INVESTIGATION OF GENETIC EFFECTS ON BIRTH WEIGHT IN

BRAHMAN-SIMMENTAL CROSSES

A Thesis

by

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ABSTRACT

Brahman cross calves exhibit unusual inheritance of birth weight: Brahman-sired crossbreds out of *Bos taurus* females are heavier with greater difference between sexes than calves of the reciprocal cross. The objective of this work was to investigate genetic effects that may influence differences in Brahman (B) × Simmental (S) crosses. 5,102 calves produced by embryo transfer (ET) (n = 2,914) and natural service/artificial insemination (n = 2,188) were born from 1983 – 1991 . Data were analyzed using an animal model. Fixed effects investigated included contemporary group (n = 87; combinations of ET status, birth year, month, and location), sex, recipient breed, and linear covariates of direct breed effects, maternal breed effects, expected breed heterozygosity of the calf (HET) and the dam, mitochondrial origin, Y chromosome effects, X chromosome effects (XCHR), genomic imprinting (GI), non-random X inactivation by breed of origin, and non-random X inactivation by parent of origin (NONRP). ET calves were constrained to 0 for maternal breed and breed heterozygosity effects. Random effects included direct and maternal additive genetic. The regression coefficient for HET (4.09 ± 0.96 kg) ($P < 0.001$) The regression coefficient for GI was -4.24 ± 0.95 kg ($P < 0.001$). XCHR has a probable role but was antagonized by the presence of NONRP in the model. This is likely due to insufficient data and structure available to partition the effects. Direct and maternal breed and breed heterozygosity effects estimated from models not including GI and XCHR are not straightforward to interpret in *Bos indicus-Bos taurus* crosses.

DEDICATION

One of my favorite poets defines patience as follows:

"Patience doesn't mean we have to wait around, it means

we respect the time it takes for things to blossom and come

into fruition."

There have been many people who have been patient with

me throughout my academic career.

To them I dedicate this work.

To my parents, who have never allowed "I can't" to be a part of my vocabulary.

To those whose influence will be replayed in my mind and on the backs of my eyelids

like an old movie reel.

To my friends, who have supported and encouraged me every step of the way.

To That which I am part of, which is greater than me.

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INTRODUCTION

Brahman cattle were developed in the United States from Zebu breeding stock imported from India and Brazil (Sanders, 1980). Since the development of the breed, Brahman cattle have become an integral part of breeding systems particularly in the Southern and Southeastern regions of the United States. In these regions, the Brahman female's mothering ability and the outstanding performance of the crossbred Brahman-*Bos taurus* female are greatly desired. In the process of producing these valuable *Bos indicus-Bos taurus* crossbred females, researchers and producers alike have noted an unusual trend in birth weights in which calves from *Bos indicus* sires and *Bos taurus* dams are typically heavier with greater differences between sexes than calves of the reciprocal cross (Cartwright et al., 1964; Roberson et al., 1986). These heavier birth weights many times result in increased incidence of calving difficulty, which, in some cases, results in death.

Research into the genetic cause of this abnormal birth weight trend will allow for directed breeding recommendations which avoid the negative effects of this phenomenon while taking advantage of its benefits.

LITERATURE REVIEW

Reciprocal Differences in Birth Weight

Due to the average superior performance of crossbred offspring as compared to the average purebred performance (heterosis), many studies have evaluated the expression of heterosis in *Bos indicus-Bos taurus* crossbred cattle (e.g., Cartwright et al, 1964; Roberson et al., 1986; Pitchford et al., 1993; Boenig, 2011). Cartwright et al. (1964) were the first to document an unusual phenomenon in birth weights of *Bos indicus-Bos taurus* crossbred offspring in a report on heterosis in Brahman-Hereford crosses. Data collected from the Texas Agricultural Experiment Stations in Lufkin and McGregor, TX, showed that at birth, calves from Brahman bulls and Hereford dams weighed on average 5.8 kg above the overall mean, while calves from Hereford bulls and Brahman dams weighed on average 2.9 kg below the overall mean. Cartwright et al. (1964) attributed this 8.6 kg difference to maternal effects, concluding that the genotype of the dam had greater influence on the birth weight of the calf than did the genotype of the sire or the heterosis due to crossbreeding. In the same study, further analysis of reciprocal backcross calves (F_1 Brahman-Hereford progeny bred back to both parental breeds) showed that birth weight tended to increase with increasing proportion of Brahman in the sire relative to the proportion in the dam. Though not reported in the discussion of results, a summary of calf birth weights by cross and sex are included in Table 1 as deduced from least squares constants provided in the appendix of the manuscript.

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In agreement with Cartwright et al. (1964), Roberson et al. (1986) reported a 7 kg difference between Brahman-sired calves out of Hereford dams and Hereford-sired calves out of Brahman dams. Numerous studies have since documented higher average birth weights in *Bos indicus*-sired calves out of *Bos taurus* dams as compared to calves from the reciprocal cross (Reynolds et al. 1980; Baker et al. 1990; Brown et al. 1993b; Thallman et al. 1993; Riley et al., 2007) (Table 1). Lemos et al. (1984) and Amen et al. (2007) also reported a trend in which birth weight differences increased proportionately as the proportion of *Bos indicus* in the sire in relation to the proportion of *Bos indicus* in the dam increased. These results deviated from those of *Bos taurus* reciprocal crosses (Long and Gregory, 1974; Gregory et al., 1979b; Riley et al., 2007).

A number of studies have shown greater sexual dimorphism for birth weight in *Bos indicus*-*Bos taurus* crosses as compared to *Bos taurus* crosses (e.g., Long and Gregory, 1974). Of particular interest is that larger differences between male and female birth weights exist for *Bos indicus*-sired calves out of *Bos taurus* dams than between calves of the reciprocal cross. In some instances, heavier birth weights in females from *Bos taurus* sires and *Bos indicus* dams than males from the same cross have been reported (Thallman et al., 1993; Riley et al., 2007; Boenig, 2011). Riley et al. (2007) reported larger sex differences in birth weight in Brahman-sired calves out of Romosinuano and Angus dams than in calves from the reciprocal crosses (4.6 kg, 5.7 kg, -0.8 kg, and -0.8 kg respectively, males – females). In a study of varying grades of crossbred Holstein-Friesian-Guzera calves, Lemos et al. (1984) reported sex differences of 4.7 kg for Guzera-sired calves and only 0.8 kg for Holstein-Friesian-sired calves.

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Table 1. Birth weight means in *Bos indicus-Bos taurus* reciprocal crosses

Breed[1]	Birth weight, kg		
	Male	Female	Mean
B × H	34.8	29.2	37.8
H × B	31.8	32.2	29.1
B × BH[2]	34.0	30.0	32.7
BH[2] × B	34.5	29.5	28.6
H × BH[2]	32.7	31.3	31.0
BH[2] × H	33.0	31.0	36.7
H × H	33.0	31.0	32.1
B × B	33.3	30.8	28.3
Cartwright et al. (1964)			
H × A			30.3
A × H			23.5
Long and Gregory (1974)			
H × A			35.0
A × H			35.8
Gregory et al. (1979b)			
B × A			32.5
A × B			27.5
Reynolds et al. (1980)			
G × ½ HF ½ G	34.6	29.9	
HF × G	28.6	29.5	
⅝ HF ⅜ G × ⅝ G ⅜ HF	34.2	33.4	
HF × ½ HF ½ G	32.4	31.9	
HF × ¾ HF ¼ G	35.0	33.6	
Lemos et al. (1984)			
B × H			37.4
H × B			30.4
B × BH[2]			34.8
BH[2] × B			29.8
H × BH[2]			32.1
BH[2] × H			37.2
Roberson et al. (1986)			

Table 1 continued.

Breed[1]	Birth weight, kg		
	Male	Female	Mean
B × B – B[3]			31.9
H × H – B			39.1
B × B – H			33.9
H × H – H			37.0
B × H – B			42.1
H × B – B			34.7
B × H – H			49.2
H × B – H			37.3
Baker et al. (1990)			
B × A	45.8	38.4	42.1
A × B	32.1	31.0	31.5
Brown et al. (1993b)			
B × BB		30.2	
B × BH		31.1	
H × BH		31.9	
H × HH		32.4	
B × HH		36.2	
Pitchford et al. (1993)			
B × AB	40.7	36.7	38.7
B × BA	40.2	36.2	38.2
AB × A	43.7	35.2	39.4
BA × A	37.5	36.0	36.8
A × AB	35.5	33.7	34.5
A × BA	34.6	33.4	34.0
AB × B	34.0	32.5	33.2
BA × B	33.8	33.2	33.5
Amen et al. (2007)			
R × B	29.3	30.1	
B × R	38.3	33.7	
R × A	31.0	28.8	
A × R	32.8	31.1	
B × A	39.1	33.4	
A × B	30.8	31.6	
Riley et al. (2007)			

Table 1 continued.

Breed[1]	Birth weight, kg		
	Male	Female	Mean
B × H	39.99	39.09	
H × B	33.31	34.47	
BH × HB	33.22	33.86	
HB × BH	36.2	31.45	
Boenig (2011)			

[1]Breeds are listed sire breed followed by dam breed, including within pairs of letters, and are represented as follows: (A) Angus, (B) Brahman, (G) Guzera, (H) Hereford, (HF) Holstein-Friesian, (R) Romosinuano

[2]Records from reciprocal crosses combined for calculation of reported means

[3]Recipient breed

Thallman et al. (1993) reported results on embryo transfer (ET) calves out of Brahman-Simmental crosses. Calves from Brahman bulls and Simmental dams had larger values than calves out of Simmental bulls and Brahman dams for birth weight, weaning weight, gestation length, yearling weight, and scrotal circumference. All embryos in the study were flushed from their natural dams and implanted into Holstein or crossbred beef recipient cows. The differences in calves from Brahman bulls and Simmental dams as compared to calves from Simmental bulls and Brahman dams were twice as large in males as in females for birth weight. These results indicated that differences may be due to some genetic mechanism occurring before the seventh day of pregnancy.

Riley and Sanders (1999) compared variances for birth weight in *Bos indicus* × *Bos taurus* cattle and their crosses (sire breed is listed first followed by dam breed where the "×" is used in conjunction with crosses). Variance of Brahman × Hereford male birth weights was larger than that of Brahman and Hereford straightbred males and females, and crossbred calves of the reciprocal cross. Brahman × Angus males had greater variance in birth weight than that of Brahman and Angus straightbred males and females, but did not differ from Brahman × Angus females. Nellore × Angus males had a birth weight variance which did not differ from straightbred or Nellore × Angus females. After log-transformation, differences in variances were removed except in the case of Brahman × Hereford males which differed only from Brahman × Hereford females, and Brahman × Angus males which had smaller variance than Brahman × Angus females.

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Reciprocal Differences in Other Traits

There are a number of additional traits reported to exhibit reciprocal differences in *Bos indicus-Bos taurus* crosses. Some of these traits are related to birth weight and for this reason, have been included in the review of the literature.

Gestation Length

Notter et al. (1978) reported that in calves out of *Bos taurus* cows, those with Brahman sires had gestation length 6 days longer than those with Hereford sires. Lemos et al. (1984) reported differences in gestation length in various grades of Holstein-Guzera crossbred cattle. F_1 backcrosses to Guzera bulls had the longest gestation length while F_1 backcrosses to Holstein bulls had the shortest gestation length. Paschal et al. (1991) reported that *Bos indicus*-sired calves out of Hereford dams had gestation length that was 7 to 12 days longer than the Angus-Hereford crosses. Paschal et al. (1991) also noted that sex differences in gestation length had a tendency to be greater in *Bos indicus*-sired calves than in *Bos taurus*-sired calves, with males gestating longer than females. Thallman et al. (1993) reported that calves from Brahman bulls and Simmental dams had longer gestation length than calves from the reciprocal cross in ET calves from Holstein and crossbred beef recipient cows. Consistent with earlier results, Amen et al. (2007) reported longer gestation lengths in Brahman-sired calves than Angus-sired calves produced by ET, and noted that gestation length increased as the proportion of Brahman in the sire increased in relation to the amount of Brahman in the dam. In contrast with

these studies involving *Bos indicus-Bos taurus* crosses, Gregory et al. (1979b) reported

no significant difference in gestation length in reciprocal *Bos taurus* crosses (Table 2).

Table 2. Gestation length in *Bos indicus-Bos taurus* and *Bos taurus-Bos taurus* crosses

Breed[1]	Gestation length, days		
	Male	Female	Mean
H × A			283.8
A × H			284.7
Gregory et al. (1979b)			
B × A			286.6
A × B			284.0
Reynolds et al. (1980)			
G × ½ HF ½ G	290.0	287.5	
HF × G	281.2	280.1	
⅝ HF ⅜ G × ⅝ HF ⅜ G	285.3	285.3	
HF × ½ HF ½ G	278.8	274.5	
HF × ¾ HF ¼ G	280.5	279.2	
Lemos et al. (1984)			
B × B – B[2]			293.0
H × H – B			289.0
B × B – H			291.0
H × H – H			284.0
B × H – B			297.0
H × B – B			287.0
B × H – H			292.0
H × B – H			284.0
Baker et al. (1990)			

Table 2 continued.

Breed[1]	Gestation length, days		
	Male	Female	Mean
B × AB			289.0
B × BA			292.6
AB × A			283.5
BA × A			285.8
A × AB			281.5
A × BA			283.9
AB × B			284.2
BA × B			286.6
Amen et al. (2007)			

[1]Breeds are listed sire breed followed by dam breed, including within pairs of letters, and are represented as follows: (A) Angus, (B) Brahman, (G) Guzera, (H) Hereford, (HF) Holstein-Friesian
[2]Recipient breed

Calving Difficulty

Research has shown calving difficulty to be strongly associated with heavier birth weight, with higher incidences of calf mortality occurring in more difficult births. In a breed comparison study of Hereford, Angus, Brahman, Sahiwal, Pinzgauer, and Tarentaise bulls bred to Hereford and Angus dams, Gregory et al. (1979b) found that Brahman-sired calves had the highest incidence of calving difficulty. In this study, 11.6% of the males, overall, required assistance as compared to 7.0% overall in females. Among Brahman-Angus crosses in the study, 19% of males as compared to 5.7% of females experienced difficult births. Paschal et al. (1991) reported greater sex differences in dystocia for *Bos indicus* crosses than for *Bos taurus* crosses, and that breeds with larger sex differences for birth weight had higher incidences of dystocia than

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what would be expected from the average breed birth weight. Most of this dystocia was in bull calves. Riley et al. (2007) reported that, while incidence of calving difficulty was relatively low overall (all possible combinations of Brahman, Romosinuano, and Angus), the greatest incidence of calving difficulty occurred in Brahman-sired calves from Angus dams (11% of the total number of difficult births), whereas no incidences of difficult calving were reported in the reciprocal cross. In that study, calving difficulty was the leading known cause of death. These results deviated from those of *Bos taurus* reciprocal crosses; for example, Gregory et al. (1979b) reported calving difficulty percentages of 5.7% and 6.1% for Hereford × Angus and Angus × Hereford crosses respectively.

Calf Vigor

Poor vigor at birth is probably seldom an issue in crossbred calves, except in difficult births. Large differences in calf vigor have not been reported in reciprocal *Bos indicus* × *Bos taurus* crosses. Cartwright et al. (1964) reported a similar relationship in calf vigor to that in birth weight, where calves with a higher proportion of Brahman in the sire as compared to the proportion in the dam had lower calf vigor scores (with lower scores being less desirable than higher scores). Riley et al. (2004) found inadequate calf vigor in high percentage and purebred Brahman calves, and reported greater odds of poor vigor in calves surviving difficult births. Riley et al. (2007) reported adequate calf vigor in Brahman × Romosinuano, Brahman × Angus, and their reciprocal crosses.

Weaning Weight and Yearling Weight

Means from the literature on weaning weights in reciprocal *Bos indicus-Bos taurus* and *Bos taurus* crosses are compiled in Table 3. Thallman et al. (1993) reported in an ET study that Brahman-sired calves out of Simmental dams were significantly heavier than Simmental-sired calves out of Brahman dams at weaning and as yearlings; differences between reciprocal crosses were almost twice as large in bulls as in heifers. Brown et al. (1993a) reported yearling weights of 298.1 kg and 279.4 kg for Brahman × Angus and Angus × Brahman calves respectively. Madrid-Bury (1994) reported a statistically significant difference in body weight at 16 months of age for reciprocal Brahman × Holstein bull calves (429 kg for Brahman-sired calves out of Holstein cows and 369 kg for Holstein-sired calves). Riley et al. (2007) reported sex differences for weaning weight in calves out of Brahman sires and Romosinuano and/or Angus dams and reciprocal crosses of these breeds, with males being heavier than females. In reciprocal Angus × *Bos indicus* (Brahman and Nellore) backcross calves, Amen et al. (2007) reported that weaning weights followed the same trend as birth weights in the study with weaning weights decreasing as the proportion of *Bos indicus* in the dam increased in relation to the proportion in the sire, although differences detected were not statistically significant. Boenig (2011) reported sex differences in weaning weights for Brahman-Hereford crosses. Of note in the results is the huge 34.9 kg difference between male and female weaning weights for Brahman × Hereford calves, with females being heavier than males. Male and female Hereford × Brahman calves had a difference of only 19.7 kg and males were larger than females. Boenig (2011) remarked that both

groups were small and had large standard deviations. Coleman et al. (2012) reported

statistically significant differences in finish weights on wheat pasture (approximately 13

months of age) for Brahman × Romosinuano (403 kg) and Romosinuano × Brahman

steers (381 kg), but not for Brahman × Angus (435 kg) and Angus × Brahman steers

(428 kg). Average finish weights for reciprocal Brahman × Angus (569 kg and 535 kg,

respectively) and Brahman × Romosinuano calves (551 kg and 466 kg, respectively) in a

feedlot differed significantly. In all instances, the Brahman-sired calf finished at a

heavier weight than the *Bos taurus*-sired calf. It should be noted that the differences in

reciprocal Brahman × Romosinuano calves can be partially attributed to a group of poor

Romosinuano × Brahman steers in one project year. These results in *Bos indicus × Bos

taurus* crosses differed from reports on weaning weight in reciprocal *Bos taurus* crosses

(Long and Gregory, 1974; Bailey et al., 1977; Gregory et al., 1979a), although some

studies have reported non-significant differences in weaning weight for *Bos indicus ×

Bos taurus* reciprocal crosses (Reynolds et al., 1982).

In many reported cases of reciprocal *Bos indicus-Bos taurus* cross weaning

weights, the calf raised by a Brahman dam was heavier than the calf weaned by the *Bos

taurus* dam, presumably due to the increased milk production of the Brahman female

(Riley et al., 2007; Boenig, 2011).

Table 3. Weaning weight in *Bos indicus* and *Bos taurus* reciprocal crosses

Breed[2]	Weaning weight[1], kg		
	Male	Female	Mean
H × A			167.0
A × H			156.2
Long and Gregory (1974)			
B × SH			184.0
SH × B			202.0
Koger et al. (1975)			
H1 × H2			181.1
H2 × H1			183.0
Bailey et al. (1977)			
H × A			210.0
A × H			195.0
Gregory et al. (1979a)			
B × A			194.2
A × B			194.6
Reynolds et al. (1982)			
B × A	224.7	212.2	218.5
A × B	218.1	202.1	210.1
Brown et al. (1993a)			
B × AB			239.4
B × BA			229.2
AB × A			240.4
BA × A			230.3
A × AB			229.6
A × BA			229.4
AB × B			228.2
BA × B			226.6
Amen et al. (2007)			

Table 3 continued.

Breed[2]	Weaning weight[1], kg		
	Male	Female	Mean
R × B	241.1	234.8	
B × R	242.2	224.9	
B × A	235.2	217.8	
A × B	258.1	246.9	
R × A	207.2	194.3	
A × R	233.8	216.0	
Riley et al. (2007)			
B × H	157.4	192.4	
H × B	243.2	227.5	
BH × HB	221.5	213.5	
HB × BH	228.5	196.8	
Boenig (2011)			

[1]Weaning weight is 200-d or 205-d weight
[2]Breeds are listed sire breed followed by dam breed, including within pairs of letters, and are represented as follows: (A) Angus, (B) Brahman, (H) Hereford, (H1) Inbred Hereford Line 1, (H2) Inbred Hereford Line 2, (R) Romosinuano, (S) Simmental, (SH) Shorthorn

Scrotal Circumference

Few publications have reported on scrotal circumference in *Bos indicus × Bos taurus* reciprocal crosses. Herring et al. (1991) detected no effect of Y chromosome origin on variation in scrotal circumference in Brangus bulls based upon pedigree information. Thallman et al. (1993) showed that Brahman-sired calves out of Simmental cows had yearling scrotal circumference 3.39 cm larger than Simmental-sired calves out of Brahman cows. In a comparison of reciprocal Brahman × Holstein bulls, Madrid-Bury et al. (1994) reported numerically larger scrotal circumference means for Brahman-

sired bulls (approximately 1 cm) at 15, 16, and 17 months of age than for Holstein-sired bulls, but these differences were not significant.

Reciprocal Differences in Other Species

Research has shown reciprocal differences in birth weight as well as placental weight in *Peromyscus polionotus* (Oldfield mouse)-*Peromyscus maniculatus* (Deer mouse) crosses (Table 4). Dawson (1965) reported that breeding Deer males to Oldfield females produced oversized offspring,—often resulting in death—while the reciprocal cross produced offspring that were smaller than either parental species (Table 4).

Sexual dimorphism (similar to that seen in *Bos indicus-Bos taurus* crosses) and reciprocal differences in placental size in interspecific hybrids of the genus *Mus* have also been reported in the literature (Zechner et al., 1996). Consistent with the literature, Hemberger et al. (1999) reported results on placental dysplasia among several congenic strains of *Mus musculus* (House mouse) and *Mus spretus* (Algerian mouse). Differences were found in placental weight, with placental weight increasing as the length of the *Mus spretus*-derived X chromosome increased. Morphological differences were also found in the spongiotrophoblast layer of the placenta and the degree of glycogen cell differentiation. Placental hyperplasia may be under the control of multiple genes with epistatic interactions.

Hemberger et al. (2001) tested three hypotheses in an attempt to explain the apparent sex effect on placental growth: (1) differences are caused by disturbed inactivation of the paternal X chromosome, (2) only specific gene(s) related to differences in placentation are active or reactivated, and (3) the Y chromosome plays

some role in contributing to sex differences in placentation. Results could not disprove

the second hypothesis, but Hemberger et al. (2001) favored a conclusion which

suggested that the Y chromosome causes the sex-specific effect.

Table 4. Weights of reciprocal crosses in mice and ducks[1]

Mouse	Birth weight, g		10-day weight, g			
P. maniculatus × *P. polionotus*	2.17		6.07			
P. polionotus × *P. maniculatus*	1.31		3.32			
Dawson (1965)						
	Placental weight, g		Embryo weight, g			
P. maniculatus × *P. polionotus*	0.49		1.10			
P. polionotus × *P. maniculatus*	0.10		0.95			
Vrana et al. (2000)						
	Week 0, g		Week 4, g		Week 10, g	
Duck	Male	Female	Male	Female	Male	Female
Muscovy × Pekin	53.9	52.1	960	906	2996	2892
Pekin × Muscovy	52.2	51.7	1024	769	3045	1989
Tai and Rouvier (1988)						

[1]Species are listed sire species first followed by dam species

Vrana et al. (2000) reported reciprocal differences in placental and embryo

weights for *P. polionotus-P. maniculatus* crosses (Table 4) and suggested a maternally

expressed X-linked locus from the Oldfield (*Peromyscus polionotus*) parent and an

imprinted paternally expressed autosomal locus from the Deer (*Peromyscus

maniculatus*) parent as an explanation for this birth weight phenomenon in mouse

hybrids. The interaction resulted in skewed X-chromosome inactivation. The relaxation

of the imprinting of paternally expressed genes was correlated with extreme overgrowth

of the fetus. *Plp* and *Peg3* were implicated as candidate genes linked to placental

overgrowth. Duselis and Vrana (2010) reported that placental weights from mice

produced from matings of Deer males and Oldfield females were larger by the sixteenth

day of embryonic growth than placental weights from Oldfield males and Deer females.

It is around this time in gestation that the majority of Deer × Oldfield conceptuses are

dead. Oldfield × Deer conceptuses also had greater fetal weight to placental weight ratio

(a method of measuring placental efficiency) than Deer × Oldfield conceptuses,

indicating that placental weight is more affected by this cross than fetal weight. *Esx1*

was implicated as a candidate gene linked to placental overgrowth.

Duselis and Vrana (2010) investigated morphological defects in placenta in

Peromyscus maniculatus-Peromyscus polionotus crosses. Deer × Oldfield crosses

produced slightly larger placentas by day 16 of gestation, which is significant because

this is also the time when most of these conceptuses are dead. In spite of this, Duselis

and Vrana (2010) remarked that little evidence for association between placental weights

and mortality was found. Differences in gene expression in the labyrinthine layer of the

placenta (the juxtaposition of the maternal and fetal circulatory systems where metabolic

exchange occurs) that inhibit maternal-fetal nutrient and waste exchange are a potential

cause of mortality after 12 days of gestation. Oldfield × Deer offspring had greater fetal

weight to placental weight ratios than Deer × Oldfield offspring. Results from this study

suggested that the X chromosome may play a role in growth retardation in Oldfield ×

Deer crosses, as had been reported by Hemberger et al. (1999) and others.

Tai and Rouver (1998) found sexual dimorphism for growth in a crossbreeding study between Muscovy and Pekin ducks. While weight differences at hatching were not significant, significant body weight sexual dimorphism occurred and increased with age in ducks from Pekin males and Muscovy females, while the reciprocal cross showed much smaller differences in body weight between sexes. Tai and Rouver (1998) suggested that the Muscovy W chromosome (females are the heterogametic sex in ZW systems) may have a depressive effect on growth.

Reports have also been made of reciprocal differences in *Panthera leo* (lion) × *Panthera tigris* (tiger) hybrids, with cats from *Panthera leo* males and *Panthera tigris* females reaching substantially greater body weights than cats from *Panthera tigris* males and *Panthera leo* females (B. Davis, Texas A&M University, College Station, TX, personal communication).

Investigation of Genetic Mechanisms Causing Reciprocal Differences in Birth Weight

Thallman et al. (1993) suggested six genetic mechanisms which may function as potential causes of reciprocal differences: (1) mitochondrial inheritance, (2) genomic imprinting, (3) X-linked inheritance with non-random X inactivation, (4) Y-linked inheritance, (5) maternal inheritance of non-genetic ova cytoplasm, and (6) maternal effect of oviduct and uterus of donor cow on embryo prior to transfer.

Baker et al. (1990) conducted a small study of reciprocal Brahman-Hereford crossbred and purebred calves (*n* = 53). Embryos from both reciprocal crosses and both purebreds were collected and implanted into Brahman and Hereford recipients, completing all eight possible embryo-recipient combinations. Recipient breed was a

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significant source of variation for gestation length, while the recipient dam's maternal effect on birth weight was dependent upon the breed type of the calf. Calves born of Brahman recipients were consistently lighter at birth than calves born of Hereford recipients, except in the case of purebred Hereford calves born to Brahman recipients. Purebred Hereford calves born to Brahman recipients were heavier at birth, likely due to being carried 5 days longer in the Brahman cow. Calves born to Brahman recipients gestated longer, on average, than calves born to Hereford recipients (Table 1; Table 2).

Rohrer et al. (1994) evaluated a herd of purebred Brangus cattle for the effect of line and breed of cytoplasm (based on pedigree) on birth and weaning weights. Results showed that line of cytoplasm origin accounted for extremely minimal amounts of phenotypic variation (< 0.002%) and as such was not considered a major factor in determining phenotype for birth or weaning weight. This, along with the likelihood that most Brahman cattle developed in the United States probably have *Bos taurus* mitochondria, cast doubt on the potential for mitochondrial inheritance as the genetic mechanism causing differences in phenotypic traits in reciprocal *Bos indicus × Bos taurus* crosses.

Ferrell (2005) reported that Charolais fetuses weighed nearly twice as much as Brahman fetuses at 232 days of gestation, regardless of cow breed. By 271 days of gestation, Charolais fetuses weighed 16.5 kg more than Brahman fetuses. However, when the Charolais fetus was in the Brahman cow at 271 days, it weighed 13 kg less than the Charolais fetus in the Charolais cow. From these results, Ferrell (2005) concluded that fetal genotype was a primary factor in regulating fetal growth, but that

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maternal environments constrained growth, with a greater constraining effect occurring on fetuses with greater genetic potential for growth than those with lesser genetic potential.

Gill et al. (2005) investigated differences in birth weight in reciprocal *Bos indicus-Bos taurus* backcross calves. A genome wide scan for QTL affecting birth weight was conducted and data were analyzed using two models: a Mendelian inheritance and an imprinting model (including parent-of-origin effects). Under the Mendelian inheritance model, five QTL (on BTA 3, 5, 8, 12, and X) were found affecting birth weight through additive and dominance effects. When parent-of-origin effects were included in the model, QTL on BTA 3, 6, 8, and X were found to be significant. Some evidence supported linkage of a QTL affecting birth weight with a marker on BTA 6, which was not detected in the Mendelian inheritance model. For the QTL on the X chromosome, heterozygous females who inherited the Brahman allele from their sire had higher birth weight than animals inheriting the Brahman allele from their dam. Markers surrounding the QTL on BTA X reported in this study have been reported to also flank XIST (Amaral et al., 2002), a gene shown to be imprinted in mice (Vrana et al., 2000).

In a study measuring fetal and maternal environment traits on calves from an Angus-Brahman diallel, Fitzsimmons et al. (2008) showed that placental weight was correlated with fetal weight, and that both placental and fetal overgrowth were only present in the Brahman-sired crossbred (out of Angus dams). Burns et al. (2010) concluded that placental traits (Droughtmaster calves) may be more useful to predict

birth weight than early fetal measurements, warranting further investigation into calf genotype × maternal genotype interactions. In a study of placental tissues of horse × donkey hybrids, results reported by Wang et al. (2012) were consistent with previous assumptions of random X inactivation in the placental tissues of eutherian animals.

OBJECTIVES

The objectives of this study were to:

1. Confirm reciprocal differences (and sexual dimorphism in those differences) in birth weight in Brahman-Simmental F_1 calves produced by ET.

2. Estimate differences in Brahman versus Simmental breed of origin for non-standard genetic (e.g., parent-of-origin, mitochondrial origin, Y-chromosome, X-chromosome) effects on birth weight, accounting for and helping to explain the sexual dimorphism that occurs in crosses of Brahman and Simmental.

MATERIALS AND METHODS

Birth weight records were collected on 5,102 calves by Granada Land and Cattle Company. Calves were weighed shortly after birth. Records were collected on private operations in central Texas from 1983 to 1991. Breed groups included purebred Brahman, Simmental, and varying proportions of Brahman and Simmental produced by the matings described in Table 5. Unadjusted means for birth weight in all possible Brahman-Simmental matings are reported in Table 6. The majority of F_1 crosses were produced by mating Simmental bulls to Brahman dams. Half-blood parents were almost exclusively F_1 Brahman-Simmental crosses. Many of the purebred and F1 parents produced more than one type of calf (e.g. some sires produced both half and three-quarter blood calves.

Calves were produced out of multiple sires by natural service or artificial insemination (AI) (n = 2,188) and ET (n = 2,914). Embryo transfer calves were assigned randomly to recipient cows comprised of multiparous Holstein or crossbred beef cows. These cattle were all part of a breeding program to produce registered Simbrah cattle and were not part of a designed experiment.

Recipient cows at Granada Cattle Company were managed in separate herds based upon their expected parturition date as calculated by adding 285 days minus age of the embryo (usually seven days) to the date that the embryo was implanted. Calves produced by ET were managed apart from those produced by natural service or AI. Among ET calves, those with registered recipients were managed separately from those

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with crossbred recipients. First calf heifers were managed separately from multiparous cows.

The pedigree file included 10,565 animals over 12 generations. There were 906 sires, 326 paternal grandsires, 419 paternal grand-dams, 2,614 dams, 645 maternal grandsires, and 1,326 maternal grand-dams.

Statistical Analysis

The data in this study were analyzed using animal models in ASReml (Gilmour et al., 2009). Two models were used in analysis of these data in order to accomplish objectives 1 & 2. Fixed effects investigated included breed effects, sex of calf, contemporary group, and recipient breed. Contemporary groups consisted of ET/non-ET (non-ET consisted of calves produced by natural service or AI; ET included a designation for calves born to registered recipients), month of birth, year of birth, and the location where the calf was born. The contemporary group definition precluded ET and non-ET calves from being in the same contemporary group; this is emphasized because the maternal effects portions of the model differed between these two types of calves. Recipient breeds were categorized as crossbred beef, Holstein, varying proportions of *Bos indicus* influence for registered recipients with reliable breed records, and unknown. Calves that were not produced by ET were assigned to one level for this fixed effect. Recipient breed and contemporary group were partially confounded. Simple t-tests were conducted for means comparison.

Table 5. Number of observations by sire breed, dam breed, and sex of calf

| | Sire Breed[1] | | | | | | | | | | | | |
| | B | | ¾ B | | ½ B | | ⅜ B | | ¼ B | | S | | |
Dam Breed	M	F	M	F	M	F	M	F	M	F	M	F	Total
B	24	10			24	24					440	410	932
¾ B					11	11		1			92	100	215
⅝ B										1	2	6	9
½ B	171	158			16	14	202	193	99	96	527	448	1924
⅜ B	1	1			185	133	325	259	55	30	24	19	1032
¼ B					241	168	90	74	4	1			578
S	48	58	100	131	46	29							412
Total	471		231		902		1144		286		2068		5102

[1]B = Brahman; S = Simmental

Table 6. Unadjusted means and standard deviations for birth weight by sire breed, dam breed, and sex of calf[1,2]

Dam Breed	Sire Breed B		¾ B		½ B		⅜ B		¼ B		S		Total
	M	F	M	F	M	F	M	F	M	F	M	F	
B	33.02	32.34			35.32	32.56					37.21	37.62	37.06
	(4.09)	(4.30)			(5.51)	(6.13)					(6.15)	(6.17)	(6.18)
¾ B					44.74	41.81		*34.02*			37.91	36.21	37.65
					(5.98)	(8.01)		*(0.00)*			(5.79)	(6.16)	(6.40)
⅝ B									*34.02*		*32.89*	30.84	31.65
									(0.00)		*(1.60)*	(3.14)	(2.84)
½ B	41.92	38.14			40.03	38.43	37.83	35.07	35.74	34.08	38.86	37.33	37.84
	(7.72)	(5.90)			(10.09)	(4.74)	(6.37)	(5.68)	(4.97)	(4.7)	(7.15)	(5.82)	(6.66)
⅜ B					40.30	38.87	38.22	37.50	40.10	36.35	*40.82*	*36.29*	38.55
					(7.34)	(7.18)	(6.30)	(6.81)	(8.79)	(6.71)	*(0.00)*	*(0.00)*	(6.98)
¼ B					40.85	38.28	36.36	34.43	35.15	*56.70*			38.57
					(8.71)	(7.32)	(7.27)	(4.15)	(7.05)	*(0.00)*			(7.97)
⅛ B	*37.19*	*27.22*			34.98	*37.19*	48.63	40.73			38.16	36.44	38.03
	(0.00)	*(0.00)*			(5.27)	*(8.98)*	(6.33)	(5.50)			(7.07)	(5.61)	(6.98)
S	50.08	44.83	47.41	41.54	44.12	40.87							44.66
	(9.06)	(7.87)	(8.52)	(6.06)	(6.90)	(4.66)							(7.95)
Total	41.14	44.08	39.72				37.12	36.14	37.70				
	(8.29)	(7.78)	(7.79)				(6.46)	(6.45)	(6.38)				

[1]Standard deviations are listed in parentheses
[2]Italicized means indicate matings with fewer than three observations
[3]B = Brahman; S = Simmental

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Breed effects were parameterized in two ways: for the prediction of least squares means in Objective 1, sire breed × dam breed combinations represented the two possible reciprocal crosses that could produce F_1 calves. The interaction between reciprocal cross and sex of calf was included in this model. For analyses in objective 2, breed effects were accounted for by genetic covariates designed to investigate potential genetic mechanisms influencing birth weight patterns reported in the literature and possibly confirmed by the analyses in Objective 1.

Random effects investigated included direct genetic, maternal genetic, and maternal permanent environmental. The direct and maternal genetic effects, and the covariance between them, were modeled as having covariance matrices proportional to the numerator relationship matrix. The maternal permanent environmental effects were modeled as independently and identically distributed and uncorrelated with the random genetic effects. Direct and maternal heritabilities and direct-maternal covariance for birth weight were estimated. The maternal permanent environmental effect was estimated to be zero and subsequently dropped from the model.

Estimation of Birth Weight Averages in F_1 Embryo Transfer Calves

In order to address Objective 1, records on reciprocal F_1 animals produced by ET were analyzed and least squares means were predicted.

*Investigation of Genetic Effects Influencing Birth Weight*

In order to address Objective 2, covariates were designed to model modes of genetic action which may be influencing the unusual response in birth weight seen in Objective 1.

All covariates representing genetic effects were probabilities or expected values calculated from pedigree information. In cases where it was not possible to trace pedigree back to a purebred individual, the probabilities were assigned based on the recorded breed composition of the earliest recorded founder. The following were fitted as covariates: (1) Direct breed effects, (2) maternal breed effects, (3) direct heterosis, (4) maternal heterosis, (5) genomic imprinting, (6) probability of Brahman mitochondrial origin, (7) probability of Brahman Y chromosome, (8) probability of Brahman X chromosome, (9) probability of non-random X inactivation due to the breed of origin, (10) probability of non-random X inactivation due to the parent of origin.

Direct Breed Effects

Proportion of Brahman in the calf for all calves in the data set is represented by the direct breed effects covariate. Values for direct breed effects were assigned from 0 to 1, with 0 indicating a calf with 0% Brahman and 1 indicating a calf with 100% Brahman. The remainder of breed proportion was nearly all Simmental. A small fraction of the founder animals had minor proportions of non-Simmental *Bos taurus* breeds. No attempt was made to estimate differences between those breeds and Simmental. The direct breed effects covariate was designed to evaluate the change in birth weight as a

function of the increase in proportion of Brahman in the calf if all other covariates were held constant. Most of the values were around 25%, 37%, 50%, and 75% Brahman. This peaking was expected and can be attributed to the ultimate goal of making these matings, which was to produce Simbrah (⅜ Brahman ⅝ Simmental) cattle (Figure 1).
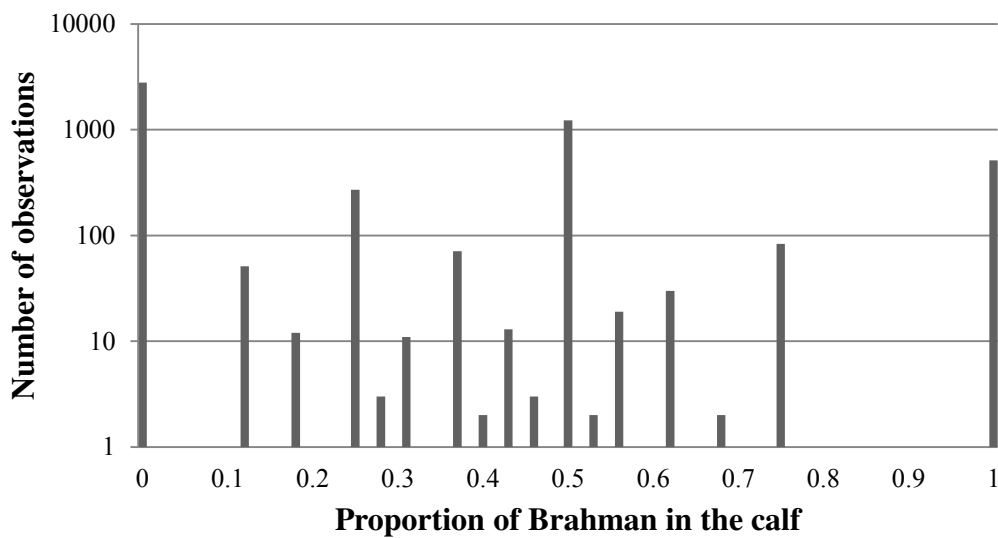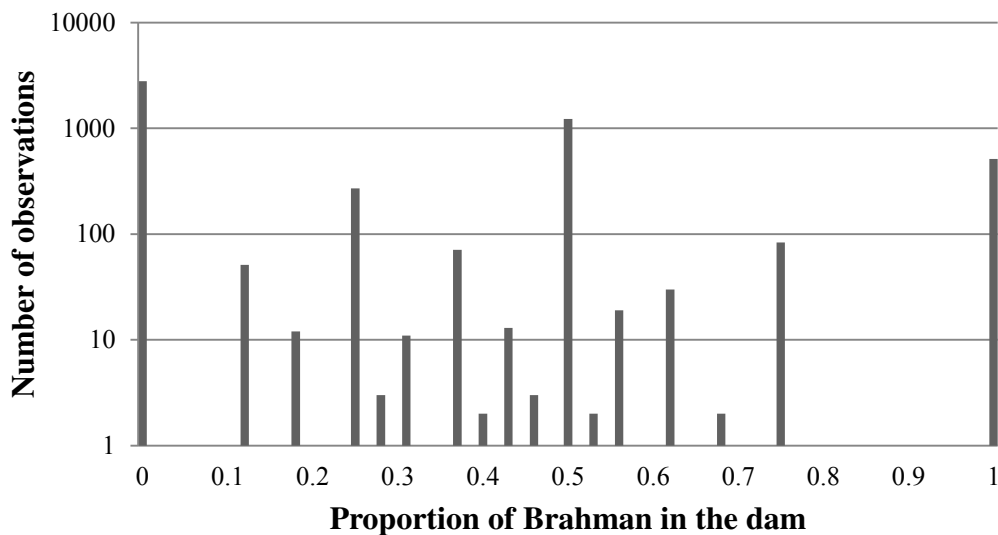

Figure 1. Frequency of covariate values for proportion of Brahman in the calf as representative of direct Brahman effects

Maternal Breed Effects

The maternal breed effects covariate is defined as the proportion of Brahman in the dam for non-ET calves. It is intended to represent the effect of the dam's maternal uterine environment on calf birth weight. It was set to zero for ET calves as the maternal

uterine effects of their recipients were modeled (to the extent possible) by recipient

breed code. Values for this covariate ranged from 0 to 1 (Figure 2), with 0 representing

a calf with 0% Brahman in the dam and 1 representing a calf with a dam that was 100%

Brahman. This covariate is interpreted as the effect of Brahman maternal uterine

environment on birth weight if all other covariates could be held constant.

Figure 2. Frequency of covariate values for the proportion of Brahman in the dam as representative of maternal breed effects. ET calves are constrained to 0 for this covariate

Direct Breed Heterozygosity

The direct breed heterozygosity covariate represents the proportion of expected

breed heterozygosity in the calf as calculated from the expected proportions of Brahman

and Simmental in the calf's sire and dam. Breed heterozygosity fractions ranged from 0

to 1 (Figure 3). This covariate is designed to estimate the effect of breed heterozygosity in the calf on the calf's birth weight while holding all other covariates constant. There is clustering of values for this covariate from 0.45 - 0.59, 0.75 - 0.79, and 1. This distribution was expected due to the types of matings producing these observations.
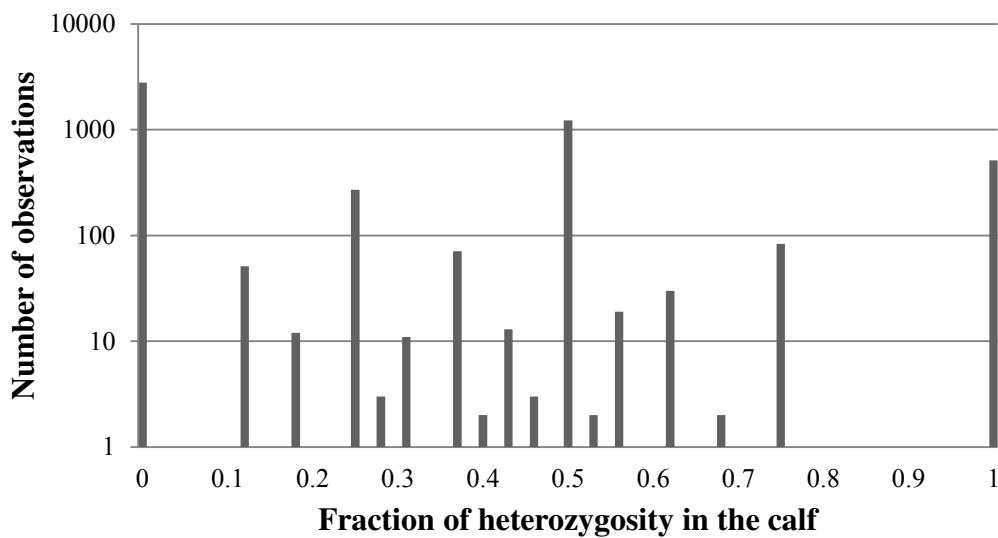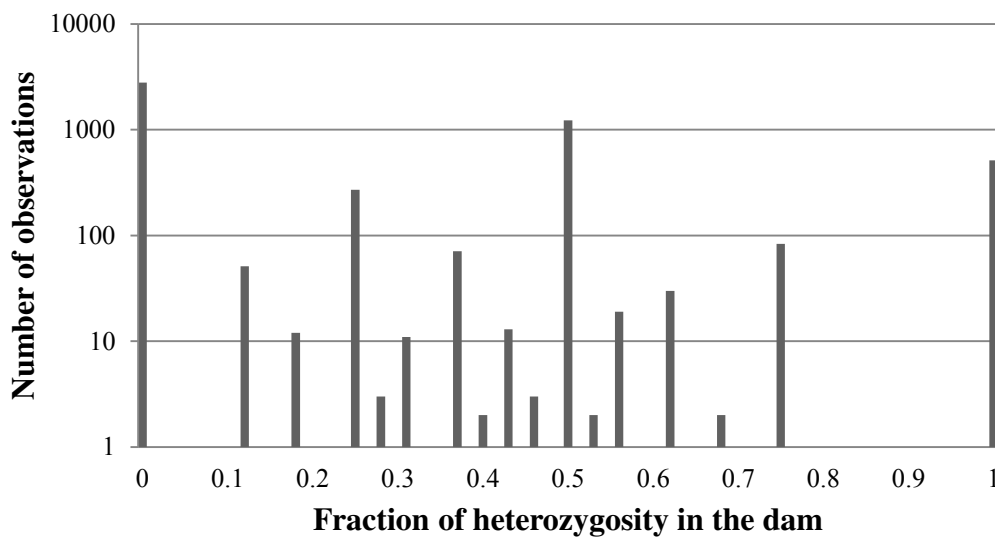

Figure 3. Frequency of covariate values for the fraction of heterozygosity in the calf as representative of direct breed heterozygosity

Maternal Breed Heterozygosity

The maternal breed heterozygosity covariate represents the proportion of breed-heterozygosity in the dam for non-ET calves. Maternal breed heterozygosity for ET calves was set to 0 because it is accounted for (as best is possible) by the recipient breed

code. This covariate is designed to estimate the effect of breed heterozygosity of the maternal uterine environment on birth weight. Values for this covariate ranged from 0 to 1 (Figure 4), with 0 representing a calf with a purebred dam (no breed-heterozygosity) and 1 representing a calf with a dam that was 100% breed-heterozygous (F_1).
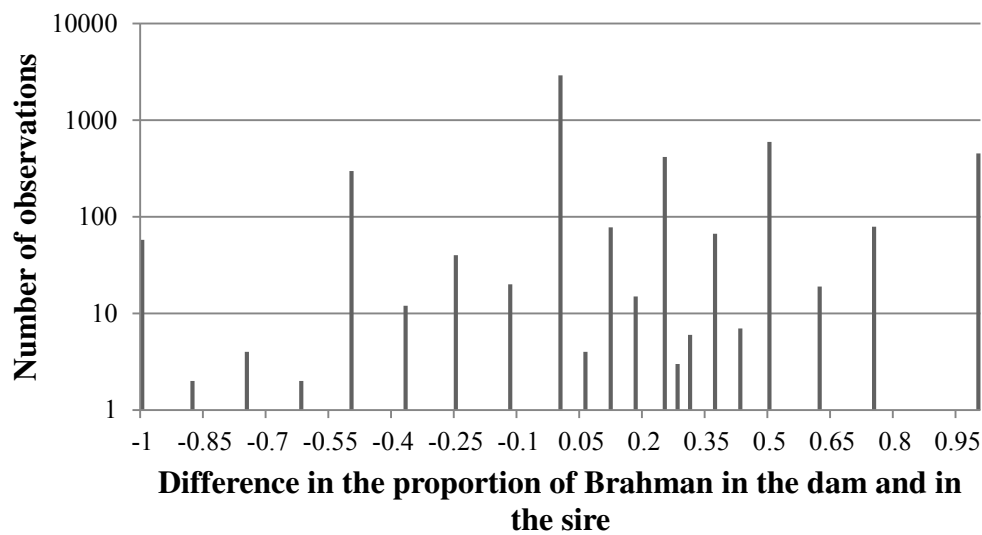

Figure 4. Frequency of covariate values for the fraction of heterozygosity in the dam as representative of maternal breed heterozygosity

Genomic Imprinting

The genomic imprinting covariate is defined as the difference between the proportion of Brahman in the genetic dam and the proportion of Brahman in the sire for all calves (regardless of ET/non-ET status). This effect is confounded by definition in

non-ET calves with the combination of direct and maternal breed effects (it is equal to twice the difference between the maternal and direct breed covariates). It is only records on ET calves in which the sire and dam have different proportions of Brahman that allows estimation of this effect without assuming a value for the direct or maternal breed effect. Values for this covariate ranged from -1 to 1 (Figure 5), with -1 representing a calf with a Simmental dam and Brahman sire, 0 representing a calf with parents of equal proportion Brahman, and 1 representing a calf with a Brahman dam and Simmental sire.

Figure 5. Frequency of covariate values for the difference in the proportion of Brahman in the dam and in the sire as representative of genomic imprinting. Values for ET and non-ET calves are included in the parameterization of this covariate

Other genetic mechanisms suggested by Thallman et al. (1993) include maternal effects of the donor cow's oviduct and uterus on the embryo prior to ET at day seven of

development and translation of mRNA transcribed from the donor's genome (and present in the cytoplasm of the oocyte) that may affect early embryonic development. Either of these two mechanisms would be modeled by the proportion of Brahman in the dam, regardless of whether the calf was produced by ET or not. Unfortunately, within the class of analyses based on expectations of breed proportions, this covariate is completely confounded (by definition) with the combination of the genomic imprinting and direct breed covariates. Therefore, any effects of these mechanisms will be reflected in the estimates for genomic imprinting and direct breed effects and those effects must be interpreted accordingly. The choice to parameterize the model to estimate genomic imprinting was made because it seems most plausible based on examples from the literature.

Mitochondrial Origin

The mitochondrial origin covariate represents the probability of an animal having mitochondria which originated from a Brahman ancestor, assuming that all mitochondria are inherited from the dam. Values for this covariate ranged from 0 to 1 (Figure 6), with 0 representing a 0% probability that a calf inherited Brahman mitochondria from its dam and 1 representing a 100% probability that a calf inherited Brahman mitochondria from its dam. The small number of records with intermediate probabilities reflects crossbred maternal founders for which no further pedigree is available.

Theoretically, Brahman dams would pass on *Bos indicus* mitochondria to their offspring. However, it should be noted that it is probable that Brahman cattle in the United States Brahman have *Bos taurus* mitochondria due to the way that the breed was

developed. This should be taken into account in interpretation of results for this covariate.
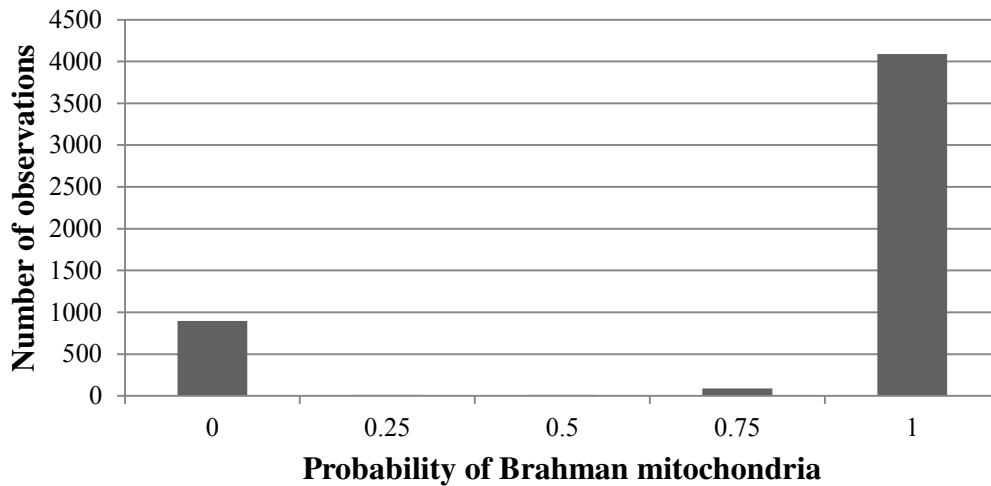
Figure 6. Frequency of covariate values for the probability of a calf inheriting a Brahman mitochondria from its dam as representative of mitochondrial origin

Y Chromosome Inheritance
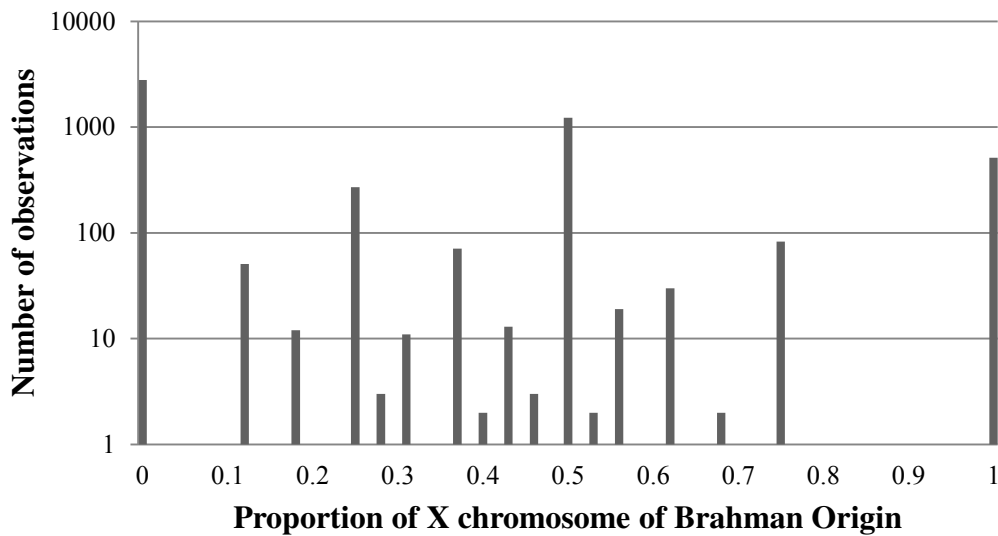
This covariate represents the probability that a calf inherited a Brahman Y chromosome from its sire. Females were set to 0 for this effect. Values for this covariate ranged from 0 to 1 (Figure 7), with 0 representing a 0% probability that a calf inherited a Brahman Y chromosome from its sire and 1 representing a 100% probability that a calf inherited a Brahman Y chromosome from its sire.

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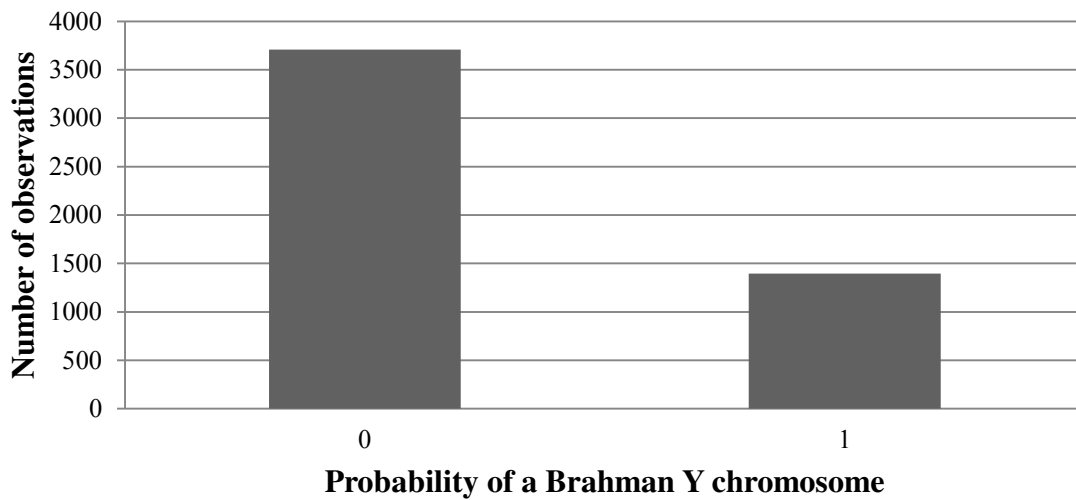
Figure 7. Frequency of covariate values for the probability of a calf inheriting a Brahman Y chromosome from its sire as representative of the Y chromosome inheritance covariate

X Chromosome Inheritance

This covariate is defined as the expected proportion of an animal's X chromosomes that are of Brahman origin. For male calves, it is equal to the probability of inheriting a Brahman X chromosome. This covariate assumes that expression in females is identical to that of males due to the silencing of one X chromosome in early female mammalian development (Avner and Heard, 2001). Values for this covariate ranged from 0 to 1 (Figure 8), with 0 representing a calf with only Simmental X chromosome(s) and 1 representing a calf with only Brahman X chromosome(s). An F_1 female, with one chromosome of each breed, would have a value of 0.5.
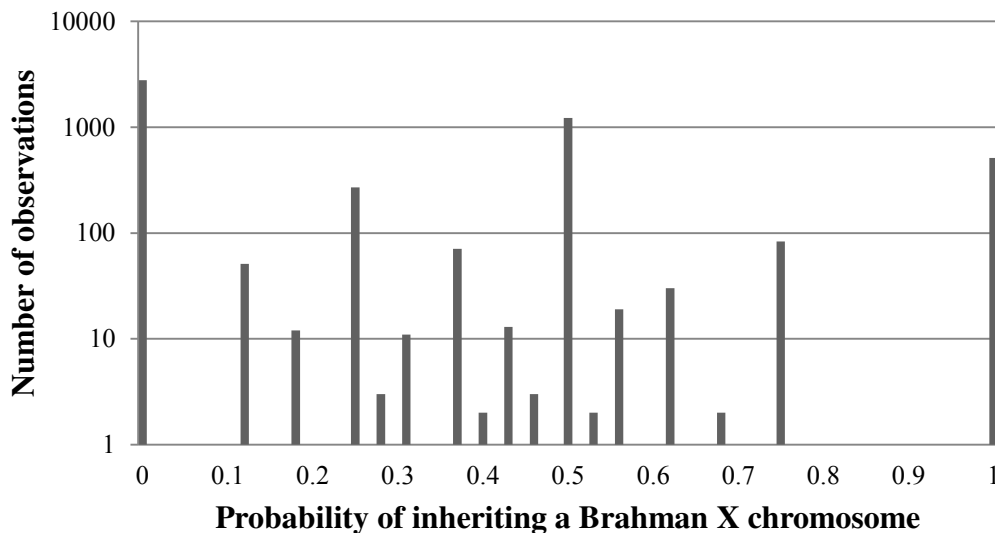
Figure 8. Frequency of covariate values for the probability of a Brahman X chromosome as representative of the X chromosome inheritance covariate

Non-random X Inactivation due to Breed of Origin

This covariate was designed to estimate the difference between females that are breed-heterozygous at the X chromosome and the average of the alternative breed homozygous females. It was the probability of breed heterozygosity of the X chromosomes of a female and is defined as 0 for males. It was statistically analogous to a dominance effect at a single locus and was motivated by examples in the literature of preferential inactivation of X chromosomes with specific alleles of an "X chromosome controlling element" in mice. For example, preferential inactivation of the Brahman X chromosome (when paired with an X of Simmental origin) would cause the breed-heterozygous female to more closely resemble a homozygous Simmental X female than

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a homozygous Brahman X female. The covariate implicitly allowed for the possibility of erosion of the primary effect by incomplete genetic linkage between the loci affecting preferential inactivation and those affecting the trait of interest. Statistically, there was no constraint to prevent the heterozygote estimate from falling outside the range of the homozygotes (similar to overdominance), but plausibility of this outcome requires an explanation (probably involving mosaicism) beyond that of non-random X inactivation.

Values for this covariate ranged from 0 to 1 (Figure 9). A value of 0 for this solution indicated that the calf did not have heterozygous X chromosomes by breed, while a value of 1 for this covariate indicated that the female was breed-heterozygous at the X chromosomes.
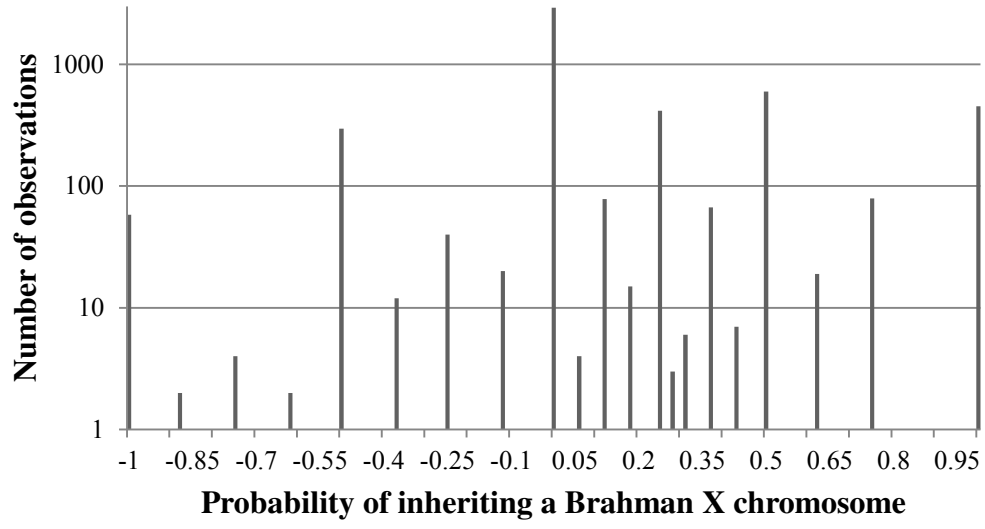

Figure 9. Frequency of covariate values for the probability of inheriting a Brahman and a non-Brahman X chromosome from the sire or the dam as representative of non-random X inactivation due to the breed of origin

Non-random X Inactivation due to Parent of Origin

Just as there are two ways in which an individual can be heterozygous at an autosomal locus (e.g., genomic imprinting can give rise to parent-of-origin effects), there are two ways that a female can be breed-heterozygous for the X chromosome, giving rise to a parent-of-origin effect for the X chromosome. The biological basis of this covariate is preferential X inactivation based on parent of origin.

This covariate accounts for whether a breed-heterozygous female inherited her Brahman X chromosome from her sire or her dam by taking the difference between the probability that she inherited a Brahman X chromosome from her dam and the probability she inherited a Brahman X chromosome from her sire. Males were assigned a value of 0 because they inherit only one X chromosome and therefore cannot be affected by non-random X inactivation. Values for this covariate ranged from -1 to 1 (Figure 10). A regression coefficient of -1 for this covariate indicates a female who inherited a Brahman X chromosome from her sire and a Simmental X chromosome from her dam. A regression coefficient of 1 for this covariate indicates she inherited a Simmental X from her sire and a Brahman X chromosome from her dam. Calves that are not breed-heterozygous for their X chromosomes and males have regression coefficients of 0. Negative regression coefficients for this covariate indicate that a calf was more likely to have inherited a Brahman X chromosome from its dam than from its sire, while positive regression coefficients for this covariate indicate that a calf was more likely to have inherited a Brahman X from its sire than from its dam.

Figure 10. Frequency of covariate values for the probability that a calf inherited a Brahman X chromosome from either the sire or the dam as representative of non-random X inactivation due to the parent of origin

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RESULTS AND DISCUSSION

Estimation of Birth Weight Averages in F_1 Embryo Transfer Calves

The model used to generate least squares means for F_1 calves included calf sex ($P < 0.001$), the interaction of sire breed × dam breed nested within sex ($P < 0.001$), and contemporary group ($P < 0.001$) as fixed effects. Recipient breed ($P = 0.88$) was dropped from the final model.

Least squares means for reciprocal F_1 calf birth weight are reported in Table 7. Brahman × Simmental males were 4.52 kg heavier than females and 12.29 kg heavier than Simmental × Brahman males. Simmental × Brahman females were 0.86 kg heavier than males on average (though sex averages were not significantly different) and 6.91 kg lighter than Brahman × Simmental females. Differences between overall birth weight means in reciprocal crosses were 9.59 kg (47.65 ± 1.59 and 38.05 ± 1.36 kg for Brahman × Simmental calves and Simmental × Brahman calves, respectively). These findings are consistent with differences reported in the literature for reciprocal *Bos indicus-Bos taurus* crosses (Cartwright et al., 1964; Brown et al., 1993b; Riley et al., 2007).

Table 7. Least squares means and standard errors by sire breed and dam breed for birth weight in F_1 reciprocal Brahman-Simmental ET calves

Cross[1]	Males			Females		
	n	Mean, kg	SE	n	Mean, kg	SE
B × S	46	49.91[a]	1.69	49	45.39[b]	1.71
S × B	292	37.62[c]	1.37	269	38.48[c]	1.38

[a-c]Means without a common superscript differ ($P < 0.05$)
[1]Cross is listed sire breed first
[2]B = Brahman; S = Simmental

Investigation of Genetic Effects Influencing Birth Weight

Covariates were designed to model various modes of genetic action proposed by Thallman et al. (1993) to influence reciprocal differences seen in *Bos indicus-Bos taurus* crosses.

Two models were used to investigate genetic effects influencing birth weight: (1) a complete model including all genetic covariates; (2) a reduced model including only significant covariates from the complete model. Fixed effects included were sex ($P < 0.001$), contemporary group ($P < 0.001$), and recipient breed ($P = 0.07$). Although $P > 0.05$ for recipient breed, it is likely that this is due to the structure of the data and the large number of ET calves with unknown recipient breeds. As such, recipient breed was retained in the model to account for any amount of variation in birth weight that may have been due to differences in this variable.

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Random effects included direct additive genetic and maternal additive genetic. The direct-maternal additive genetic covariance was estimated. The maternal permanent environmental effect was not included in the final model as it failed to significantly increase log-likelihood values and did not change estimates of the other components when additive and maternal genetic effects were already in the model. Estimates for all variance components are reported in Table 8. Estimates of direct and maternal heritability were 0.65 ± 0.07 and 0.36 ± 0.03. The direct-maternal correlation for birth weight was large and negative ($r = -0.70 \pm 0.04$). Estimates for direct heritability were much higher than those reported by Kriese et al. (1991) for purebred Brahman and Brangus cattle (0.37 kg^2 and 0.28 kg^2, respectively). The estimate for the direct-maternal correlation was also larger than the reported correlations of -0.15 for Brahman and -0.52 for Brangus. Estimates of this magnitude suggest that birth weight is largely influenced by additive gene action, however, the non-Mendelian nature of inheritance that appears to be influencing birth weight in these traits may be affecting the unusually large estimates in these data and as such, reported heritabilities should be interpreted appropriately.

Table 8. Estimates of variance components for birth weight from the final model

Component[1,2]	Estimate	SE
σ_A^2	21.13	2.59
σ_M^2	11.82	1.10
$\sigma_{A,M}$	-10.99	1.36
σ_E^2	10.48	1.57
σ_P^2	32.44	0.86
h_A^2	0.65	0.07
h_M^2	0.36	0.03
r	-0.70	0.04

[1]Subscripts indicate proportions of variance: A = additive genetic; M = maternal genetic; E = residual; P = phenotypic
[2]h_A^2 = direct heritability; h_M^2 = maternal heritability

Estimates, standard errors, and *P*-values for all genetic covariates are reported in Table 9. Direct breed-heterozygosity (fraction of heterozygosity in the calf) and genomic imprinting (the difference in proportion of Brahman in the dam and in the sire) were sources of variation in the model ($P < 0.001$). Direct breed effects (proportion of Brahman in the calf), maternal breed effects (proportion of Brahman in the dam), maternal breed heterozygosity (fraction of heterozygosity in the dam), mitochondrial origin, probability of a Brahman Y chromosome, probability of a Brahman X chromosome, non-random X inactivation by breed of origin, and non-random X inactivation by parent of origin were all excluded from the reduced model ($P > 0.05$).

Table 9. Levels of significance, least squares constant solutions for regression coefficients and SE for genetic covariates from analysis of birth weight

Genetic Effect	Complete Model[1]			Reduced Model[2]		
	P	Estimate	SE	P	Estimate	SE
Direct breed effects	0.239	−2.75	2.32	—	—	—
Maternal breed effects	0.997	0.01	1.32	—	—	—
Direct breed heterozygosity	< 0.001	4.09	0.96	< 0.001	3.75	0.82
Maternal breed heterozygosity	0.169	0.75	0.54	—	—	—
Genomic imprinting	< 0.001	−4.24	0.95	< 0.001	−4.13	0.44
Mitochondrial origin	0.359	−0.40	0.43	—	—	—
Probability of Brahman Y	0.937	0.03	0.37	—	—	—
Probability of Brahman X	0.226	−2.06	1.69	—	—	—
Non-random X inactivation (breed of origin)	0.257	0.74	0.65	—	—	—
Non-random X inactivation (parent of origin)	0.089	1.56	0.91	—	—	—

[1]Complete model includes all genetic effects covariates in the model
[2]Reduced model includes only significant genetic effects covariates from the complete model

Direct Breed Heterozygosity

Estimates of direct breed heterozygosity in *Bos indicus-Bos taurus* crosses are not straightforward to interpret, as results may be accounting for more than simply the difference in performance of the crossbred offspring over that of their purebred parents due to increased breed heterozygosity. Results indicated a 4.09 kg increase in birth weight ($P < 0.001$) associated with increasing proportion of breed heterozygosity at each locus from 0 to 1. Estimates for direct breed heterozygosity in these data coincide with those reported by Prayaga (2003), who also employed an animal model (but with modeled random dominance effects both as direct and maternal) and investigated additive and nonadditive genetic effects influencing birth weight in *Bos indicus, Bos taurus,* and *Bos indicus-Bos taurus* crosses. Riley et al. (2007) reported direct heterosis effects of 2.6 ± 0.3 kg and 3.7 ± 0.4 kg for Romosinuano-Brahman and Brahman-Angus crosses, respectively.

Genomic Imprinting

The estimate for the covariate designed to represent genomic imprinting was – 4.24 ± 0.95 kg. This solution suggests that as an animal moves from having parents with equal proportions of Brahman to having a greater proportion of Brahman in the dam than in the sire, birth weight is decreased. Previous studies have commented that this appeared to be the relationship observed, based upon changes in least squares means by breed group (Cartwright et al., 1964; Amen et al., 2007).

This covariate attempts to estimate the Brahman dam's genetic contribution to birth weight, regardless of ET status. However, there is some ambiguity as to precisely which mode of action is being influenced by the dam. Thallman et al. (1993) proposed three genetic mechanisms which may be explained by the design of this covariate: (1) genomic imprinting, (2) maternal effects of the donor ovary, oviduct, or uterus on the early stages of the embryo, and (3) maternal transmission of non-genetic ova cytoplasmic components (e.g. messenger RNA in the oocyte). While these three explanations cannot be partitioned out in the present parameterization, findings in the literature related to crossbreeding studies in interspecific hybrids have pointed to the potential for imprinting as the more likely predominant genetic mode of action (Vrana et al., 2000), and provides justification for the design of this covariate to model the potential effect of genomic imprinting.

Subsequent analyses within sex (for covariates where regression coefficients for one sex were not constrained to a single value) returned only the interaction with genomic imprinting as significant. The estimate for the genomic imprinting × sex interaction in this scenario was -5.4 ± 1.10 kg for males and -2.7 ± 1.25 kg for females.

These results build evidence for genomic imprinting as a genetic mechanism causing reciprocal differences in crosses of this nature. However, this model cannot tell us whether the imprinting effect was a negative effect expressed from the maternal genome, a positive effect expressed from the paternal genome, a combination of both, or more likely, the combination of both overriding a smaller combination of opposing effects.

Antagonism of the X Chromosome and Non-Random Inactivation Covariates

The model showed an antagonistic relationship between the covariates modeling the probability of a Brahman X chromosome and non-random X inactivation due to the parent of origin. When the X chromosome covariate was included in the model, estimates for each effect were -2.06 ± 1.69, 0.74 ± 0.65, and 1.56 ± 0.91 kg for X chromosome ($P = 0.23$), non-random by breed of origin ($P = 0.26$), and non-random by parent of origin ($P = 0.09$), respectively. When the X chromosome covariate was in a model with non-random X inactivation by breed of origin, the estimates were -4.68 ± 0.72 and 0.96 ± 0.64 for the X chromosome ($P < 0.001$) and non-random by breed of origin ($P = 0.14$) effects, respectively. However, when the X chromosome covariate was in a model with non-random X inactivation by parent of origin, the least squares constant solutions were -1.90 ± 1.68 and 1.76 ± 0.89 for X chromosome ($P = 0.26$) and non-random by breed of origin ($P = 0.05$), respectively. The model appeared to prefer the non-random X inactivation by parent covariate to the X chromosome covariate, but the X chromosome covariate was significant when the non-random X inactivation by parent covariate was not in the model. Biologically, an effect representing non-random X inactivation does not seem plausible in the absence of an overall effect of the X chromosome. The relationship between these three covariates is due to confounding and a limited number of females that are informative for the two non-random inactivation covariates.

CONCLUSION

In summary, reciprocal differences and sexual dimorphism existed in the reciprocal F_1 ET Brahman × Simmental crosses in this data set. A difference of 9.59 kg existed between reciprocal breeding groups. Males weighed 4.52 kg more than females for Brahman-sired crosses out of Simmental dams, and 0.86 kg lighter than females in the reciprocal cross.

Covariates designed to represent direct breed effects, maternal breed effects, maternal heterosis, mitochondrial origin, and Y chromosome effects were not statistically significant sources of variation in these data. Findings related to mitochondrial origin and Y chromosome effects coincide with those reported by Rohrer et al. (1994) and Herring et al. (1991), who also developed covariates designed to estimate probabilities of these covariates based upon pedigree information in Brangus cattle. Statistically insignificant results for direct and maternal breed effects in this model contradict results reported by Ferrell (2005), who concluded that maternal environments constrained growth, with a greater effect exerted on fetuses with a greater growth potential than on those with lesser growth potential. This may be due to the design of the model, as variance usually accounted for by the inclusion of "breed" as representative of direct and maternal breed effects in studies of this nature have likely shifted to the genetic covariates included in the parameterization of this model.

Covariates designed to model direct breed heterozygosity and genomic imprinting were significant sources of variation in the model. Direct breed

heterozygosity may not be straightforward to interpret in *Bos indicus-Bos taurus* crosses due to the apparent deviation from expectations on how cattle inherit genes that influence birth weight. Confounding between the covariates designed to evaluate the probability of inheriting a Brahman X chromosome and non-random X inactivation was due to insufficient data and structure to partition the effects. Findings in mice suggest that imprinting resulting in skewing of X-chromosome inactivation (Vrana et al., 2000) may be an explanatory model for reciprocal differences in weight and placentation in interspecific mouse hybrids. It is possible that reciprocal differences in birth weight in *Bos indicus-Bos taurus* crosses is occurring by a similar method.

Results from these data warrant further investigation into genomic imprinting and X chromosome effects in future research projects.

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