87 ± 0.12[abc]	0.92 ± 0.05[a]
⅜ N ⅝ A[5]	0.92 ± 0.04[a, xy]	0.85 ± 0.04[y]	0.83 ± 0.04[bc, y]	0.95 ± 0.02[a, x]
⅜ N ⅝ A-2[6]	0.94 ± 0.04[a]	0.86 ± 0.04	0.90 ± 0.05[ab]	0.88 ± 0.03[a]

[1] A = Angus, N = Nellore,
[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams
[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams
[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.
[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.
[6] Second generation ⅜ Nellore ⅝ Angus cows.
[7] Age category 2 = 2 yr-old-cows, 3 = 3 yr-old-cows, 4 = 4 yr-old-cows,
≥ 5 = cows 5 yr of age and older.
[a,b,c] Means within a column that do not share a superscript differ ($P < 0.05$).
[x,y,z] Means within a row that do not share a superscript differ ($P < 0.05$).

lowest calving rate ($P < 0.05$), while the other breedtypes did not differ ($P > 0.05$). Age did not have significant effects on calving rate of ⅜ Nellore ⅝ Angus produced by ¾ Nellore ¼ Angus sires and Angus dams, or the second generation ⅜ Nellore ⅝ Angus. The F_1 Nellore-Angus had a significantly higher calving rate as 4 yr of age and as mature cows compared to their calving rate at 3 yr of age. As mature cows the first generation ⅜ Nellore ⅝ Angus calving rate was significantly higher than their calving rate as 3- and 4- yr-olds. Angus calving rate as mature cows was significantly higher than their calving rate as 2-yr-old heifers.

To evaluate another parameterization of the effect of cow age, an analysis was done using the actual cow age rather than dividing cows into four age categories. Unadjusted means for calving rate of cow's breedtype within actual cow age are presented in Table 7, and adjusted means are presented in Table 8. The F_1 Nellore-Angus and the first generation ⅜ Nellore ⅝ Angus had high calving rates at 5 yr of age , while Nellore cows had the lowest ($P < 0.001$) calving rate. The second generation ⅜ Nellore ⅝ Angus and the Angus cows were intermediate. At 6 yr of age Nellore cows had 0.65 ± 0.05 calving rate and it was the lowest ($P < 0.001$) among all cow groups, however, no significant differences were detected between the other groups.

At 6-, 7-, and 8-yr of age the means of the ⅜ Nellore ⅝ Angus produced by ¾ Nellore ¼ Angus sires and Angus dams, and the ⅜ Nellore ⅝ Angus produced by ½ Nellore ½ Angus sires and ¾ Angus ¼ Nellore dams did not differ ($P > 0.05$) from any breedtype group; this may be a result of their few numbers. The high calving rates in the older ages may be due to culling of inferior cows at younger ages, but these higher rates are also due to the natural tendency for young cows to be under more nutritional stress because of the nutritional requirements for growth in the young cows.

Estimates of heterosis for calving rate are presented in Table 9. The estimates were based on the analysis done by dividing the data into 4 age categories. All crossbred cows expressed significant heterosis for calving rate, except the ⅜ Nellore ⅝ Angus produced out of ½ Nellore ½ Angus sires and ¾ Angus ¼ Nellore dams. The F_1 Nellore-Angus cows expressed 0.20 ± 0.02 heterosis for calving rate, and it was numerically the largest of all crossbred groups.

Table 7. Unadjusted means, SD, and numbers of records for calving rate by breedtype and actual cow age[1].

	Age (yr)					
Breedtype	**2**	**3**	**4**	**5**	**6**	**7**
A	0.78 (0.42)	0.86 (0.35)	0.85 (0.37)	0.83 (0.38)	0.94 (0.25)	0.92 (0.27)
	51	42	39	36	31	26
N	0.05 (0.21)	0.86 (0.35)	0.72 (0.45)	0.75 (0.44)	0.65 (0.48)	0.90 (0.30)
	50	50	50	48	44	40
F_1 NA	0.94 (0.24)	0.84 (0.37)	0.98 (0.14)	0.98 (0.14)	0.96 (0.21)	0.98 (0.15)
	50	50	50	48	46	46
⅜ N ⅝ A[2]	0.88 (0.35)	0.86 (0.38)	0.67 (0.52)	1.00	0.80 (0.45)	1.00
	8	7	6	5	5	5
⅜ N ⅝ A[3]	0.91 (0.28)	0.87 (0.34)	0.84 (0.37)	0.98 (0.15)	0.93 (0.27)	0.97 (0.19)
	47	47	45	43	40	29
⅜ N ⅝ A[4]	1.00	0.75 (0.46)	0.86 (0.38)	0.86 (0.38)	0.83 (0.41)	1.00
	8	8	7	7	6	5
⅜ N ⅝ A[5]	0.92 (0.27)	0.85 (0.36)	0.83 (0.38)	0.96 (0.19)	0.90 (0.30)	0.97 (0.16)
	63	62	58	55	51	39
⅜ N ⅝ A-2[6]	0.90 (0.30)	0.85 (0.36)	0.90 (0.31)	0.85 (0.36)	0.92 (0.28)	1.00
	52	52	49	47	36	17

[1] A = Angus, N = Nellore,

[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams

[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams

[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.

[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.

[6] Second generation ⅜ Nellore ⅝ Angus cows.

Table 7. Continued

	Age (yr)						
Breedtype	**8**	**9**	**10**	**11**	**12**	**13**	**14**
A	0.96 (0.21)	0.95 (0.22)	0.86 (0.36)	0.88 (0.35)	1.00	1.00	1.00
	23	20	14	8	6	3	2
N	0.79 (0.41)	0.88 (0.34)	0.86 (0.36)	0.86 (0.38)	1.00	0.67 (0.58)	1.00
	30	24	15	7	4	3	1
F_1 NA	0.96 (0.21)	0.91 (0.29)	0.90 (0.30)	1.00	0.94 (0.24)	0.95 (0.22)	1.00
	45	45	41	37	35	20	4
⅜ N ⅝ A[2]	1.00	1.00	1.00	1.00	1.00	-	-
	5	5	3	1	1		
⅜ N ⅝ A[3]	1.00	0.95 (0.22)	0.92 (0.29)	1.00	-	-	-
	24	20	12	2			
⅜ N ⅝ A[4]	1.00	1.00	1.00	0.75 (0.50)	1.00	1.00	1.00
	5	5	5	4	2	1	1
⅜ N ⅝ A[5]	1.00	0.97 (0.18)	0.95 (0.22)	0.86 (0.38)	1.00	1.00	1.00
	34	30	20	7	3	1	1
⅜ N ⅝ A-2[6]	1.00	-	-	-	-	-	-
	4						

Table 8. Least squares means and SE for calving rate by breedtype and actual cow age[1].

	Age ± yr					
Breedtype	**2**	**3**	**4**	**5**	**6**	**7**
A	$0.78 \pm 0.05^{b, z}$	0.85 ± 0.05^{zy}	$0.85 \pm 0.05^{ab, zy}$	$0.81 \pm 0.05^{b, zy}$	$0.91 \pm 0.06^{a, zy}$	0.91 ± 0.06^{zy}
N	$0.03 \pm 0.05^{c, z}$	0.86 ± 0.05^{x}	$0.72 \pm 0.05^{c, y}$	$0.76 \pm 0.05^{b, y}$	$0.65 \pm 0.05^{b, y}$	0.90 ± 0.05^{x}
F_1 NA	$0.94 \pm 0.05^{a, xy}$	0.84 ± 0.05^{y}	$0.97 \pm 0.05^{a, x}$	$0.96 \pm 0.05^{ac, xy}$	$0.93 \pm 0.05^{a, xy}$	0.98 ± 0.05^{x}
⅜ N ⅝ A[2]	0.86 ± 0.12^{ab}	0.83 ± 0.12	0.65 ± 0.13^{bc}	1.01 ± 0.14^{ab}	0.87 ± 0.14^{ab}	0.98 ± 0.14
⅜ N ⅝ A[3]	$0.91 \pm 0.05^{a, xy}$	0.86 ± 0.05^{y}	$0.85 \pm 0.05^{b, y}$	$0.99 \pm 0.05^{a, x}$	$0.95 \pm 0.05^{a, xy}$	0.98 ± 0.06^{xy}
⅜ N ⅝ A[4]	0.98 ± 0.12^{ab}	0.74 ± 0.12	0.86 ± 0.12^{abc}	0.84 ± 0.12^{ab}	0.82 ± 0.12^{ab}	1.02 ± 0.14
⅜ N ⅝ A[5]	$0.92 \pm 0.04^{a, xy}$	0.85 ± 0.04^{y}	$0.83 \pm 0.04^{bc, y}$	$0.97 \pm 0.04^{a, x}$	$0.92 \pm 0.04^{a, xy}$	0.98 ± 0.05^{x}
⅜ N ⅝ A-2[6]	0.94 ± 0.05^{a}	0.86 ± 0.05	0.90 ± 0.05^{ab}	0.84 ± 0.05^{bc}	0.90 ± 0.05^{a}	0.99 ± 0.08

[1] A = Angus, N = Nellore,
[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams
[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams
[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.
[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.
[6] Second generation ⅜ Nellore ⅝ Angus cows.
^{a,b,c} Means within a column that do not share a superscript differ ($P < 0.05$).
^{x,y,z} Means within a row that do not share a superscript differ ($P < 0.05$).

Table 8. Continued

Breedtype	Age (yr)						
	8	9	10	11	12	13	14
A	$0.97 \pm 0.07^{a, xy}$	0.98 ± 0.07^{xy}	0.92 ± 0.08^{zy}	0.86 ± 0.11^{zy}	0.99 ± 0.13^{zy}	0.99 ± 0.18^{zy}	0.99 ± 0.21^{zy}
N	$0.79 \pm 0.06^{b, xy}$	0.88 ± 0.06^{x}	0.85 ± 0.08^{xy}	0.85 ± 0.12^{xy}	0.99 ± 0.15^{xy}	0.66 ± 0.17^{xy}	0.99 ± 0.30^{xy}
F_1 NA	$0.99 \pm 0.05^{a, x}$	0.94 ± 0.05^{xy}	0.91 ± 0.05^{xy}	0.99 ± 0.05^{xy}	0.93 ± 0.05^{xy}	0.94 ± 0.07^{xy}	0.99 ± 0.15^{xy}
⅜ N ⅝ A[2]	1.02 ± 0.14^{ab}	0.98 ± 0.14	1.00 ± 0.18	0.98 ± 0.30	0.99 ± 0.30	-	-
⅜ N ⅝ A[3]	$0.99 \pm 0.06^{a, xy}$	0.94 ± 0.07^{xy}	0.91 ± 0.09^{xy}	0.99 ± 0.21^{xy}	-	-	-
⅜ N ⅝ A[4]	0.99 ± 0.14^{ab}	1.03 ± 0.14	1.02 ± 0.14	0.74 ± 0.15	1.00 ± 0.21	0.98 ± 0.30	0.99 ± 0.30
⅜ N ⅝ A[5]	$0.99 \pm 0.05^{a, x}$	0.96 ± 0.06^{xy}	0.94 ± 0.07^{xy}	0.84 ± 0.12^{xy}	0.99 ± 0.17^{xy}	0.98 ± 0.30^{xy}	0.99 ± 0.30^{xy}
⅜ N ⅝ A-2[6]	0.99 ± 0.20^{ab}	-	-	-	-	-	-

First generation ⅜ Nellore ⅝ Angus expressed 0.11 ± 0.03 heterosis for calving rate and second generation ⅜ Nellore ⅝ Angus expressed 0.13 ± 0.02. Heterosis expressed by the non-F_1 crossbred cows did not differ ($P > 0.05$) from the dominance model expectations.

Additional analyses were performed by dividing the data into subsets by age groups for separate analyses. Fixed effects modeled in these analyses were the same as the effects used in the original model including age, the only difference was by analyzing the data for each age group separately The first data set included records of 2- and 3-yr-olds, the second included records from females that were 4 yr of age and older, and the third set included all records except those of 2-yr-old females. The purpose of these analyses was to determine the ages that were most influential on estimates of heterosis, as it was possible that a very low mean, such as that of the 2-yr-old Nellore was responsible for the large heterosis estimates. Estimates of heterosis from analyses of these data sets are presented in Table 10. All expressed heterosis ($P < 0.001$) in the first data set (2 and 3 yr of age), but the only two groups that expressed heterosis at 4 and older (the second data set) were the F_1 Nellore-Angus and the ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sire and ½ Nellore ½ Angus dam. The third group (excluding records of 2-yr-olds) shows that the only breedtype that expressed heterosis was the F_1 Nellore-Angus ($P < 0.001$). From these results we can conclude that the very low calving rate mean of the Nellore cows at 2 yr of age resulted in lowering the average of the purebreds, and resulted in high levels of heterosis.

The first generation ⅜ Nellore ⅝ Angus was produced in three different ways as presented in Table 1. A subsequent analysis was conducted to evaluate the effect of those ways this crossbred was produced on the heterosis expressed for calving rate. For this purpose, data were analyzed using only the records from the ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams, which represent the majority of the first generation ⅜ Nellore ⅝ Angus cows (n = 47). The heterosis estimate for calving rate from this analysis in the first generation ⅜ Nellore ⅝ Angus was 0.14 ± 0.03 (Table 11), which was similar to that expressed when all data were included in the analysis. The type of mating used to produce first generation ⅜ Nellore ⅝ Angus cows did not appear to substantially influence estimates of heterosis for calving rate.

Table 9. Estimates of heterosis for calving rate and SE by breedtype.

Breedtype	**N**	**Heterosis**
F_1 ½ Nellore ½ Angus	50	0.20 ± 0.02***
First generation ⅜ Nellore ⅝ Angus		
½ Nellore ½ Angus sires × ¾ Angus ¼ Nellore dams	8	0.07 ± 0.05
¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams	47	0.14 ± 0.03***
¾ Nellore ¼ Angus sires × Angus dams	8	0.12 ± 0.05*
All first generation ⅜ Nellore ⅝ Angus females	63	0.11 ± 0.03**
Second generation ⅜ Nellore ⅝ Angus	52	0.13 ± 0.03***
Observed heterosis vs Dominance model expectations		
½ Nellore ½ Angus sires × ¾ Angus ¼ Nellore dams	8	− 0.03 ± 0.05
¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams	47	0.04 ± 0.03
¾ Nellore ¼ Angus sires × Angus dams	8	− 0.03 ± 0.05
All first generation ⅜ Nellore ⅝ Angus females	63	0.003 ± 0.03
Second generation ⅜ Nellore ⅝ Angus	52	0.04 ± 0.03

*** $P < 0.001$
** $P < 0.01$
* $P < 0.05$

Table 10. Estimates of heterosis for calving rate and SE by in data sets of different groupings of records by age of cow[1]

	Data grouping[7]		
Breedtype	**1**	**2**	**3**
F_1 NA	0.26 ± 0.04***	0.14 ± 0.03***	0.09 ± 0.06**
⅜ N ⅝ A[2]	0.19 ± 0.09***	−0.02 ± 0.07	− 0.03 ± 0.03
⅜ N ⅝ A[3]	0.21 ± 0.04***	0.07 ± 0.03*	0.04 ± 0.03
⅜ N ⅝ A[4]	0.19 ± 0.09***	0.06 ± 0.06	0.01 ± 0.06
⅜ N ⅝ A[5]	0.19 ± 0.05***	0.04 ± 0.04	0.01 ± 0.03
⅜ N ⅝ A-2[6]	0.19 ± 0.05***	0.06 ± 0.03	0.04 ± 0.03

[1] A = Angus, N = Nellore,
[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams
[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams
[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams
[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.
[6] Second generation ⅜ Nellore ⅝ Angus cows
[7] Data groupings: **1** had records from 2- and 3-yr-old females; **2** had records of females age 4 and older; and **3** had records of all females except 2-yr-olds.
*** $P < 0.001$
** $P < 0.01$
* $P < 0.05$

Table 11. Estimates of heterosis for calving rate and SE produced from analyses in which first generation records were limited to those cows produced by ¾ A ¼ N sires and ½ A ½ N dams.

Breedtype	Heterosis
F_1 ½ Nellore ½ Angus	$0.20 \pm 0.02^{***}$
¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams	$0.14 \pm 0.03^{***}$
Second generation ⅜ Nellore ⅝ Angus	$0.14 \pm 0.03^{***}$

*** $P < 0.001$

Weaning Rate

The final model for weaning rate contained sire breed of the cow, dam breed of the cow, cow age, and the three-way interaction of these ($P < 0.05$). Unadjusted means and SD for weaning rate of cow's breedtype within age categories are presented in Table 12, and the corresponding adjusted means are presented in Table 13. As was the case for calving rate, Nellore cows had the lowest ($P < 0.05$) weaning rate at 2 yr of age (0.03 ± 0.06), which is a result of their relatively late age at sexual maturity. The F_1 Nellore-Angus cows had 0.83 ± 0.06 weaning rate at 2 yr of age which was greater than Angus weaning rate ($P < 0.05$). Unlike calving rate, weaning rate for all breedtypes improved at 3 yr of age, and there were no differences ($P > 0.05$) among breedtypes. Again, the greatest improvement was the Nellore weaning rate (0.77 ± 0.06). Weaning rate means for the Nellore in age categories 4 and 5 yr or older were significantly lower than all breed groups except the two small (n = 8 cows each) first generation ⅜ Nellore ⅝ Angus groups (¾ Nellore ¼ Angus sires × Angus dams and the ½ Nellore ½ Angus sires × ¾ Angus ¼ Nellore dams). Age category means did not significantly differ for F_1 Nellore-Angus, two of the three first generation ⅜ Nellore ⅝ Angus (produced by ¾ Nellore ¼ Angus sires and Angus dams, or by ½ Nellore ½ Angus sires and ¾ Angus ¼ Nellore dams), and the second generation ⅜ Nellore ⅝ Angus. Weaning rate means for the other breedtypes were lowest when they were heifers and different ($P < 0.001$) from the age 5 or older category means. With the exception of Nellore, as 3- and 4- yr-olds the weaning rate means for these breedtypes did not differ ($P > 0.05$) from either their heifer weaning rate means or age 5 or older category. The pattern of means for Nellore was oscillatory

(Koger, 1963; Crockett et al., 1968; Riley et al., 2005) and means in a given category appeared to depend on the lactation status of the majority of cows in the previous age category.

Unadjusted means for weaning rate of cow's breedtype within actual cow age are presented in Table 14, and adjusted means are presented in Table 15. Modeling cow age as actual ages in years permitted evaluation of those ages greater than 5 (means for 2-, 3-, and 4-yr-old cows were similar to those results from modeling cow ages greater than 5 in a single category). All breedtypes had cows with records through age 8. In those ages, Nellore cows had significantly lower weaning rate means than the other groups, except for the first generation ⅜ Nellore ⅝ Angus cows produced by ¾ Nellore ¼ Angus sires and Angus dams as 5-, and 6-yr-olds Differences at older ages were minimal; this may be due to the removal of cows by culling procedures leaving superior cows, and most likely, the smaller number of cows with records and consequently, the larger SE of those means at older ages. The lack of differences at these older ages is not surprising, because the cows were past the stressful years as 2 and 3-yr-olds.

Table 12. Unadjusted means (SD) and number of records for weaning rate by breedtype and age group[1]

	Age Category[7]			
Breedtype	**2**	**3**	**4**	**≥ 5**
A	0.57 (0.50)	0.81 (0.40)	0.79 (0.41)	0.85 (0.36)
	51	42	39	169
N	0.02 (0.15)	0.76(0.43)	0.42 (0.50)	0.72 (0.45)
	44	50	50	213
F_1 NA	0.82 (0.39)	0.80 (0.40)	0.84 (0.37)	0.90 (0.30)
	50	50	50	367
⅜ N ⅝ A[2]	0.50 (0.53)	0.71 (0.49)	0.67 (0.52)	0.83 (0.38)
	8	7	6	30
⅜ N ⅝ A[3]	0.68 (0.47)	0.83 (0.38)	0.80 (0.40)	0.88 (0.32)
	47	47	45	170
⅜ N ⅝ A[4]	0.75 (0.46)	0.75 (0.46)	0.57 (0.53)	0.76 (0.43)
	8	8	7	41
⅜ N ⅝ A[5]	0.67 (0.48)	0.81 (0.40)	0.76 (0.43)	0.85 (0.35)
	63	62	58	241
⅜ N ⅝ A-2[6]	0.73 (0.45)	0.77 (0.43)	0.84 (0.37)	0.89 (0.31)
	52	52	49	104

[1] A = Angus, N = Nellore,

[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams

[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams

[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.

[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.

[6] Second generation ⅜ Nellore ⅝ Angus cows.

[7] Age category 2 = 2 yr-old-cows, 3 = 3 yr-old-cows, 4 = 4 yr-old-cows, ≥ 5 = cows 5 yr of age and older.

Table 13. Least squares means and SE for weaning rate by breedtype and age category[1]

	Age Category[7]			
Breedtype	**2**	**3**	**4**	**≥ 5**
A	0.57 ± 0.06[b, y]	0.81 ± 0.06[x]	0.83 ± 0.06[a, x]	0.84 ± 0.04[ab, x]
N	0.03 ± 0.06[c, z]	0.77 ± 0.06[x]	0.43 ± 0.06[b, y]	0.71 ± 0.03[c, x]
F_1 NA	0.83 ± 0.06[a]	0.81 ± 0.06	0.87 ± 0.06[a]	0.90 ± 0.03[a]
⅜ N ⅝ A[2]	0.55 ± 0.14[ab]	0.71 ± 0.15	0.65 ± 0.16[ab]	0.81 ± 0.07[abc]
⅜ N ⅝ A[3]	0.70 ± 0.06[a, y]	0.84 ± 0.06[xy]	0.79 ± 0.06[a, xy]	0.87 ± 0.04[a, x]
⅜ N ⅝ A[4]	0.72 ± 0.14[ab]	0.78 ± 0.14	0.59 ± 0.14[ab]	0.74 ± 0.07[bc]
⅜ N ⅝ A[5]	0.69 ± 0.05[ab, y]	0.82 ± 0.05[xy]	0.75 ± 0.05[a, xy]	0.84 ± 0.03[a, x]
⅜ N ⅝ A-2[6]	0.75 ± 0.04[a]	0.77 ± 0.04	0.83 ± 0.05[a]	0.86 ± 0.03[a]

[1] A = Angus, N = Nellore,
[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams
[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams
[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.
[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.
[6] Second generation ⅜ Nellore ⅝ Angus cows.
[7] Age category 2 = 2 yr-old-cows, 3 = 3 yr-old-cows, 4 = 4 yr-old-cows,
≥ 5 = cows 5 yr of age and older.
[a,b,c] Means within a column that do not share a superscript differ ($P < 0.05$).
[x,y,z] Means within a row that do not share a superscript differ ($P < 0.05$).

Table 14. Unadjusted means, SD, and numbers of records for weaning rate by breedtype and actual cow age[1]

	Age (yr)					
Breedtype	**2**	**3**	**4**	**5**	**6**	**7**
A	0.57 (0.50)	0.81 (0.40)	0.79 (0.41)	0.81 (0.40)	0.87 (0.34)	0.85 (0.37)
	51	42	39	36	31	26
N	0.02 (0.15)	0.76 (0.43)	0.42 (0.50)	0.61 (0.49)	0.60 (0.49)	0.80 (0.41)
	44	50	50	48	44	40
F_1 NA	0.82 (0.39)	0.80 (0.40)	0.84 (0.37)	0.88 (0.33)	0.89 (0.31)	0.93 (0.25)
	50	50	50	48	46	46
⅜ N ⅝ A[2]	0.50 (0.53)	0.71 (0.49)	0.67 (0.52)	1.00 (0.00)	0.80 (0.45)	1.00
	8	7	6	5	5	5
⅜ N ⅝ A[3]	0.68 (0.47)	0.83 (0.38)	0.80 (0.40)	0.88 (0.32)	0.85 (0.36)	0.93 (0.26)
	47	47	45	43	40	29
⅜ N ⅝ A[4]	0.75 (0.46)	0.75 (0.46)	0.57 (0.53)	0.57 (0.53)	0.50 (0.55)	1.00
	8	8	7	7	6	5
⅜ N ⅝ A[5]	0.67 (0.43)	0.81 (0.40)	0.76 (0.43)	0.85 (0.36)	0.80 (0.40)	0.95 (0.22)
	63	62	58	55	51	39
⅜ N ⅝ A-2[6]	0.73 (0.45)	0.77 (0.43)	0.84 (0.37)	0.83 (0.38)	0.92 (0.28)	1.00
	52	52	49	47	36	17

[1] A = Angus, N = Nellore,

[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams

[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams

[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.

[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.

[6] Second generation ⅜ Nellore ⅝ Angus cows.

Table 14. Continued

Breedtype	Age (yr) 8	9	10	11	12	13	14
A	0.83 (0.39)	0.90 (0.31)	0.79 (0.43)	0.88 (0.35)	0.83 (0.41)	1.00	1.00
	23	20	14	8	6	3	2
N	0.73 (0.45)	0.88 (0.33)	0.80 (0.41)	0.86 (0.38)	1.00 (0.00)	0.67 (0.58)	1.00
	30	24	15	7	4	3	1
F_1 NA	0.91 (0.29)	0.89 (0.32)	0.88 (0.33)	0.92 (0.28)	0.91 (0.28)	0.90 (0.31)	1.00
	45	45	41	37	35	20	4
⅜ N ⅝ A[2]	1.00	0.20 (0.45)	1.00	1.00	1.00	-	-
	5	5	3	1	1		
⅜ N ⅝ A[3]	0.88 (0.34)	0.90 (0.31)	0.83 (0.39)	1.00	-	-	-
	24	20	12	2			
⅜ N ⅝ A[4]	1.00	1.00	1.00	0.25 (0.50)	0.50 (0.71)	1.00	1.00
	5	5	5	4	2	1	1
⅜ N ⅝ A[5]	0.91 (0.29)	0.80 (0.41)	0.90 (0.31)	0.57 (0.53)	0.67 (0.58)	1.00	1.00
	34	30	20	7	3	1	1
⅜ N ⅝ A-2[6]	1.00	-	-	-	-	-	-
	4						

Table 15. Least squares means and SE for weaning rate by breedtype and actual cow age[1].

	Age ± yr					
Breedtype	**2**	**3**	**4**	**5**	**6**	**7**
A	$0.57 \pm 0.06^{b, y}$	0.81 ± 0.06^{x}	$0.83 \pm 0.06^{a, x}$	$0.80 \pm 0.07^{a, x}$	$0.88 \pm 0.07^{a, x}$	$0.83 \pm 0.08^{ab, x}$
N	$0.03 \pm 0.06^{c, z}$	0.76 ± 0.06^{x}	$0.43 \pm 0.06^{b, y}$	$0.62 \pm 0.06^{b, x}$	$0.60 \pm 0.06^{b, x}$	$0.78 \pm 0.06^{b, x}$
F_1 NA	0.83 ± 0.06^{a}	0.81 ± 0.06	0.86 ± 0.06^{a}	0.89 ± 0.06^{a}	0.89 ± 0.06^{a}	0.92 ± 0.06^{a}
⅜ N ⅝ A[2]	$0.54 \pm 0.14^{ab, yz}$	0.71 ± 0.14	$0.65 \pm 0.16^{ab, xy}$	$1.00 \pm 0.17^{a, x}$	$0.84 \pm 0.17^{a, x}$	$0.97 \pm 0.17^{ab, x}$
⅜ N ⅝ A[3]	$0.69 \pm 0.06^{a, y}$	0.84 ± 0.06^{xy}	$0.80 \pm 0.06^{a, xy}$	$0.89 \pm 0.06^{a, x}$	$0.85 \pm 0.06^{a, xy}$	$0.93 \pm 0.07^{a, x}$
⅜ N ⅝ A[4]	$0.72 \pm 0.14^{ab, x}$	0.77 ± 0.14^{x}	$0.59 \pm 0.14^{ab, x}$	$0.56 \pm 0.14^{b, x}$	$0.51 \pm 0.16^{b, x}$	$1.00 \pm 0.17^{ab, x}$
⅜ N ⅝ A[5]	$0.68 \pm 0.05^{ab, yz}$	0.82 ± 0.05^{xy}	$0.75 \pm 0.05^{a, y}$	$0.85 \pm 0.05^{a, xy}$	$0.81 \pm 0.06^{a, xy}$	$0.94 \pm 0.06^{a, x}$
⅜ N ⅝ A-2[6]	0.75 ± 0.06^{a}	0.78 ± 0.06	0.83 ± 0.06^{a}	0.81 ± 0.06^{a}	0.89 ± 0.07^{a}	0.97 ± 0.10^{a}

[1] A = Angus, N = Nellore,
[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams
[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams
[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams.
[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.
[6] Second generation ⅜ Nellore ⅝ Angus cows.
[a,b,c] Means within a column that do not share a superscript differ ($P < 0.05$).
[x,y,z] Means within a row that do not share a superscript differ ($P < 0.05$).

Table 15. Continued

Breedtype	Age (yr) 8	9	10	11	12	13	14
A	$0.82 \pm 0.08^{a, x}$	$0.90 \pm 0.09^{a, x}$	0.81 ± 0.10^{x}	$0.84 \pm 0.14^{ab, x}$	0.81 ± 0.16^{x}	0.96 ± 0.22^{x}	0.94 ± 0.27^{x}
N	$0.72 \pm 0.07^{b, x}$	$0.86 \pm 0.08^{a, x}$	0.77 ± 0.10^{x}	$0.83 \pm 0.14^{ab, x}$	0.98 ± 0.19^{x}	0.63 ± 0.22^{y}	0.94 ± 0.38^{y}
F_1 NA	0.93 ± 0.06^{a}	0.90 ± 0.06^{a}	0.87 ± 0.06	0.90 ± 0.07^{a}	0.89 ± 0.07	0.86 ± 0.09	0.96 ± 0.19
⅜ N ⅝ A[2]	$1.00 \pm 0.17^{a, x}$	$0.18 \pm 0.17^{b, z}$	0.97 ± 0.22^{xy}	$0.96 \pm 0.38^{ab, xy}$	0.94 ± 0.38^{xy}	-	-
⅜ N ⅝ A[3]	$0.85 \pm 0.08^{a, xy}$	0.87 ± 0.09^{a}	0.80 ± 0.11	0.95 ± 0.27^{ab}	-	-	-
⅜ N ⅝ A[4]	$0.97 \pm 0.17^{a, x}$	$1.00 \pm 0.17^{a, x}$	1.00 ± 0.17^{x}	$0.23 \pm 0.19^{c, y}$	0.48 ± 0.27^{xy}	0.96 ± 0.38^{xy}	0.94 ± 0.38^{xy}
⅜ N ⅝ A[5]	$0.89 \pm 0.07^{a, xy}$	$0.77 \pm 0.07^{a, yz}$	0.87 ± 0.09^{xy}	$0.53 \pm 0.15^{bc, z}$	0.63 ± 0.22^{xyz}	0.97 ± 0.38^{xy}	0.93 ± 0.38^{xy}
⅜ N ⅝ A-2[6]	0.96 ± 0.19^{a}	-	-	-	-	-	-

Estimates of heterosis for weaning rate are presented in Table 16. The estimates were based on the analysis performed by dividing the data into 4 age categories. All crossbred cow groups expressed significant heterosis for weaning rate, except the ⅜ Nellore ⅝ Angus produced out of ½ Nellore ½ Angus sires and ¾ Angus ¼ Nellore dams, the ⅜ Nellore ⅝ Angus produced out of ¾ Nellore ¼ Angus sires × Angus dams, and as a consequence to that the first generation ⅜ Nellore ⅝ Angus were not found to express significant heterosis for weaning rate. The F_1 Nellore-Angus expressed 0.23 ± 0.03 heterosis for weaning rate, and it was numerically the largest among the crossbred groups. The ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams and the second generation ⅜ Nellore ⅝ Angus expressed 0.14 ± 0.07 and 0.15 ± 0.05 heterosis for weaning rate, respectively. Heterosis expressed by the non-F_1 crossbred cows did not differ ($P > 0.05$) from the dominance model expectations.

As was done for calving rate, additional analyses were done by dividing the data into subsets by age groups for separate analyses. Fixed effects modeled in these analyses were the same as the effects used in the original model including age. The first data grouping included records of 2- and 3-yr-olds, the second included records from females that were 4 yr of age and older, and the third set included all records except those of 2-yr-old females. Estimates of heterosis from analyses of these data sets are presented in Table 17. All crossbred groups expressed heterosis ($P < 0.001$) in the first data set (2 and 3 yr of age) except for the two small first generation ⅜ Nellore ⅝ Angus groups (produced by ½ Nellore ½ Angus sires × ¾ Angus ¼ Nellore dams, and by ¾ Nellore ¼ Angus sires × Angus dams). Only three groups expressed heterosis at ages 4 and older (the second data set): F_1 Nellore-Angus, the first generation ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams (the largest of the three first generation groups; n = 47), and the second generation ⅜ Nellore ⅝ Angus. Only two breedtypes expressed heterosis in the third group (excluding records of 2-yr-olds): the F_1 Nellore-Angus and the first generation ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams ($P < 0.001$). As was the case for calving rate, the records of 2-yr-old cows appeared to be responsible for heterosis. The very low mean for Nellore (a consequence of late maturity, not reproductive failure) resulted in lowering the average of the purebreds, and therefore high levels of heterosis.

Data were analyzed using only the records from the ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams, which represent the majority of the first generation ⅜ Nellore ⅝ Angus cows (n = 47). The estimate of heterosis for calving rate from this analysis in the first generation ⅜ Nellore ⅝ Angus was 0.14 ± 0.03 (Table 18). The result from this analysis differed from that for calving rate in that the only breedtype of the three first generation ⅜ Nellore ⅝ Angus cows that had a significant heterosis estimate for weaning rate was the ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams (Table 16). Although the heterosis for first generation ⅜ Nellore ⅝ Angus cows (Table 18) did not differ substantially from that when all three different mating systems were included (Table 16), the non-significant heterosis for the two other mating systems seems to negatively affect the estimate of overall heterosis.

Table 16. Estimates of heterosis and SE for weaning rate by breedtype.

Breedtype	N	Heterosis
F_1 ½ Nellore ½ Angus	50	$0.23 \pm 0.03^{***}$
First generation ⅜ Nellore ⅝ Angus		
½ Nellore ½ Angus sires × ¾ Angus ¼ Nellore dams	8	0.02 ± 0.04
¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams	47	$0.14 \pm 0.07^{***}$
¾ Nellore ¼ Angus sires × Angus dams	8	0.05 ± 0.07
All first generation ⅜ Nellore ⅝ Angus females	63	0.11 ± 0.04
Second generation ⅜ Nellore ⅝ Angus	52	$0.15 \pm 0.05^{***}$
Observed heterosis vs Dominance model expectations		
½ Nellore ½ Angus sires × ¾ Angus ¼ Nellore dams	8	-0.09 ± 0.08
¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams	47	0.02 ± 0.04
¾ Nellore ¼ Angus sires × Angus dams	8	-0.15 ± 0.07
All first generation ⅜ Nellore ⅝ Angus females	63	-0.07 ± 0.03
Second generation ⅜ Nellore ⅝ Angus	52	0.01 ± 0.04

*** $P < 0.001$

Table 17. Estimates of heterosis for weaning rate and SE by in data sets of different groupings of records by age of cow[1].

	Data grouping[7]		
Breedtype	**1**	**2**	**3**
F_1 NA	$0.28 \pm 0.05^{***}$	$0.18 \pm 0.04^{***}$	$0.13 \pm 0.03^{**}$
⅜ N ⅝ A[2]	0.06 ± 0.11	0.01 ± 0.09	-0.03 ± 0.08
⅜ N ⅝ A[3]	$0.18 \pm 0.06^{**}$	$0.11 \pm 0.04^{**}$	$0.08 \pm 0.04^{*}$
⅜ N ⅝ A[4]	0.17 ± 0.11	-0.07 ± 0.08	-0.05 ± 0.07
⅜ N ⅝ A[5]	$0.14 \pm 0.06^{*}$	0.05 ± 0.04	0.03 ± 0.04
⅜ N ⅝ A-2[6]	$0.17 \pm 0.06^{**}$	$0.12 \pm 0.04^{**}$	0.07 ± 0.04

[1] A = Angus, N = Nellore,

[2] ⅜ N ⅝ A produced by ½ N ½ A sires and ¾ A ¼ N dams

[3] ⅜ N ⅝ A produced by ¾ A ¼ N sires and ½ A ½ N dams

[4] ⅜ N ⅝ A produced by ¾ N ¼ A sires and A dams

[5] ⅜ N ⅝ A all first generation ⅜ Nellore ⅝ Angus cows.

[6] Second generation ⅜ Nellore ⅝ Angus cows

[7] Data groupings: **1** had records from 2- and 3-yr-old females; **2** had records of females age 4 and older; and **3** had records of all females except 2-yr-olds.

*** $P < 0.001$

** $P < 0.01$

* $P < 0.05$

Table 18. Estimates of heterosis and SE for weaning rate produced from analyses in which first generation records were limited to those cows produced by ¾ Angus ¼ Nellore sires and ½ Angus ½ Nellore dams.

Breedtype	Heterosis
F_1 ½ Nellore ½ Angus	$0.23 \pm 0.03^{***}$
¾ Angus ¼ Nellore sires × ½ Nellore ½ Angus dams	$0.14 \pm 0.03^{**}$
Second generation ⅜ Nellore ⅝ Angus	$0.15 \pm 0.04^{**}$

*** $P < 0.001$

Birth Weight

Birth weight was analyzed using a final model that contained breedtype of the cow, cow age (divided into four age categories: 2 yr, 3 yr, 4 yr, and 5 yr and older cows), sire of the calf breed, and calf sex, and the three-way interaction of breedtype of the cow, sire of the calf breed, and calf sex ($P < 0.05$). Age had a significant effect on birth weight; among all breedtypes heifers produced the lightest ($P < 0.001$) calves compared to calves produced by older cows. Unadjusted means for calf birth weight, SD, and number of records by cow breedtype and sire of the calf breed are presented in Tables 19 and 20, and the corresponding adjusted means are presented in Tables 21 and 22. Means were grouped by sire breed of calf: Angus, Nellore, and Charolais in Tables 19 and 21 and ¾ Angus ¼ Nellore, ⅜ Nellore ⅝ Angus, and F_1 sires in Tables 20 and 22. Large reciprocal differences were found in F_1 calves produced out of Nellore and Angus breeds (Table 21), and these were consistent with earlier work in Brahman-*Bos taurus* crossbred calves (Cartwright et al., 1964; Roberson et al., 1986; Riley et al., 2007). Nellore-sired calves born to Angus cows were significantly heavier at birth than Angus-sired calves born to Nellore cows. In addition, among the Nellore-sired crossbred calves, bull calves were much heavier than heifer calves, but the sex difference ($P < 0.05$) in the reciprocal cross was of smaller magnitude, and the heifer calves were numerically heavier than the bull calves, which has often been reported in *Bos indicus* sired F1 calves out of *Bos taurus* females (Roberson et al., 1986; Riley et al., 2007) Others reported no significant difference between birth weights of males and females born to Brahman dams and sired by *Bos taurus* bulls (Roberson et al., 1986; Riley et al., 2007).

There were other notable differences between cow breedtype-sire breed of calf-sex combinations (Tables 21 and 22). Bulls were heavier ($P < 0.05$) for all cow breedtype-sire breed combinations except for calves born to these cows: Nellore, F_1, and second generation ⅜ Nellore ⅝ Angus cows bred to Angus; F_1 and first generation ⅜ Nellore ⅝ Angus cows bred to Charolais; a small group of second generation ⅜ Nellore ⅝ Angus cows bred to ⅜ Nellore ⅝ Angus bulls; and another small group of first generation ⅜ Nellore ⅝ Angus cows bred to F_1 bulls. This result (absence of sex difference in birth weight) in general was not consistent with almost all sex differences reported in literature (except for F_1 calves sired by *Bos taurus*, and out of *Bos indicus*, primarily Brahman, cows); however, in most cases bull calves had numerically larger means. Angus-sired bull calves born to Nellore cows were lighter ($P < 0.05$) at birth than Angus-sired bull calves born to cows in all other breed groups (Table 21). Angus-sired heifer calves born to Nellore cows were lighter ($P < 0.05$) at birth than Angus-sired heifers born to second generation ⅜ Nellore ⅝ Angus cows. Charolais-sired bull calves born to second generation ⅜ Nellore ⅝ Angus cows were heavier at birth than those born to first generation ⅜ Nellore ⅝ Angus cows; however, Charolais-sired heifers born to F_1 Nellore-Angus, first and second generations ⅜ Nellore ⅝ Angus did not differ ($P > 0.05$).

No breedtype expressed significant maternal heterosis for birth weight (Table 23). This result is in agreement with the result found by (Gaines et al., 1966; Spelbring et al., 1977a; McElhenney et al., 1986) when they reported that maternal heterosis for birth weight is either zero or very little.

Table 19. Unadjusted means for calf birth weight (SD) and number of records by breedtype for calves sired by Angus, Nellore, and Charolais

	Sire breed					
	Angus		Nellore		Charolais	
Breedtype	M	F	M	F	M	F
Angus	36.4 (5.70) 122	34.2 (5.20) 124	48.8 (6.90) 8	41.1 (5.40) 5	-	-
Nellore	31.8 (4.80) 76	32.5 (3.80) 59	33.5 (4.80) 58	28.4 (4.90) 56	-	-
F_1 Nellore-Angus	36.8 (5.01) 27	36.0 (3.70) 26	-	-	40.0 (4.40) 19	37.8 (4.90) 22
⅜ Nellore ⅝ Angus	35.1 (6.70) 53	33.1 (4.90) 64	-	-	37.4 (4.80) 63	36.9 (4.60) 77
⅜ Nellore ⅝ Angus[1]	35.6 (4.00) 47	33.8 (5.91) 47	-	-	39.0 (4.80) 66	36.0 (4.50) 59

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 20. Unadjusted means for calf birth weight (SD) and number of records by breedtype for calves sired by crossbred bulls

	Sire breed					
	¾ Angus ¼ Nellore		⅜ Nellore ⅝ Angus		F_1 Nellore-Angus	
Breedtype	M	F	M	F	M	F
Angus	-	-	-	-	-	-
Nellore	-	-	-	-	-	-
F_1 Nellore-Angus	35.0 (7.00) 124	32.2 (5.30) 128	-	-	34.4 (5.80) 79	32.5 (4.70) 62
⅜ Nellore ⅝ Angus	-	-	36.0 (6.30) 68	34.1 (4.70) 53	31.0 (6.60) 3	36.0 (3.70) 7
⅜ Nellore ⅝ Angus[1]	-	-	37.7 (3.10) 4	37.3 (0.91) 3	-	-

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 21. Least squares means for calf birth weight and SE by breedtype for calves sired by Angus, Nellore, an Charolais[1]

	Sire breed					
	Angus		Nellore		Charolais	
Breedtype	M	F	M	F	M	F
Angus	36.0 ± 0.76$^{a, y}$	33.1 ± 0.75$^{ab, z}$	46.6 ± 2.0$^{a, x}$	40.0 ± 2.4$^{a, y}$	-	-
Nellore	31.0 ± 0.85$^{b, x}$	31.4 ± 0.90$^{b, x}$	32.0 ± 0.90$^{b, x}$	26.6 ± 0.90$^{b, y}$	-	-
F_1 Nellore-Angus	36.0 ± 1.14$^{a, x}$	33.8 ± 1.20$^{ab, xy}$	-	-	36.1 ± 1.30$^{ab, x}$	34.4 ± 1.20^{x}
⅜ Nellore ⅝ Angus	35.0 ± 0.90$^{a, xy}$	32.6 ± 0.90$^{b, zw}$	-	-	36.3 ± 0.91$^{b, x}$	36.6 ± 0.90^{x}
⅜ Nellore ⅝ Angus[2]	36.5 ± 0.97$^{a, y}$	34.5 ± 0.97$^{a, y}$	-	-	39.0 ± 0.90$^{a, x}$	35.7 ± 0.92^{y}

[1]Means in this table and Table 22 were produced in the same analyses, but are presented separately to enhance clarity.

[2] Second generation ⅜ Nellore ⅝ Angus cows.

^{a,b,c} Means within a column that do not share a superscript differ ($P < 0.05$).

^{w,x,y,z} Means within a row in this table and in the corresponding row in Table 22 that do not share a superscript differ ($P < 0.05$).

Table 22. Least squares means for calf birth weight and SE by breedtype for calves sired by crossbred bulls

	Sire breed					
	¾ Angus ¼ Nellore		⅜ Nellore ⅝ Angus		F_1 Nellore-Angus	
Breedtype	M	F	M	F	M	F
Angus	-	-	-	-	-	-
Nellore	-	-	-	-	-	-
F_1 Nellore-Angus	34.0 ± 0.76^{x}	30.8 ± 0.75^{z}	-	-	34.0 ± 0.87^{x}	$31.4 \pm 0.90^{b,\ yz}$
⅜ Nellore ⅝ Angus	-	-	34.1 ± 0.85^{yw}	32.1 ± 0.90^{z}	33.0 ± 2.90^{yz}	$37.5 \pm 2.00^{a,\ xy}$
⅜ Nellore ⅝ Angus[2]	-	-	37.6 ± 2.60^{xy}	34.8 ± 2.90^{xy}	-	-

[1]Means in this table and Table 21 were produced in the same analyses, but are presented separately to enhance clarity.

[2] Second generation ⅜ Nellore ⅝ Angus cows.

[a,b,c] Means within a column that do not share a superscript differ ($P < 0.05$).

[w,x,y,z] Means within a row in this table and in the corresponding row in Table 22 that do not share a superscript differ ($P < 0.05$).

Table 23. Estimates of maternal heterosis for birth weight and SE by breedtype

Breedtype	Heterosis
F_1 ½ Nellore ½ Angus	− 0.72 ± 0.57
First generation ⅜ Nellore ⅝ Angus	− 0.86 ± 0.73
Second generation ⅜ Nellore ⅝ Angus	0.82 ± 0.93

Weaning Weight

Multiple model parameterizations of fixed effect combinations were attempted. All models produced some least squares means for certain cow breedtype-sire breed of calf-calf sex combinations that were excessively adjusted. This may be due to several characteristics of these data. Sire breed of calf was in part confounded with age or age categories. Two combinations of these effects (first generation ⅜ Nellore ⅝ Angus cows bred to F_1 bulls and second generation ⅜ Nellore ⅝ Angus cows bred to first generation ⅜ Nellore ⅝ Angus bulls) had very few numbers of records and low weaning weight means. The linear regression on weaning age in days appeared to be responsible in many cases for excessive adjustment; particularly the mean weaning age of straightbred Nellore calves (198.6 ± 22.5 days) was much lower than that of other groups (216.3 ± 25.0 days). Other analyses of subsets of these data were conducted with similar undesirable results. As a result of the above it was concluded that more could be learned from examination of unadjusted means for this trait.

Unadjusted means for calf weaning weight, SD and number of records by cow breedtype and cow age are presented in Table 24. In general, young cows and the oldest cows weaned lighter calves than others. Not surprisingly, F_1 Nellore-Angus cows weaned heavier calves than the straightbred cows and for most ages of the first and second generation ⅜ Nellore ⅝ Angus cows. It is noteworthy that at several ages, those cows, especially first generation, weaned calves that were as heavy as those of the outstanding F_1 cows. Older cows are expected to wean heavier calves than younger cows; in these data, this effect probably is augmented because mature cows in the crossbred groups were mated to Charolais sires that would contribute large direct effect for weaning weight.

Unadjusted means for calf weaning weight, SD, and number of records by cow breedtype and sire of the calf breed are presented in Tables 25 and 26. As for birth weight, means were grouped by sire breed of calf: Angus, Nellore, and Charolais in Table 25 and ¾ Angus ¼ Nellore, ⅜ Nellore ⅝ Angus, and F_1 sires in Table 26. As was the case for birth weight, there appeared to be no sex difference in the means for F_1 calves out of Nellore cows and sired by Angus bulls (Table 25). Nellore-sired calves out of Angus cows were heavier than the reciprocal cross, but perhaps not as large a difference as might have been expected to be consistent with the birth weights; however, in some cases (e.g., Roberson et al., 1986), *Bos indicus* sired F1 calves out of *Bos taurus* cows have been reported to be heavier than the reciprocal cross at birth, but lighter at weaning. This difference in rank in birth weight and weaning weight between reciprocal

F_1s has generally been interpreted as differences in the milk production of the two particular breeds. Among the Nellore-sired F_1 calves, bulls were heavier than heifers, but again, of a magnitude much lower than the birth weight sex difference for these groups. Among the other groups (with substantial numbers of records), the small (or no) sex difference seemed unusual in calves from first generation ⅜ Nellore ⅝ Angus cows bred to Charolais bulls and the second generation ⅜ Nellore ⅝ Angus cows bred to Angus bulls. However, lack of sex differences, and even heavier weights in females than males, in calves where there is more *Bos indicus* in the dam than in the sire, are an interesting result that has previously been reported (e.g., Roberson et al., 1986). The extremely heavy Charolais-sired calves out of F_1 cows (Table 25) would be consistent with the large combination of direct effects and direct and maternal heterosis expected to be expressed by a terminal 3-breed cross for a trait such as weaning weight (Gregory and Cundiff, 1980).

Table 24. Unadjusted means (SD) for calf weaning weight by breedtype and cow age

	Age					
Breedtype	2	3	4	5	6	7
Angus	172 (26.0)	183 (33.0)	214 (35.0)	233 (29.0)	236 (29.0)	216 (27.0)
	29	34	31	29	27	22
Nellore	177	185 (29.0)	190 (36.0)	196 (34.0)	210 (34.0)	210 (33.0)
	1	37	21	28	26	32
F_1 Nellore-Angus	214 (25.0)	233 (27.0)	247 (25.0)	240 (28.0)	257 (36.0)	257 (23.0)
	41	40	42	42	41	43
⅜ Nellore ⅝ Angus	207 (26.0)	202 (36.0)	225 (28.0)	239 (35.0)	244 (34.0)	258 (28.0)
	44	50	45	48	41	37
⅜ Nellore ⅝ Angus[1]	204 (37.0)	224 (33.0)	235 (40.0)	250 (42.0)	235 (36.0)	224 (40.0)
	43	40	41	37	33	17

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 24. Continued

Breedtype	Age 8	9	10	11	12	13	14
Angus	212 (37.0) 19	209 (33.0) 18	208 (36.0) 11	189 (38.0) 7	193 (56.0) 5	218 (12.0) 3	193 (9.0) 2
Nellore	217 (46.0) 22	209 (44.0) 20	198 (33.0) 12	227 (35.0) 6	224 (51.0) 4	197 (52.0) 2	117 1
F_1 Nellore-Angus	264 (29.0) 41	249 (35.0) 40	233 (33.0) 36	234 (27.0) 34	212 (41.0) 32	205 (35.0) 18	202 (22.0) 4
⅜ Nellore ⅝ Angus	250 (36.0) 31	245 (34.0) 24	238 (29.0) 18	241 (54.0) 4	233 (30.0) 2	250 1	218 1
⅜ Nellore ⅝ Angus[1]	210 (21.0) 4	-	-	-	-	-	-

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 25. Unadjusted means for calf weaning weight (SD) and number of records by breedtype for calves sired by Angus, Nellore, and Charolais

	Sire breed					
	Angus		Nellore		Charolais	
Breedtype	M	F	M	F	M	F
Angus	211 (38.4)	202 (37.2)	233 (33.5)	219 (30.8)	-	-
	108	114	7	5		
Nellore	214 (37.0)	213 (39.0)	193 (31.3)	175 (25.7)	-	-
	70	55	46	40		
F_1 Nellore-Angus	248 (33.2)	242 (23.2)	-	-	281 (25.4)	269 (25.7)
	25	25			19	22
⅜ Nellore ⅝ Angus	240 (31.7)	224 (33.4)	-	-	252 (36.3)	253 (29.0)
	42	57			55	71
⅜ Nellore ⅝ Angus[1]	211 (41.1)	218 (29.0)	-	-	250 (40.8)	228 (36.3)
	45	46			64	55

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 26. Unadjusted means for calf weaning weight (SD) and number of records by breedtype for calves sired by crossbred bulls

	Sire breed					
	¾ Angus ¼ Nellore		⅜ Nellore ⅝ Angus		F_1 Nellore-Angus	
Breedtype	M	F	M	F	M	F
Angus	-	-	-	-	-	-
Nellore	-	-	-	-	-	-
F_1 Nellore-Angus	250 (35.4) 113	234 (31.8) 114	-	-	228 (34.1) 76	212 (30.5) 60
⅜ Nellore ⅝ Angus	-	-	216 (30.2) 61	207 (31.8) 51	188 (37.3) 3	187 (32.0) 6
⅜ Nellore ⅝ Angus[1]	-	-	168 (4.5) 2	211 (28.1) 3	-	-

[1] Second generation ⅜ Nellore ⅝ Angus cows

Preweaning Average Daily Gain

The same attempts were conducted in the analysis of ADG as in the case of weaning weight and all models resulted in excessive adjustments, which may be due in part to the reasons discussed earlier in weaning weight section. Unadjusted means for calf ADG, SD, and numbers of records by cow breedtype and cow age are presented in Table 27. In general, calves out of cows of intermediate ages had larger ADG than calves born to 2- and 3-yr-old cows and to aged cows. As for weaning weight, calves out of F_1 Nellore-Angus cows had larger ADG than calves born to straightbred cows and in many cases more than calves born to both first and second generation ⅜ Nellore ⅝ Angus cows. Calves out of first and second generation ⅜ Nellore ⅝ Angus cows had similar ADG to calves out of F_1 Nellore-Angus cows at some ages, and larger ADG at others. As discussed for weaning weight, the large ADG means for calves out of the mature crossbred cows would be expected to be positively influenced by Charolais direct effects.

Unadjusted means for calf ADG, SD, and numbers of records by cow breedtype and sire of the calf breed are presented in Tables 28 and 29. Interestingly, large reciprocal differences in ADG were observed in the F_1 heifer calves. Nellore-sired F_1 heifer calves had lower ADG than Angus-sired F_1 heifers calves(Table 28); reciprocal males had similar ADG. Among other groups, bull calves had slightly larger ADG than heifer calves except for Angus-sired calves out of second generation ⅜ Nellore ⅝ Angus cows and the small group of calves born to second generation ⅜ Nellore ⅝ Angus cows and sired by first generation bulls.

Table 27. Unadjusted means (SD) (kg) and number of records for calf ADG by breedtype and cow age

	Age					
Breedtype	2	3	4	5	6	7
Angus	0.609 (0.118)	0.651 (0.148)	0.806 (0.158)	0.895 (0.102)	0.913 (0.103)	0.832 (0.118)
	29	34	31	29	27	22
Nellore	0.791	0.774 (0.107)	0.794 (0.122)	0.806 (0.134)	0.879 (0.134)	0.899 (0.106)
	1	37	21	28	26	32
F_1 Nellore-Angus	0.829 (0.075)	0.884 (0.101)	0.934 (0.087)	0.927 (0.090)	1.000 (0.130)	1.004 (0.090)
	41	40	42	42	41	43
⅜ Nellore ⅝ Angus	0.782 (0.096)	0.824 (0.120)	0.887 (0.105)	0.919 (0.111)	0.953 (0.121)	1.000 (0.095)
	44	50	45	48	41	37
⅜ Nellore ⅝ Angus[1]	0.785 (0.144)	0.891 (0.130)	0.912 (0.136)	0.951 (0.131)	0.965 (0.118)	0.936 (0.116)
	43	40	41	37	33	17

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 27: Continued

Breedtype	Age 8	9	10	11	12	13	14
Angus	0.825 (0.121)	0.795 (0.138)	0.766 (0.201)	0.745 (0.135)	0.745 (0.263)	0.856 (0.089)	1.033 (0.083)
	19	18	11	7	5	3	2
Nellore	0.897 (0.164)	0.937 (0.103)	0.890 (0.100)	0.950 (0.081)	0.978 (0.080)	0.901 (0.056)	0.665
	22	20	12	6	4	2	1
F_1 Nellore-Angus	1.037 (0.102)	0.978 (0.134)	0.933 (0.107)	0.921 (0.102)	0.890 (0.099)	0.915 (0.079)	0.966 (0.071)
	41	40	36	34	32	18	4
⅜ Nellore ⅝ Angus	0.972 (0.130)	0.975 (0.112)	0.993 (0.115)	0.942 (0.154)	0.963 (0.037)	0.834	0.949
	31	24	18	4	2	1	1
⅜ Nellore ⅝ Angus[1]	0.950 (0.110)	-	-	-	-	-	-
	4						

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 28. Unadjusted means for calf ADG (SD) (kg) and number of records by breedtype for calves sired by Angus, Nellore, and Charolais

	Sire breed					
	Angus		Nellore		Charolais	
Breedtype	M	F	M	F	M	F
Angus	0.794 (0.172)	0.764 (0.158)	0.974 (0.102)	0.755 (0.266)	-	-
	108	114	7	5		
Nellore	0.926 (0.109)	0.908 (0.102)	0.794 (0.121)	0.728 (0.098)	-	-
	70	55	46	40		
F_1 Nellore-Angus	0.996 (0.114)	0.958 (0.092)	-	-	1.085 (0.092)	1.022 (0.094)
	25	25			19	22
⅜ Nellore ⅝ Angus	0.907 (0.108)	0.843 (0.127)	-	-	1.021 (0.101)	0.985 (.103)
	42	57			55	71
⅜ Nellore ⅝ Angus[1]	0.829 (0.142)	0.832 (0.125)	-	-	0.984 (0.136)	0.923 (0.115)
	45	46			64	55

[1] Second generation ⅜ Nellore ⅝ Angus cows.

Table 29. Unadjusted means for calf ADG (SD) (kg) and number of records by breedtype for calves sired by crossbred bulls

	Sire breed					
	¾ Angus ¼ Nellore		⅜ Nellore ⅝ Angus		F_1 Nellore-Angus	
Breedtype	M	F	M	F	M	F
Angus	-	-	-	-	-	-
Nellore	-	-	-	-	-	-
F_1 Nellore-Angus	0.957 (0.147) 113	0.895 (0.110) 114	-	-	0.932 (0.093) 76	0.879 (0.100) 60
⅜ Nellore ⅝ Angus	-	-	0.889 (0.105) 61	0.826 (0.110) 51	0.748 (0.092) 3	0.694 (0.120) 6
⅜ Nellore ⅝ Angus[1]	-	-	0.767 (0.081) 2	0.877 (0.054) 3	-	-

[1] Second generation ⅜ Nellore ⅝ Angus cows

SUMMARY AND CONCLUSIONS

Calving and Weaning Rate

The primary reason for this research was to evaluate the heterosis expressed for these reproductive traits in crossbred (non-F1) Nellore-Angus cows. First and second generation ⅜ Nellore ⅝ Angus cows expressed substantial heterosis ($P < 0.001$) for both calving and weaning rate.

The type of mating used to produce first generation ⅜ Nellore ⅝ Angus cows did not appear to substantially influence estimates of heterosis for calving and weaning rate. The first generation ⅜ Nellore ⅝ Angus cows were made using three distinct types of matings. The majority of these (n = 47) were sired by ¾ Angus ¼ Nellore bulls and out of F_1 dams; another set (n = 8) was produced as the reciprocal of that mating. A third set (n = 8) of cows was produced by mating ¾ Nellore ¼ Angus sires and Angus dams. When these two small groups were considered as distinct breedtypes, heterosis for calving and weaning rate was not detected for cows produced by ½ Nellore ½ Angus sires and ¾ Angus ¼ Nellore dams for either trait, nor for those produced by ¾ Nellore ¼ Angus sires and Angus dams. This is not surprising given the limited numbers of records in these two small groups. Heterosis estimated from the reduced data set (cows produced ¾ Angus ¼ Nellore bulls and out of F_1 dams) was very similar to that estimated from the entire data.

Heterosis for calving and weaning rate was also estimated within cow age groups. At 2- and 3-yr of age, F_1 Nellore-Angus, first generation ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams, and first and second generation ⅜ Nellore ⅝ Angus expressed heterosis ($P < 0.05$) for calving and weaning rate. The first generation ⅜ Nellore ⅝ Angus produced out of ½ Nellore ½ Angus sires and ¾ Angus ¼ Nellore dams, and that produced out of ¾ Nellore ¼ Angus sires and Angus dams expressed heterosis ($P < 0.001$) for calving rate at 2- and 3-yr of age. The F_1 Nellore-Angus, first generation ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams expressed heterosis ($P < 0.05$) for calving and weaning rate at 4-yr of age and older. For the same age category, second generation ⅜ Nellore ⅝ Angus cows expressed heterosis ($P < 0.01$) for weaning rate. Excluding the records of 2-yr old cows; F_1 Nellore-Angus cows expressed heterosis ($P < 0.01$) for both calving and weaning rate. However, first generation ⅜ Nellore ⅝ Angus produced out of ¾ Angus ¼ Nellore sires and ½ Nellore ½ Angus dams expressed heterosis ($P < 0.05$) for weaning rate only. It appears that heterosis for these reproductive traits from these data were primarily due to breedtype differences at young ages.

For both calving and weaning rate, heterosis expressed by the crossbred cows other than the F_1 cows did not differ from what would be expected by the dominance model. The very low mean for Nellore 2-yr-old cows due to their late age at maturity resulted in lowering the average of the purebreds, and therefore may have agumented high levels of heterosis. As 2-yr old cows, heterosis expressed by second generation ⅜ Nellore ⅝ Angus did not appear to differ from that expressed by first generation ⅜ Nellore ⅝ Angus for calving and weaning rate. However, overall weaning rate heterosis expressed by second generation ⅜ Nellore ⅝ Angus was greater than that expressed by first generation ⅜ Nellore ⅝ Angus as mature cows but it was very similar to that expressed by first generation ⅜ Nellore ⅝ Angus cows produced by ¾ Angus ¼ Nellore sires and ½ Angus ½ Nellore dams.

Birth Weight, Weaning Weight, and ADG

No breedtype group expressed significant maternal heterosis for birth weight. The influence of age was obvious as the lightest calves were produced out of heifers for all breedtypes. Reciprocal birth weight differences were large in F_1 calves. Nellore-sired F_1 calves were heavier than Angus-sired calves and these were in agreement with the previous findings in Brahman-*Bos taurus* crosses (Cartwright et al., 1964; Roberson et al., 1986; Thallman et al., 1993; Riley et al., 2007). Among these Nellore-sired F_1 calves, males were much heavier than females at birth. Among the Angus-sired F_1 calves, males appeared to be slightly lighter than females at birth, and this have previously been reported in Brahman F_1 crosses (Cartwright et al., 1964; Roberson et al., 1986; Thallman et al., 1993; Riley et al., 2007). In calves from most other breedtypes, males were heavier than females at birth.

Several models with different parameterizations of fixed effect combinations were attempted to analyze weaning weight and ADG traits. All models produced some least squares means for certain cow breedtype-sire breed of calf-calf sex combinations that were excessively adjusted. As a result it was determined to learn from these data by examination of unadjusted means for these traits.

Calves out of cows at intermediate ages had larger ADG and were heavier at weaning compared to those out of young (2- and 3-yr old) and aged cows. Nellore-sired

F_1 calves were heavier at weaning than the reciprocal cross. Angus-sired F_1 heifers had larger ADG than the reciprocal cross, while averages for the reciprocal F_1 males were similar. Calves out of F_1 Nellore-Angus cows were heavier at weaning and gained more than those out of the straightbred and the first and second generation ⅜ Nellore ⅝ Angus. In some cases, calves out of first generation ⅜ Nellore ⅝ Angus cows were as heavy as calves out of F_1 Nellore-Angus cows. For most of the cow breedtype-sire breed of calf combinations bull calves were heavier at weaning and gained more than heifer calves except for Angus-sired calves out of second generation ⅜ Nellore ⅝ Angus.

Nellore-Angus crossbred cows, especially the F_1 cows, performed very well for reproductive traits. Both first and second generation ⅜ Nellore ⅝ Angus cows performed very well, although not quite to the level of the F_1 cows, and raised very heavy calves, especially when bred to Charolais. The mating system used to produce the first generation ⅜ Nellore ⅝ Angus cows did not influence their performance for reproductive traits, however, the sample size was very small for two groups produced by different systems and may be responsible for this result. Heterosis expressed by non-F_1 cows for reproductive traits did not differ ($P > 0.05$) from the dominance model expectations.

LITERATURE CITED

Alenda, R., T. G. Martin, J. F. Lasley, and M. R. Ellersieck. 1980. Estimation of genetic and maternal effects in crossbred cattle of Angus, Charolais and Hereford parentage. I. Birth and weaning weights. J. Anim. Sci. 50:226-234.

Arthur, P. F., H. Hearnshaw, P. J. Kohun, and R. Barlow. 1994. Evaluation of *Bos indicus* and *Bos taurus* straightbreds and crosses. III. Direct and maternal effects on growth traits. Aust. J. Agric. Res. 45:807-815.

Boenig, L. 2011. Heterosis and heterosis retention for reproductive and maternal traits in Brahman × Hereford crossbred cows. M. S. Thesis, Texas A&M University.

Cartwright, T. C., G. F. Ellis, Jr., W. E. Kruse, and E. K. Crouch. 1964. Hybrid vigor in Brahman-Hereford crosses. Tech. Monograph 1. Texas Agric. Exp. Sta., College Station.

Cartwright, T. C. 1970. Selection criteria for beef cattle for the future. J. Anim. Sci. 30: 706-711.

Corva, P. M., E. L. Villarreal, C. A. Mezzadra, and L. M. Melucci. 1995. Reproductive traits of Angus, Criollo and reciprocal crossbred females in the temperate area of Argentina. Animal Science. 61:241-249.

Crow, J. F. 1948. Alternative hypothesis of hybrid vigor. Genet. 33:477-487.

Cundiff, L. V., K. E. Gregory, and R. M. Koch. 1974a. Effects of heterosis on reproduction in Hereford, Angus and Shorthorn cattle. J. Anim. Sci. 38:711-727.

Cundiff, L. V., K. E. Gregory, F. J. Schwulst and R. M. Koch. 1974b. Effects of heterosis on maternal performance and milk production in Hereford, Angus and Shorthorn cattle. J. Anim. Sci. 38:728-745.

Cundiff, L. V., R. Nunez-Dominguez, G. E. Dickerson, K. E. Gregory, and R. M. Koch. 1992. Heterosis for lifetime production in Hereford, Angus, Shorthorn, and crossbred cows. J. Anim. Sci. 70:2397-2410.

Cunningham, E. P. 1982. The genetic basis of heterosis. Proc. of the 2nd World Congress on Genetics Applied to Livestock Production. Vol. VI:190-205. Madrid, Spain.

Dearborn, D. D., K. E. Gregory, L. V. Cundiff, and R. M. Koch. 1987. Maternal heterosis and grandmaternal effects in beef cattle: Preweaning traits. J. Anim. Sci. 65:33-41.

Dickerson, G. E. 1952. Inbred lines for heterosis tests? In: Heterosis. Ed. J. W. Gowen. Iowa State College Press, Ames.

Dickerson, G. E. 1969. Experimental approaches in utilizing breed resources. Anim. Breed. Abstr. 37:191-202.

Dickerson, G.E. 1973. Inbreeding and heterosis in animals. Proc. Anim. Breed. Genet. Symposium in honour of Dr. J. L. Lush, ASAS, ADSA. 111:54-77.

Dillard, E. U., O. Rodriguez, and O. W. Robison. 1980. Estimation of additive and nonadditive direct and maternal genetic effects for crossbreeding beef cattle. J. Anim. Sci. 50:653-663.

Gaines, J. A., W. H. McClure, D. W. Vogt, R. C. Carter, and C. M. Kincaid. 1966. Heterosis from crosses among British breeds of beef cattle: fertility and calf performance to weaning. J. Anim. Sci. 25:5-13.

Gregory, K. E. and L. V. Cundiff. 1980. Crossbreeding in beef cattle: Evaluation of systems. J. Anim. Sci. 51:1224-1242.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1991a. Breed effects and heterosis in advanced generations of composite populations for preweaning traits of beef cattle. J. Anim. Sci. 69:947-960.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1991b. Breed effects and heterosis in advanced generations of composite populations for birth weight, birth date, dystocia, and survival as traits of dam in beef cattle. J. Anim. Sci. 69:3574-3589.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1992a. Breed effects and heterosis in advanced generations of composite populations for reproduction and maternal traits of beef cattle. J. Anim. Sci. 70:656-672.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1992b. Breed effects and heterosis in advanced generations of composite populations on actual weight, adjusted weight, hip height, and condition score of beef cows. J. Anim. Sci. 70:1742-1754.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1992c. Effects of breed and retained heterosis on milk yield and 200-day weight in advanced generations of composite populations of beef cattle. J. Anim. Sci. 70:2366-2372.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1999. Composite breeds to use heterosis and breed differences to improve efficiency of beef production. Tech. Bull. No. 1875. USDA Agri. Res. Service., Nat. Tech. Info. Serv., Springfield, Virginia.

Gregory, K. E., L. V. Cundiff, R. M. Koch, D. B. Laster, and G. M. Smith. 1978. Heterosis and breed maternal and transmitted effects in beef cattle. I. Preweaning traits. J. Anim. Sci. 47:1031-1041.

Gregory, K. E., J. C. M. Trail, H. J. S. Marples, and J. Kakonge. 1985. Heterosis and breed effects on maternal and individual traits of *Bos indicus* breeds of cattle. J. Anim. Sci. 60:1175-1180.

Haile, A., B.K. Joshi, W. Ayalew, A. Tegegne, and A. Singh. 2011. Genetic evaluation of Ethiopian Boran cattle and their crosses with Holstein Friesian for growth performance in central Ethiopia. J. Anim. Breed. Genet. 128:133–140.

Hargrove, D. D., A. Pourrain, J. R. Crockett, F. M. Pate, and T. T. Marshall. 1991. Comparison of *inter se* mated $^3/_8$ Brahman: $^5/_8$ Angus and ½ Brahman: ½ Angus. I. Reproduction and cow productivity. Florida Beef Cattle Research Report. Florida Agri. Exp. Sta., Florida Coop. Ext. Serv., Inst. Food and Agri. Sci., Univ. of Florida, Gainesville.

Hill, W. G. 1982. Dominance and epistasis as components of heterosis. Z. Tierzüchtg. Züchtgsbiol. 99:161-168.

Hohenboken, W. D., and D. W. Weber. 1989. Crossbreeding among British and Continental European dual-purpose breeds in the coastal Pacific Northwest. J. Anim. Sci. 67:2841-2847.

Jenkins, T. G., and C. L. Ferrell. 2004. Preweaning efficiency for mature cows of breed crosses from tropically adapted *Bos indicus* and *Bos taurus* and unadapted *Bos taurus* breeds. J. Anim. Sci. 82:1876-1881.

Jones, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genet. 2:466-479.

Key, K. L. 2004. Heterosis and heterosis retention for reproductive and maternal traits in Brahman-British crossbred cows. Ph.D. Diss., Texas A&M University, College Station.

Kinghorn, B. 1980. The expression of “recombination loss” in quantitative traits. Z. Tierzüchtg. Züchtgsbiol. 97:138-143.

Kinghorn, B. P., and J. E. Vercoe. 1989. The effect of using the wrong genetic model to predict the merit of crossbred genotypes. Anim. Prod. 49:209-216.

Knapp, B. W., O. F. Pahnish, J. J. Urick, J. S. Brinks, and G. V. Richardson. 1980. Preweaning and weaning heterosis for maternal effects of beef × beef and beef × dairy crosses. J. Anim. Sci. 50:800-807.

Koch, R. M., G. E. Dickerson, L. V. Cundiff, and K. E. Gregory. 1985. Heterosis retained in advanced generations of crosses among Angus and Hereford cattle. J. Anim. Sci. 60:1117-1132.

Koger, M. 1973. Summary. In: Crossbreeding Beef Cattle, Series II. Eds: M. Koger, T. J. Cunhua, and A. C. Warnick. Univ. Florida Press, Gainesville. pp. 434-447.

Koger, M., F. M. Peacock, W. G. Kirk, and J. R. Crockett. 1975. Heterosis effects on weaning performance of Brahman-Shorthorn calves. J. Anim. Sci. 40:826-833.

Kress, D. D., D. E. Doornbos, and D. C. Anderson. 1986. Empirical validation of the dominance model for beef cattle. In: Proc. of the 3rd World Congress on Genetics Applied to Livestock Production. Vol. IX:295-300. Lincoln, Nebraska.

Kress, D. D., D. E. Doornbos, and D. C. Anderson. 1990. Performance of crosses among Hereford, Angus, and Simmental cattle with different levels of Simmental breeding. Maternal heterosis and calf production by two-year-old dams. J. Anim. Sci. 68:54-63.

Kress, D. D., D. E. Doornbos, D. C. Anderson, and D. Rossi. 1992. Performance of crosses among Hereford, Angus and Simmental cattle with different levels of Simmental breeding. VI. Maternal heterosis of 3- to 8-year-old dams and the dominance model. J. Anim. Sci. 70:7682-7687.

Long, C. R. 1980. Crossbreeding for beef production: Experimental results. J. Anim. Sci. 51:1197-1223.

Lush, J. L. 1945. Animal Breeding Plans. Iowa State Univ. Press, Ames.

Mackinnon, M. J., D. J. S. Hetzel, and J. F. Taylor. 1989. Genetic and environmental effects on the fertility of beef cattle in a tropical environment. Austr. J. Agric. Res. 40:1085-1097.

Mackinnon, M.J., W. Thorpe, L. Baker. 1996. Source of genetic variation for milk production in a crossbred herd in the tropics. Anim. Sci. 62:5–16.

MacNeil, M. D., D. D. Dearborn, L. V. Cundiff, C. A. Dinkel, and K. E. Gregory. 1989. Effects of inbreeding and heterosis in Hereford females on fertility, calf survival and preweaning growth. J. Anim. Sci. 67:895-901.

Madalena, F. E., A. M. Lemos, R. L. Teodoro, R. T. Barbosa, and J. B. N. Monteiro. 1990. Dairy production and reproduction in Holstein-Friesian and Guzera crosses. J. Dairy Sci. 73:1872-1886.

Magaña J. G and J. C. Segura. 2003. Estimates of breed average direct, maternal and heterosis effects for some pre-weaning traits of zebu breeds and their crosses in southeastern Mexico. Trop. Anim. Health and Prod. 35:342-350.

McDonald, R. P. and J. W. Turner. 1972. Estimation of maternal heterosis in preweaning traits of beef cattle. J. Anim. Sci. 35:1146-1154.

McElhenney, W.H., C.R. Long, J.F. Baker, and T.C. Cartwright. 1986. Production characters of first generation cows of a five-breed diallel: Reproduction of mature cows and pre-weaning performance of calves by two third-breed sires. J. Anim. Sci. 63:59-67.

Meuchel, M. C. 2005. Evaluation of heterosis and heterosis retention in *Bos taurus-Bos indicus* crossbred cattle for productivity traits in cows. M.S. thesis, Texas A&M University, College Station.

Meyer, K., K. Hammond, P. F. Parnell, M. J. MacKinnon, and S. Sivarajasingam. 1990. Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. Livest. Prod. Sci. 25:15–30.

Morris, C. A., R. L. Baker, S. M. Hickey, D. L. Johnson, N. G. Cullen, and J. A. Wilson. 1993. Evidence of genotype by environment interaction for reproductive and maternal traits in beef cattle. Anim Prod. 56:69-83.

Neville, W. E., Jr., B. G. Mullinix, Jr., and W. C. McCormick. 1984a. Grading and rotational crossbreeding of beef cattle. I. Reproductive performance. J. Anim. Sci. 58:25-37.

Neville, W. E., Jr., B. G. Mullinix, Jr., and W. C. McCormick. 1984b. Grading and rotational crossbreeding of beef cattle. II. Calf performance to weaning. J. Anim. Sci. 58:38-46.

Newman, S., M. D. MacNeil, W. L. Reynolds, B. W. Knapp, and J. J. Urick. 1993. Fixed effects in the formation of a composite line of beef cattle. I. Experimental design and reproductive performance. J. Anim. Sci. 71:2026-2032.

Neufeld-Arce, R. O. 2006. Evaluation of heterosis and heterosis retention in *Bos taurus-Bos indicus* crossbred cattle for reproductive and maternal traits in cows. M. S. Thesis, Texas A&M University.

Olson, T. A., M. A. Elzo, M. Koger, W. T. Butts, Jr., and E. L. Adams. 1990. Direct and maternal genetic effects due to the introduction of *Bos taurus* alleles into Brahman cattle in Florida. I. Reproduction and calf survival. J. Anim. Sci. 68:317-323.

Olson, T. A., F. M. Peacock, and M. Koger. 1993. Reproductive and maternal performance of rotational, three-breed, and *inter se* crossbred cows in Florida. 1993. J. Anim. Sci. 71:2322-2329.

Olson, T. A., A. Van Dijk, M. Koger, D. D. Hargrove, and D. E. Franke. 1985. Additive and heterosis effects on preweaning traits, maternal ability and reproduction from crossing of the Angus and Brown Swiss breeds in Florida. J. Anim. Sci. 61:1121-1131.

Oklahoma State University Website. 2011. Breeds of Livestock- Cattle Breeds. Available: http://www.ansi.okstate.edu/breeds/cattle/. Accessed March 3, 2011.

Oxford, E. L., A. H. Brown Jr., Z. B. Johnson, G. T. Tabler , and B. R. Kutz. 2009. Preweaning performance, heterosis, and direct and maternal breed effects in angus, hereford, red poll, santa gertrudis, and reciprocal-cross calves. Prof. Anim.Sci. 25:529–535

Peacock, F. M., and M. Koger. 1980. Reproductive performance of Angus, Brahman, Charolais and crossbred dams. J. Anim. Sci. 50:689-693.

Perotto, E., J. L. Moletta, C. Lesskiu, N. A. deSilva. 1994. Additive and heterozygotic effects on body weight traits of Charolais, Caracu and Charolais × Caracu crosses in Parana – Brazil. In: Proc. of the 5th World Congress on Genetics Applied to Livestock Production. Vol. XVII:292-295. Guelph, Ontario, Canada.

Prayaga, K. C. 2003. Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment. 1. Growth traits. Aust. J. Agric. Res. 54:1013–1025.

Rendel, J. M. 1980. Low calving rates in Brahman cross cattle. Theor. Appl. Genet. 58:207-210.

Riley, D.G. 2000. Heterosis and heterosis retention in reproductive traits, weight and condition of Brahman – British crossbred cows. Ph.D. Diss., Texas A&M University.

Riley, D.G., and J.R. Crockett. 2006. Heterosis retention and the dominance model in Florida beef research. Florida Cattleman. 70(6):42, 44, 46.

Riley, D. G., C. C. Chase Jr, S. W. Coleman, T. A. Olson, and R. D. Randel. 2010. Evaluation of tropically adapted straightbred and crossbred beef cattle: Heifer age and size at first conception and characteristics of their first calves. J. Anim. Sci, 88:3173-3182.

Roberson, R. L., J. O. Sanders, and T. C. Cartwright. 1986. Direct and maternal genetic effects on preweaning characters of Brahman, Hereford and Brahman-Hereford crossbred cattle. J. Anim. Sci. 63:438-446.

Robison, O. W., B. T. MacDaniel, and E. J. Rincon. 1981. Estimation of direct and maternal additive and heterotic effects from crossbreeding experiments in animals. J. Anim. Sci. 52:44-50.

Sacco, R. E., J. F. Baker, T. C. Cartwright, C. R. Long, and J. O. Sanders. 1989. Production characteristics of straightbred F_1 and F_2 cows: Birth and weaning characters of terminal-cross calves. J. Anim. Sci. 69:1972-1979.

Sagebiel, J. A., G. F. Krause, B. Sibbit, L. Langford, A. J. Dyer and J. F. Lasley. 1973. Effect of heterosis and maternal influence on gestation length and birth weight in reciprocal crosses among Angus, Charolais, and Hereford cattle. J. Anim. Sci. 37:1273.

Sanders, J. O. 1980. History and development of Zebu cattle in the United States. J. Anim. Sci. 50:1188-1200.

Sanders, J. O., D. G. Riley, J. Paschal, and D. K. Lunt. 2005. Evaluation of the F_1 crosses of five Bos indicus breeds with Hereford for birth, growth, carcass, cow productivity, and longevity characteristics. A Compilation Of Research Results Involving Tropically Adapted Beef Cattle Breeds, S-243 and S-277 Multistate Research Projects Southern Cooperative Series Bulletin 405. ISBN: 1-58161 405-5. Pp. 96-107.

Schmitt, A., and O. Distl. 1992. Heterosis und rekombinationseffekte für abkalbe- und fruchtbarkeitsmerkmale bei kreuzungen mit Deutschem Gelbvieh. Züchtungskunde. 64:458-476.

Schoenan, S. J., J. G. E. van Zyl and R. de Wet. 1993. Direct and maternal additive and heterotic effects in crossbreeding Hereford, Simmental, and Africander cattle. S. African J. Anim. Sci. 23:61-66.

Seebeck, R. M. 1973. Sources of variation in the fertility of a herd of Zebu, British, and Zebu x British cattle in Northern Australia. J. Agric. Sci., U. K. 81:253-262.

Sheridan, A. K. 1981. Crossbreeding and heterosis. Anim. Breed. Abstr. 49:131-144.

Semel, Y., Nissenbaum, J., Menda, N., Zinder, M., Krieger, U., Issman, N., Pleban, T., Lippman, Z., Gur, A., and Zamir, D. 2006. Overdominant quantitative trait loci for yield and fitness in tomato. Proc. Natl. Acad. Sci. 103: 12981–12986.

Seifert, G.W., and J. F. Kennedy. 1972. A comparison of British breed crosses with F_1 and F_2 Zebu x British cattle on the basis of a productivity index. Proc. Aust. Soc. Anim. Prod. 9:143-146.

Sheridan, A. K. 1981. Crossbreeding and heterosis. Anim. Breed. Abstr. 49:131-144.

Shrestha, J. N. B. 2010. Heterosis retention and recombination loss. Egyptian J. Sheep Goat Sci. 5:35-82.

Shull, G. H. 1908. The composition of a field of maize. Am. Breeders Assoc. Rep. 4 :296-301.

Shull, G. H. 1952. Beginnings of the heterosis concept. In: Heterosis, Ed. J. W. Gowen, Iowa State College Press, Ames. pp. 14-48.

Spelbring, M. C., T. G. Martin, and K. J. Drewry. 1977a. Maternal productivity of crossbred Angus × Milking Shorthorn cows. I. Cow and calf weight and scores. J. Anim. Sci. 45:969-975.

Spelbring, M. C., T. G. Martin, and K. J. Drewry. 1977b. Maternal productivity of crossbred Angus × Milking Shorthorn cows. II. Cow reproduction and longevity. J. Anim. Sci. 45:976-982.

Springer N. M., and R. M. Stupar. 2007. Allelic variation and heterosis in maize: How do two halves make more than a whole? Genome Res. 17: 264-275.

Tawonezvi, H. P. R., H. K. Ward, J. C. M. Trail, and D. Light. 1988. Evaluation of beef breeds for rangeland weaner production in Zimbabwe 2. Productivity of crossbred cows and heterosis estimates. Anim Prod. 47: 361-367.

Teixeira, R.A., and L.G. Albuquerque. 2005. Maternal and individual heterosis for preweaning dailygain in Nellore × Hereford and Nellore × Angus cattle. Arq. Bras. Med. Vet. Zootec. 57:518-523.

Trail, J. C. M., K. E. Gregory, H. J. S. Marples, and J. Kakonge. 1985. Comparison of

Bos taurus-Bos indicus breed crosses with straightbred *Bos indicus* breeds for maternal and individual traits. J. Anim. Sci. 60:181-187.

Trematore, R. L., M. M. de Alencar, P. F. Barbosa , J. d. A. L. Oliveira, M. A. de Almeida. 1998. Estimates of additive and heterotic effects for preweaning growth traits of Charolais - Nellore cattle. R. Bras. Zootec. 27:87-94.

Turner, J. W., B. R. Farthing, and G. L. Robinson. 1968. Heterosis in reproductive performance of beef cows. J. Anim. Sci. 27:336-338.

Vostrý, L., V. Jakubec, W. Schlote, M. Bjelka, J. Bezdíček, and I. Majzlík. 2008. Analysis of population and heterosis effects in crossbred cattle of Czech Fleckvieh and beef Simmental parentage for growth traits. Arch. Tierz., Dummerstorf 51:207-215.

Williams, A. R., D. E., Franke, A. M. Saxton, and J. W. Turner. 1990. Two-, three and four-breed rotational crossbreeding of beef cattle: Reproductive traits. J. Anim. Sci. 68:1536-1546.

Williams, A. R., D. E. Franke, and A. M. Saxton. 1991. Genetic effects for reproductive traits in beef cattle and predicted performance. J. Anim. Sci. 69:531-542.

Winder, J. A., B. J. Rankin, and C. C. Bailey. 1992. Maternal performance of Hereford, Brangus, and reciprocal crossbred cows under semidesert conditions. J. Anim. Sci. 70:1032-1038.

Wright, S. 1922. The effects of inbreeding and crossbreeding on guinea pigs. USDA Bulletin 1121.

Wyatt, W. E. and D. E. Franke. 1986. Estimation of direct and maternal additive and heterotic effects for preweaning growth traits in cattle breeds represented in the Southern region. Bull. 310. Southern Cooperative Series. Louisiana Agri. Exp. Sta., Louisiana State Univ. Agri. Center, Baton Rouge.