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Growth and pubertal development in Brahman-, Boran-, Tuli-, Belgian Blue-, Hereford- and Angus-sired F1 bulls^{1,2}

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ABSTRACT: Growth and testicular development between 7 and 15 mo of age were evaluated in bulls produced by mating sires of six breeds (Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli) to Angus, Hereford, and MARC III (four-breed composite) cows. At 12 mo of age, Angus- and Hereford-sired bulls had the heaviest body weight ($P < 0.08$ to 0.001), whereas Brahman- and Belgian Blue-sired bulls were intermediate, and Boran- and Tuli-sired bulls weighed the least. Bulls sired by European breeds grew more rapidly after weaning ($P < 0.01$) than did Brahman-, Boran-, and Tuli-sired bulls, and these differences in growth rate were maintained through 15 mo of age, indicating that offspring of heat-adapted sire breeds (Brahman, Boran, and Tuli) have lower postweaning rates of gain, particularly during winter months, than do offspring of non-heat adapted sire breeds. Testis size was smaller initially ($P < 0.01$) and remained smaller in offspring of heat-adapted sire breeds through yearling age. By 15 mo of age, testis size was largest ($P < 0.06$ to 0.001)

in Angus-sired bulls and had become similar among Hereford-, Brahman-, Boran- and Belgian Blue-sired bulls but remained smaller ($P < 0.02$ to 0.001) in Tuli-sired bulls. Thus, offspring of heat-adapted sire breeds had delayed testicular development compared with that of nonheat adapted sire breeds, particularly through yearling age. At puberty, Angus-sired bulls were 23 to 82 d younger ($P < 0.05$ to 0.001) than all other sire breeds except Hereford, and Brahman-sired bulls were older at puberty ($P < 0.05$ to 0.001) than were bulls of all other sire breeds except Boran. Testis size at puberty was quite similar among breeds of bulls (scrotal circumference = 27.9 ± 0.1 cm) despite large breed differences in age, body weight, and hip height. Thus, measurement of yearling testis size was a reliable indicator of age at puberty among widely divergent breeds of bulls. In addition, the lower postweaning rates of gain and the smaller and slower testicular development in offspring of heat-adapted sire breeds should be noted by cattle producers considering use of such breeds in crossbreeding and breed improvement programs.

Key Words: Beef Cattle, Bulls, Puberty, Semen, Testes

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Introduction

Breed differences in performance characteristics are an important genetic resource for improving efficiency of beef production, and crossbreeding is a widely accepted means of incorporating desirable traits from var-

ious breeds. No single breed excels in all traits of importance, and beef cattle producers in the United States are under increasing pressure to exploit new breeds in order to match genetic potential with divergent climates, feed resources, and consumer preferences. Often, little comparative data on reproductive traits in these diverse breeds is available to the U.S. producer. In addition, the increasing use of EPD and artificial insemination by beef cattle producers has placed greater value on earlier puberty, larger testis size, and increased sperm production by individual bulls. Thus, there is a need for characterization of reproductive traits in bulls representing diverse beef breeds.

In this study, we compare reproductive development in beef bulls from six diverse biological types of cattle. Three heat-tolerant breeds (Brahman, Boran, and Tuli) and one continental breed (Belgian Blue) were compared to two British breeds (Hereford and Angus) widely used in the United States. The Boran is an ancient African Zebu breed that reportedly matures early,

¹Mention of trade names is necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the same by USDA implies no approval of the product to the exclusion of others that may also be suitable.

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Table 1. Numbers of F₁ bulls (n = 234) evaluated for pubertal development during 3-yr Germplasm Evaluation Project (Cycle V; born 1992 to 1994)^a

Sire breed	Dam breed			Total F ₁ bulls (n)
	Hereford	Angus	MARC-III	
Hereford	0	18	14	32
Angus	8	0	16	24
Brahman	9	16	22	47
Boran	9	15	19	43
Tuli	11	15	18	44
Belgian Blue	10	14	20	44
All F ₁ bulls	47	78	109	234

^aBulls were born between March and May of each spring, number of bulls evaluated from each sire breed and dam breed was balanced each year, and total bulls was very similar each year (79, 78, and 77 bulls born in 1992, 1993, and 1994, respectively).

has high fertility, and is highly adapted to stressful tropical conditions (Frisch et al., 1997; Gaughan et al., 1999). The Tuli is a *Sanga* breed believed to have been developed from *Bos taurus* cattle thousands of years ago in Africa, and it has demonstrated high fertility and maternal performance (Frisch et al., 1997; Gaughan et al., 1999). Belgian Blue is a continental European breed exhibiting a propensity for increased muscling (Arthur, 1995; Casas et al., 2001; Wheeler et al., 2001). This report presents results from Cycle V of the Germplasm Evaluation Project at Clay Center characterizing F₁ bulls of these breeds compared to Hereford- and Angus-sired crosses for testicular development and puberty.

Materials and Methods

This study was conducted at the U.S. Meat Animal Research Center (40° 51' N latitude, 98° 04' W longitude) located near Clay Center, Nebraska. Six breeds of sires were evaluated by topcrossing on Angus (n = ~500), Hereford (n = ~350), and MARC III (1/4 Angus, 1/4 Hereford, 1/4 Pinzgauer, 1/4 Red Poll) composite (n = ~550) cows each year, as described by Cundiff et al. (1998). All cows were 4 yr of age or older. Angus sires were bred to Hereford and MARC III cows, and Hereford sires were bred to Angus and MARC III cows. All other sire breeds were mated to Angus, Hereford, and MARC III cows. Matings were made over a 3-yr period, and a sample of about 80 males (8 to 11 males sired by Hereford or Angus; 14 to 16 by Brahman, Tuli, Boran, or Belgian Blue sires) were left intact each year (1992 to 1994) to evaluate growth and pubertal development in F₁ bulls (Table 1). Bulls were born between March and May of each spring. To obtain a representative sample of about 80 males each year, approximately every third bull calf born within sire breed was left intact each year. For sire breeds with relatively large numbers of sires (Hereford, Angus, Brahman, and Belgian Blue), each sire was represented by one to two male offspring per year, while each Tuli and Boran sire was represented by two to five male offspring each year. Number of bulls evaluated from each sire breed and dam breed was balanced each year, and total bulls evaluated was

very similar each year (79, 78, and 77 bulls born in 1992, 1993, and 1994, respectively). Range of F₁ bull age was 42 to 47 d within each year, and age range within sire breed was 32 to 37 d in each of the 3 yr. A total of 234 F₁ bulls were evaluated in this study.

Sire Breeds

Hereford. Semen from 14 polled- and four horned-Hereford sires was used with Angus and MARC III cows to produce F₁ intact male progeny. Eight of the Hereford sires were born from 1982 to 1984 and were used in previous evaluations (Cundiff et al., 1990), and 10 sires were born after 1985.

Angus. Semen from 18 Angus sires was used with Hereford and MARC III cows to produce F₁ intact male progeny. Four Angus sires were born between 1982 and 1984 and had been used in a previous evaluation (Cundiff et al., 1990), and 14 sires were born after 1985 and used for the first time in Cycle V of the Germplasm Evaluation Project program.

Brahman. To estimate genetic trends in the Brahman breed, semen from 16 sires born between 1984 and 1989 (current) and from 12 sires born between 1964 and 1976 (original, Gregory et al., 1979a) was used to produce F₁ intact male progeny.

Boran. Semen from seven Boran sires was imported from Australia and used to produce F₁ intact male progeny. The Boran traces its origin to *Bos indicus* introduced from the Indian subcontinent into East Africa about 400 A.D. (Hetzl, 1988).

Tuli. Semen from nine Tuli bulls was imported from Australia and used to produce F₁ intact male progeny. The Tuli is a *Sanga* breed indigenous to Eastern and Southern Africa with either no or minimal *Bos indicus* germplasm (Frisch et al., 1997).

Belgian Blue. Semen from 23 sires was used to produce F₁ intact male progeny. The Belgian Blue has historically been selected to establish a high frequency for a major gene that causes muscle hypertrophy (Hanset and Michaux, 1985).

Management and Data Collection

Bull calves were weaned at 185 ± 1 d of age. Following weaning each year, about 80 bull calves were randomly assigned to two drylot pens of approximately 40 bulls each with all sire and dam breeds represented in each pen. Bulls were fed a diet of corn silage, rolled corn, and protein-mineral-vitamin supplement (2.69 Mcal of ME/kg of DM, 12.88% crude protein) for 10 mo. After a 42-d acclimation period, body weight, hip height, scrotal circumference, and length of each testicle were measured at 28-d intervals for 9 mo. All testis measurements were performed by one technician using procedures as described by Lunstra et al. (1988). Concurrent with these measurements, electroejaculated semen collections were begun when bulls reached a scrotal circumference of 26 cm and continued at 28-d intervals. Ejaculate volume, sperm concentration, and progressive motility were assessed for each ejaculate, using the methods described by Lunstra and Echterkamp (1982). Briefly, semen was maintained at 37°C, and progressive motility was determined from duplicate estimates using a microscope (400× magnification). Sperm concentration was determined from spectrophotometer (550 nm) readings of duplicate semen aliquots diluted 1:200 with 1% formalin in 0.9% saline (Lunstra and Coulter, 1997). Puberty was defined as the age at which a bull first produced an ejaculate containing at least 50×10^6 sperm with >10% progressive motility (Lunstra et al., 1978). First freezable semen was defined as the age at which a bull first produced an ejaculate containing at least 500×10^6 sperm with >50% progressive motility (Lunstra et al., 1993), since these numbers represent a threshold above which freezing of semen becomes economically feasible. After 500×10^6 sperm with at least 50% motility were detected in an ejaculate, semen collection ceased for that bull. To calculate paired testicular volume, scrotal circumference (SC) was assumed to represent the connected circumference of two apposed circles of equal radius, r , using the following formula (Lunstra et al., 1988):

$$SC = 4r + 2\pi r$$

No adjustment for thickness of the scrotum was used. Average testicular length (**AvgTL**) was calculated by averaging the lengths of the left and right testicles. Assuming each testicle was a prolate spheroid, paired testicular volume (**PTV**) was then calculated using the following formula (Lunstra et al., 1988):

$$PTV = 0.0396 (\text{AvgTL}) (\text{SC})^2$$

Approximately 14 d after collection of final data, bulls were slaughtered (~16 mo of age) at a local packing plant (total = 136; $n = 75$ and 61 bulls born in 1992 and 1994, respectively; no slaughter data were collected from bulls born in 1993). Testes and epididymides obtained at slaughter were weighed, and a 10-g subsample

of testicular parenchyma was snap-frozen for subsequent homogenization to determine daily sperm production (**DSP**) per gram of testis and total DSP per paired testes (**TDSP**) (5.32 d was used as constant for DSP calculations; Amann et al., 1974). Salim and Entwistle (1982) have suggested that a constant of 5.11 d should be used for calculating DSP in *Bos indicus*-cross bulls. Initial calculation and analysis of DSP and TDSP using a constant of 5.11 d for Brahman- and Boran-sired bulls increased their DSP and TDSP values by approximately 4% but had no significant effects on differences among sire breeds. Therefore, a DSP constant of 5.32 d was used for all analyses in the present report.

Data Analyses

Data were analyzed with a least squares procedure (Harvey, 1985), and least squares means and SE are presented in text and tables. Data for BW, ADG, age, hip height, testicular measurements, age at puberty, and percentage pubescent were analyzed with a model that included sire breed, sire nested within sire breed, dam breed, dam age, year, sire breed × dam breed, sire breed × year, dam breed × year, dam age × year, and linear effects for birth date. All other possible interactions were included in the initial analyses, but interactions with nonsignificant effects were dropped from the final model. Level of significance for interactions retained in analyses is indicated within tables in the Results section. Sire breed, dam breed, dam age, and year were treated as fixed effects. All variables, except age, were adjusted for differences in calendar age using birth date as a linear covariate. Sire breed was tested using sire nested within sire breed (sire/sire breed) as the source of error. All other fixed effects were tested using the residual error variation for each trait. Sire breed means were tested with nonorthogonal contrast. Current and original Brahman types were tested with the same model, but no differences between types were observed for growth or puberty traits, and subsequently, both types were treated as a single-sire breed. Responses with probabilities less than 0.05 were considered to be different. Residual correlations among growth and testis traits at slaughter were derived from a model that included the fixed effects and all interactions that were significant for at least one trait.

Results

Birth and Weaning Weights

Sire breed and year had significant effects on birth weight of F1 bulls, but dam breed and the various interactions had no significant effects (Table 2). Brahman- and Boran-sired bulls had the highest birth weights, and Tuli-sired bulls had the lowest ($P < 0.01$), while Hereford-, Angus- and Belgian Blue-sired bull calves were intermediate (Table 2). Sire breed, dam breed, dam age, year, and their interactions had no effect (P

Table 2. Least squares means and standard errors for birth and weaning weight in F₁ bulls (n = 234) evaluated for pubertal development during 3-yr Germplasm Evaluation Project (Cycle V; born 1992 to 1994)^a

Sire breed	n	Variable			
		Birth wt, kg	Age at weaning, d	Adjusted 200 d wt, kg	ADG (birth to weaning), kg
Hereford	32	44.1 ± 1.1	185.2 ± 2.2	252 ± 6	1.04 ± 0.03
Angus	24	43.0 ± 1.3	189.6 ± 2.5	254 ± 6	1.06 ± 0.03
Brahman	47	49.7 ± 0.9	184.4 ± 1.7	260 ± 5	1.06 ± 0.02
Boran	43	46.1 ± 1.1	185.8 ± 1.5	254 ± 7	1.04 ± 0.03
Tuli	44	38.9 ± 1.0	185.4 ± 1.8	242 ± 6	1.02 ± 0.03
Belgian Blue	44	44.2 ± 0.9	184.1 ± 2.1	244 ± 5	1.00 ± 0.02
All F ₁ bulls	234	44.4 ± 0.5	185.4 ± 0.8	251 ± 3	1.04 ± 0.01
Average sire breed					
LSD 0.05 ^b		2.73	5.09	14.0	0.07
	df	Probability levels			
Sire breed (SB)	5	<0.001	0.755	0.069	0.512
Sire/sire breed	97	0.182	0.080	0.002	0.004
Dam breed (DB)	2	0.129	0.550	0.006	0.005
Dam age	3	0.846	0.806	0.685	0.638
Year (Y)	2	0.005	0.114	0.549	0.152
SB × DB	8	0.251	0.148	0.078	0.039
SB × Y	10	—	—	—	—
Dam age × Y	6	—	—	—	—
Birth date linear	1	0.039	—	0.006	0.019

^aAll means were adjusted for “age differences” by running birth date as a covariate (i.e., adjusted to average “age” of all bulls).

^bBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

> 0.10) on age that F1 bulls were weaned (185 ± 1 d) in this study (Table 2). Brahman-sired bulls had the highest while Tuli- and Belgian Blue-sired bulls had the lowest weaning weight (adjusted 200-d weight) and lowest ADG from birth to weaning; dam breed and sire within sire breed had significant effects on these weight characteristics, while the effect of sire breed approached significance only for 200-d weight ($P = 0.07$, Table 2).

Characteristics at Initial Measurement

The F1 bulls averaged 230 ± 1 d of age at the beginning of evaluation each year (Table 3), and there was no significant effect of sire breed, dam breed, dam age, year, or their interactions on age of bulls at monthly evaluations throughout the study. At 230 d of age, sire breed, sire within sire breed, dam breed, and year all had significant effects on initial body weight of F1 bulls, but dam age and the various interactions had no significant effects (Table 3). Initial body weight did not differ between Angus-, Hereford-, Brahman-, Boran-, and Belgian Blue-sired F1 bulls at 230 d of age ($P > 0.15$). However, initial body weight of Tuli-sired bulls was less than Hereford-, Angus-, and Brahman-sired bulls ($P < 0.01$) and less than Boran-sired bulls ($P = 0.03$) but did not differ from Belgian Blue-sired bulls ($P = 0.09$) at 230 d of age (Table 3). Numerically, initial body weight was heaviest in Angus- and Brahman-sired bulls, intermediate in Hereford-, Boran-, and Belgian Blue-sired bulls, and lowest in Tuli-sired bulls at 230 d of age. Bulls from Angus (309 ± 4) cows weighed more at 230 d of age ($P < 0.05$) than did bulls from Hereford

(296 ± 5) or MARC III (290 ± 4) cows. Fixed effects influenced initial hip height of F1 bulls in a manner similar to effects on initial body weight, except that the effect of dam breed was not significant (Table 3). Brahman-sired bulls were taller ($P < 0.01$) than other breeds, Boran-sired bulls were taller ($P = 0.04$) than Tuli-sired bulls, and all other F1 bulls were of similar hip height at 230 d of age.

All indicators of testis size (SC, AvgTL, and PTV) were smaller ($P < 0.01$) in Brahman- and Boran-sired bulls than in Hereford-, Angus-, and Belgian Blue-sired bulls at initial measurement (Table 3). Testis size was largest in Angus-sired bulls and was similar among Hereford-, Tuli-, and Belgian Blue-sired bulls at 230 d of age. Sire breed and year had consistent significant effects on all three indicators of testis size (SC, AvgTL, and PTV). Average testicular length also was influenced by sire within sire breed and dam breed, and PTV was influenced by sire within sire breed and dam age (Table 3).

Characteristics at Yearling Measurement

Sire breed, sire within sire breed, and dam breed had significant effects on yearling body weight of F1 bulls, and the sire breed × year and dam age × year interactions also had significant effects (Table 4). Angus- and Hereford-sired bulls were the heaviest, while Brahman- and Belgian Blue- were intermediate, and Boran- and Tuli-sired bulls weighed the least at yearling age. Yearling body weight of Tuli-sired bulls did not differ from Boran-sired bulls ($P = 0.11$), but both weighed less than Angus-, Hereford-, Belgian Blue-, and Brahman-sired

Table 3. Least squares means and standard errors of variables at initial measurement (230 d of age) in F₁ bulls (n = 234) evaluated for pubertal development between 7 and 15 mo of age during Germplasm Evaluation Project (Cycle V)

Sire breed	Variable at initial measurement ^a						
	n	Age, d	BW, kg	Hip height, cm	SC, cm	Avg TL, cm	PTV, cm ³
Hereford	32	230.2 ± 2.1	302 ± 6	114.1 ± 0.7	25.3 ± 0.4	8.2 ± 0.2	219 ± 11
Angus	24	233.5 ± 2.4	307 ± 7	113.4 ± 0.8	27.1 ± 0.5	8.8 ± 0.2	259 ± 12
Brahman	47	229.8 ± 1.7	305 ± 5	120.2 ± 0.6	21.7 ± 0.3	6.7 ± 0.2	134 ± 9
Boran	43	229.8 ± 2.3	299 ± 7	114.9 ± 0.8	22.6 ± 0.4	7.0 ± 0.2	148 ± 12
Tuli	44	229.7 ± 2.1	282 ± 7	113.1 ± 0.8	25.4 ± 0.4	8.5 ± 0.2	222 ± 11
Belgian Blue	44	228.8 ± 1.7	294 ± 5	113.2 ± 0.6	24.7 ± 0.3	8.0 ± 0.2	202 ± 9
All F ₁ bulls	234	230.3 ± 0.9	298 ± 3	114.8 ± 0.3	24.5 ± 0.2	7.9 ± 0.1	197 ± 5
Average sire breed							
LSD 0.05 ^b		5.1	15.2	1.80	1.01	0.53	26.8
	df	Probability levels					
Sire breed (SB)	5	0.755	0.021	<0.001	<0.001	<0.001	<0.001
Sire/sire breed	97	0.080	0.008	0.034	0.094	0.026	0.043
Dam breed (DB)	2	0.550	0.005	0.145	0.101	0.010	0.089
Dam age	3	0.806	0.408	0.149	0.094	0.207	0.044
Year (Y)	2	0.114	<0.001	0.018	0.003	<0.001	<0.001
SB × DB	8	0.148	0.158	0.0780	0.380	0.029	0.268
SB × Y	10	—	—	—	—	—	—
Dam age × Y	6	—	—	—	—	—	0.043
Birth date linear	1	—	0.165	0.25	0.016	0.125	0.019

^aSC = scrotal circumference, Avg TL = average testis length, PTV = paired testicular volume.

^bBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

bulls ($P < 0.01$). Angus- and Hereford-sired F₁ bulls did not differ in yearling body weight, but both Angus- ($P = 0.06$) and Hereford-sired bulls ($P = 0.08$) tended to be

heavier than Belgian Blue-sired bulls (Table 4). Dam breed influenced F₁-bull yearling weight, and bulls from Angus (458 ± 6) and Hereford (451 ± 7) cows

Table 4. Least squares means and standard errors of variables at yearling measurement (370 d of age) in F₁ bulls (n = 234) evaluated for pubertal development between 7 and 15 mo of age during Germplasm Evaluation Project (Cycle V)

Sire breed	Variable at yearling measurement ^a							
	n	Age, d	BW, kg	ADG (weaning to yearling), kg	Hip height, cm	SC, cm	Avg TL, cm	PTV, cm ³
Hereford	32	370.2 ± 2.1	476 ± 9	1.30 ± 0.03	126.1 ± 0.7	33.0 ± 0.4	11.4 ± 0.2	498 ± 20
Angus	24	373.5 ± 2.4	481 ± 10	1.33 ± 0.03	125.9 ± 0.8	34.4 ± 0.5	11.8 ± 0.2	556 ± 22
Brahman	47	369.8 ± 1.7	443 ± 7	1.08 ± 0.02	130.9 ± 0.6	30.7 ± 0.4	10.7 ± 0.2	409 ± 16
Boran	43	369.8 ± 2.3	424 ± 12	1.01 ± 0.04	124.6 ± 0.8	31.3 ± 0.5	10.9 ± 0.3	430 ± 23
Tuli	44	369.7 ± 2.1	408 ± 10	0.99 ± 0.03	123.8 ± 0.7	30.2 ± 0.4	10.6 ± 0.2	394 ± 21
Belgian Blue	44	368.8 ± 1.7	457 ± 8	1.23 ± 0.03	126.0 ± 0.6	32.4 ± 0.4	11.4 ± 0.2	482 ± 17
All F ₁ bulls	234	370.3 ± 0.9	448 ± 4	1.16 ± 0.01	126.2 ± 0.3	32.0 ± 0.2	11.1 ± 0.1	462 ± 9
Average sire breed								
LSD 0.05 ^b		5.09	21.2	0.07	1.74	1.11	0.52	48.4
	df	Probability levels						
Sire breed (SB)	5	0.755	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Sire/sire breed	97	0.080	<0.001	0.006	0.093	0.196	0.002	0.017
Dam breed (DB)	2	0.550	0.012	0.003	0.007	0.219	0.002	0.069
Dam age	3	0.806	0.126	0.003	0.042	0.376	0.314	0.196
Year (Y)	2	0.114	0.251	0.561	<0.001	0.012	<0.001	<0.001
SB × DB	8	0.148	0.178	0.216	0.526	0.865	0.634	0.714
SB × Y	10	—	0.034	—	—	—	—	—
Dam age × Y	6	—	0.022	0.009	0.010	—	—	—
Birth date linear	1	—	0.203	0.602	0.131	0.783	0.087	0.329

^aSC = scrotal circumference, Avg TL = average testis length, PTV = paired testicular volume.

^bBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

weighed more ($P < 0.05$) than did bulls from MARC III (436 ± 6) cows. In general, differences in yearling body weight reflected breed differences in ADG from weaning to yearling age; Brahman-, Boran-, and Tuli-sired bulls exhibited the lowest ADG, while the ADG of Angus-, Hereford-, and Belgian Blue-sired bulls was higher ($P < 0.01$; Table 4). The fixed effects of sire breed, sire within sire breed, dam breed, and year influenced yearling hip height of F1 bulls, and the interaction of dam age \times year also was significant (Table 4). Brahman-sired bulls continued to have the tallest hip height ($P < 0.01$), while Tuli- and Boran-sired bulls were smallest, and Angus-, Hereford-, and Belgian Blue-sired bulls were of intermediate hip height at yearling age (Table 4).

At yearling age, all indicators of testis size (SC, AvgTL, and PTV) were smaller ($P < 0.05$) in Brahman-, Boran-, and Tuli-sired bulls than in bulls of other sire breeds (Table 4). Testis size was largest in Angus-sired bulls ($P < 0.05$), intermediate in Hereford- and Belgian Blue-sired bulls, and smallest ($P < 0.05$) and relatively similar ($P > 0.25$) among Brahman-, Boran-, and Tuli-sired bulls. Sire breed and year had consistent significant effects on all three indicators of yearling testis size (SC, AvgTL, and PTV). Yearling AvgTL also was influenced by sire within sire breed and dam breed, and yearling PTV was influenced by sire within sire breed (Table 4).

Characteristics at Final Measurement and at Slaughter

Sire breed, sire within sire breed, and dam breed had significant effects on final body weight of F1 bulls at 454 d of age, and the sire breed \times year and dam age \times year interactions also had significant effects (Table 5). As at yearling age, Angus- and Hereford-sired bulls were the heaviest, while Brahman- and Belgian Blue-sired bulls were intermediate, and Boran- and Tuli-sired bulls weighed the least at 454 d of age. Final body weight of Tuli-sired bulls did not differ from Boran-sired bulls ($P = 0.62$), but both weighed less than Angus-, Hereford-, Belgian Blue-, and Brahman-sired bulls ($P < 0.01$). Angus- and Hereford-sired F1 bulls did not differ in final body weight ($P = 0.32$), but both Angus- ($P < 0.01$, $P < 0.01$) and Hereford-sired bulls ($P = 0.06$, $P < 0.01$) were heavier than Belgian Blue- and Brahman-sired bulls (Table 5). Dam breed influenced F1-bull body weight at 454 d of age, and bulls from Angus (557 ± 7) cows weighed more ($P < 0.05$) than did bulls from Hereford (538 ± 8) and MARC III (524 ± 7) cows. Similar to results at yearling age, the fixed effects of sire breed, sire within sire breed, dam breed, and year influenced final hip height of F1 bulls at 454 d of age, and the interaction of dam age \times year remained significant (Table 5). Brahman-sired bulls continued to have the tallest hip height ($P < 0.001$), while Tuli- and Boran-sired bulls were smallest, and Angus-, Hereford-, and Belgian Blue-sired bulls were of intermediate and similar hip height at 454 d of age (Table 5).

At 454 d of age, testis size was more similar among breeds than at previous timepoints. However, all indicators of testis size (SC, AvgTL, and PTV) were smaller ($P < 0.02$ to 0.001) in Tuli-sired bulls than in bulls of other sire breeds (Table 5). Testis size was larger in Angus-sired bulls ($P < 0.06$ to 0.001) than in other breeds except Hereford and was relatively similar ($P > 0.25$) among Hereford-, Brahman-, Boran-, and Belgian Blue-sired bulls. Sire breed and sire within sire breed had consistent significant effects on all three indicators of testis size (SC, AvgTL, and PTV) at 454 d of age. Final AvgTL also was influenced by dam breed, and final PTV was influenced by dam breed and dam age (Table 5).

At slaughter (Table 6) of a representative portion of these bulls ($n = 136$) approximately 2 wk after final measurement, paired testes weight and paired epididymal weight were smaller ($P < 0.05$ to 0.001) in Tuli-sired bulls than in bulls of other sire breeds. Paired testes weight was larger in Angus-sired bulls ($P < 0.04$ to 0.001) than in Tuli-, Boran-, and Belgian Blue-sired bulls. Paired testes weight and paired epididymal weight were relatively similar ($P > 0.25$) among Angus- and Hereford-sired bulls, among Brahman- and Boran-sired bulls, and among Belgian Blue- and Tuli-sired bulls (Table 6). While DSP per gram of testis did not differ ($P > 0.06$) among sire breed groups (Table 6), TDSP was markedly lower in Tuli-sired bulls ($P < 0.01$ to 0.001) than in bulls of other sire breeds except Belgian Blue-sired bulls ($P > 0.15$). Thus, sire breed differences in TDSP reflected the major differences in paired testes weight among sire breeds. Sperm production (DSP and TDSP) in Belgian Blue-sired bulls did not differ ($P > 0.15$) from that of bulls of any other sire breeds (Table 6). Residual correlations indicated that paired testes weight at slaughter had little relationship to bull body weight and hip height, but paired testes weight was well correlated with TDSP ($r = 0.65$) and highly correlated with live animal measurement of scrotal circumference ($r = 0.84$) and estimates of paired testes volume ($r = 0.87$). Since testis weight and sperm production were highly correlated to live animal testes measurements, the significance of statistical fixed effects were reflected at final measurement (Table 5) and are not presented again here.

Characteristics at Puberty

At puberty, large breed differences in age, body weight, and hip height were present (Table 7). Angus-sired bulls were 23 to 82 d younger at puberty than were bulls of all other sire breeds, which was earlier ($P < 0.05$ to 0.001) than in any other breed except Hereford ($P = 0.09$), and Brahman-sired bulls were older at puberty ($P < 0.05$ to 0.001) than were bulls of all other sire breeds except Boran ($P = 0.08$). With their older age at puberty, Brahman-sired bulls were taller and heavier at puberty ($P < 0.01$ to 0.001) than were bulls of all other sire breeds, and Boran-sired

Table 5. Least squares means and standard errors of variables at final measurement (454 d of age) in F₁ bulls (n = 234) evaluated for pubertal development between 7 and 15 mo of age during Germplasm Evaluation Project (Cycle V)

Sire breed	n	Variable at final measurement ^a					
		Age, d	BW, kg	Hip height, cm	SC, cm	Avg TL, cm	PTV, cm ³
Hereford	32	454.5 ± 2.0	575 ± 10	128.8 ± 0.8	35.7 ± 0.5	11.5 ± 0.2	587 ± 21
Angus	24	457.3 ± 2.3	591 ± 12	128.3 ± 0.9	36.2 ± 0.6	11.9 ± 0.2	618 ± 24
Brahman	47	453.9 ± 1.6	532 ± 9	135.0 ± 0.7	35.0 ± 0.4	11.3 ± 0.2	550 ± 18
Boran	43	453.8 ± 2.0	500 ± 14	127.2 ± 0.9	34.7 ± 0.5	11.5 ± 0.2	549 ± 26
Tuli	44	453.8 ± 1.9	494 ± 12	127.3 ± 0.8	33.1 ± 0.5	10.9 ± 0.2	478 ± 23
Belgian Blue	44	452.8 ± 2.1	547 ± 11	129.3 ± 0.8	34.9 ± 0.5	11.1 ± 0.2	542 ± 22
All F ₁ bulls	234	454.3 ± 0.9	540 ± 5	129.3 ± 0.4	34.9 ± 0.2	11.4 ± 0.1	554 ± 10
Average sire breed							
LSD 0.05 ^b		5.04	25.8	2.04	1.18	0.49	54.0
	df	Probability levels					
Sire breed (SB)	5	0.781	<0.001	<0.001	<0.001	0.012	<0.001
Sire/sire breed	97	0.188	<0.001	0.032	0.025	0.001	0.004
Dam breed (DB)	2	0.402	0.003	0.010	0.264	0.006	0.043
Dam age	3	0.667	0.063	0.133	0.015	0.130	0.025
Year (Y)	2	0.092	0.363	0.028	0.362	0.115	0.267
SB × DB	8	0.174	0.059	0.519	0.534	0.579	0.388
SB × Y	10	—	0.052	—	—	—	—
Dam age × Y	6	—	0.010	0.029	—	—	—
Birth date linear	1	—	0.303	0.068	0.807	0.346	0.643

^aSC = scrotal circumference, Avg TL = average testis length, PTV = paired testicular volume.

^bBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

Table 6. Least squares means and standard errors of variables at slaughter (n = 136; 470 d of age) in F₁ bulls evaluated for pubertal development between 7 and 15 mo of age during Germplasm Evaluation Project (Cycle V)

Sire breed	n	Variable at slaughter ^a				
		Slaughter age, d	Paired testes weight, g	Paired epididymal wt, g	Daily sperm production/g ^b	Total daily sperm production ^b
Hereford	22	470.9 ± 2.0	568 ± 23	58.2 ± 1.9	10.4 ± 0.7	5,637 ± 409
Angus	15	471.7 ± 2.3	609 ± 26	57.7 ± 2.3	9.9 ± 0.8	5,836 ± 495
Brahman	28	470.4 ± 1.6	564 ± 19	50.9 ± 1.7	9.4 ± 0.6	5,144 ± 362
Boran	29	470.8 ± 2.0	543 ± 19	52.1 ± 1.6	9.6 ± 0.6	5,059 ± 356
Tuli	29	470.3 ± 1.9	426 ± 19	44.3 ± 1.6	8.7 ± 0.6	3,657 ± 358
Belgian Blue	13	469.1 ± 2.1	495 ± 29	48.6 ± 2.5	10.3 ± 0.9	4,611 ± 545
All F ₁ bulls	136	470.6 ± 0.9	529 ± 25	51.4 ± 2.0	9.6 ± 0.5	4,914 ± 322
Average sire breed						
LSD 0.05 ^c		5.0	64	6.2	1.8	1,280
Residual correlations (all bulls) ^d						
Final body wt ^e		0.171	0.347	0.342	-0.078	0.127
Final hip height ^e		0.272	0.173	0.238	-0.116	-0.004
Final scrotal circumference ^e		0.020	0.839	0.675	0.078	0.477
Final paired testes volume ^e		-0.220	0.870	0.685	0.053	0.480
Slaughter age ^a		—	0.052	0.092	-0.145	-0.038
Paired testes wt ^a		—	—	0.764	0.201	0.651
Paired epididymal wt ^a		—	—	—	0.168	0.517
Daily sperm production/g ^a		—	—	—	—	0.845
Total daily sperm production ^a		—	—	—	—	—

^aObtained at slaughter at 470 d of age.

^bExpressed as sperm production × 10⁶.

^cBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

^dPearson residual correlations, after analysis to remove the effects of sire, sire breed, dam breed, year, age of dam, and appropriate interactions ($P < 0.01 = \geq 0.210$; $P < 0.001 = \geq 0.270$).

^eObtained at 454 d of age. See Table 5 (i.e., final live animal measurement).

Table 7. Least squares means and standard errors of variables at puberty (50×10^6 sperm with >10% progressive motility) in F₁ bulls (n = 234) evaluated for pubertal development between 7 and 15 mo of age during Germplasm Evaluation Project (Cycle V)^a

Sire breed	n	Variable at puberty ^b						
		Age, d	BW, kg	ADG (weaning to puberty), kg	Hip height, cm	SC, cm	Avg TL, cm	PTV, cm ³
Hereford	32	261 ± 9	339 ± 9	1.38 ± 0.17	117.1 ± 1.0	27.9 ± 0.2	9.4 ± 0.1	293 ± 6
Angus	24	238 ± 10	323 ± 11	1.89 ± 0.17	114.2 ± 1.1	28.1 ± 0.2	9.4 ± 0.2	292 ± 7
Brahman	47	320 ± 7	391 ± 8	1.13 ± 0.14	127.7 ± 0.8	27.9 ± 0.1	9.6 ± 0.1	298 ± 5
Boran	43	302 ± 8	362 ± 9	1.10 ± 0.25	120.6 ± 1.3	27.8 ± 0.1	9.6 ± 0.1	296 ± 5
Tuli	44	284 ± 8	331 ± 9	1.09 ± 0.21	117.4 ± 1.1	27.7 ± 0.1	9.6 ± 0.1	294 ± 5
Belgian Blue	44	273 ± 7	347 ± 8	1.38 ± 0.10	117.6 ± 0.9	27.9 ± 0.1	9.6 ± 0.1	297 ± 5
All F ₁ bulls	234	279 ± 4	349 ± 4	1.33 ± 0.08	119.1 ± 0.5	27.9 ± 0.1	9.5 ± 0.1	295 ± 2
Average sire breed								
LSD 0.05 ^c		21.7	23.0	0.39	2.49	0.31	0.32	13.8
	df	Probability levels						
Sire breed (SB)	5	<0.001	<0.001	0.008	<0.001	0.623	0.756	0.958
Sire/sire breed	97	0.288	0.217	<0.001	0.014	0.981	0.089	0.348
Dam breed (DB)	2	0.098	0.382	0.257	0.785	0.822	0.052	0.419
Dam age	3	0.564	0.179	0.284	0.099	0.863	0.127	0.237
Year (Y)	2	0.205	0.258	0.002	0.480	0.628	<0.001	<0.001
SB × DB	8	0.936	0.941	0.860	0.972	0.775	0.461	0.316
SB × Y	10	—	—	0.002	—	—	—	—
Dam age × Y	6	—	—	—	—	—	—	—
Birth date linear	1	0.230	0.805	0.797	0.287	0.792	0.945	0.839

^aPuberty occurred when a bull first produced an ejaculate containing at least 50×10^6 sperm with >10% progressive motility.

^bSC = scrotal circumference, Avg TL = average testis length, PTR = paired testicular volume.

^cBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

bulls were taller and heavier at puberty ($P < 0.05$ to 0.001) than were breeds other than Brahman (Table 7). Hereford-, Tuli-, and Belgian Blue-sired bulls were similar in age, body weight, and hip height at puberty (Table 7). In general, differences in body weight at puberty reflected breed differences in ADG from weaning to puberty; Brahman-, Boran-, and Tuli-sired bulls exhibited the lowest ADG, while the ADG of other breeds tended to be higher, and Angus-sired bulls had the highest ADG ($P < 0.05$ to 0.001; Table 7). Only sire breed had a significant effect on age at puberty and body weight at puberty in F₁ bulls (Table 7), while sire breed and sire within sire breed had significant effects on ADG and hip height at puberty.

At puberty, defined as the age when a bull first produced an ejaculate containing at least 50×10^6 sperm with >10% progressive motility, neither sire breed nor sire within sire breed had any effect on testis size, and the means for SC, AvgTL, and PTV at puberty each were very similar ($P > 0.21$) among breeds (Table 7). Scrotal circumference at puberty was not influenced by any fixed effects or interactions, and year was the only factor that had a significant effect on AvgTL at puberty and PTV at puberty (Table 7). Scrotal circumference at puberty averaged 28 cm in all sire breed groups.

Since sire breed was the only fixed effect that influenced age at puberty in F₁ bulls, sire breed differences in the patterns of pubertal development in F₁ bulls are shown in Figure 1. A greater proportion of Angus-sired F₁ bulls had reached puberty by 7, 8, and 9 mo of age

than in other sire breeds (Figure 1). The Angus pattern was followed closely by Hereford-sired bulls, and 100 percent of Angus- and Hereford-sired bulls were pubescent by 11 mo of age and beyond. Brahman- and Boran-sired bulls were the slowest to reach puberty, and the proportion pubertal lagged behind that of Angus-, Here-

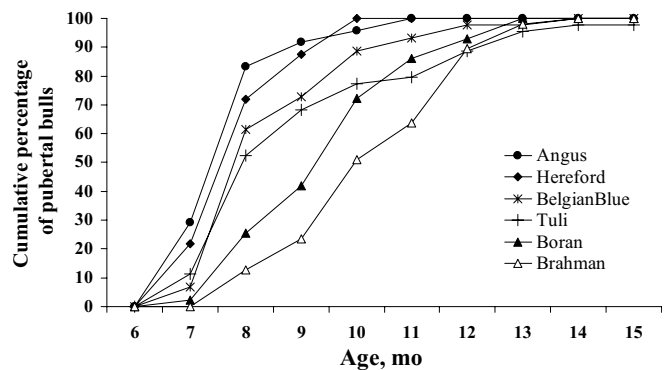


Figure 1. Graphic comparison of the differences among six sire breeds in proportions (patterns of cumulative percentage becoming pubescent) of F₁ beef bulls reaching puberty (defined as the age at which a bull first produced an ejaculate containing at least 50×10^6 sperm with >10% progressive motility). Data were obtained from 234 F₁ bulls evaluated monthly from weaning through 15 mo of age and the number of F₁ bulls evaluated per sire breed ranged from 24 to 47.

Table 8. Least squares means and standard errors of variables at freezable semen (500×10^6 sperm with $> 50\%$ progressive motility) in F₁ bulls (n = 234) evaluated for pubertal development between 7 and 15 mo of age during Germplasm Evaluation Project (Cycle V)^a

Sire breed	n	Variable at freezable semen ^b						
		Age, d	BW, kg	ADG (weaning to freezable semen), kg	Hip height, cm	SC, cm	Avg TL, cm	PTV, cm ³
Hereford	32	326 ± 10	420 ± 12	1.30 ± 0.03	122.4 ± 0.9	31.4 ± 0.4	10.8 ± 0.2	428 ± 17
Angus	24	311 ± 11	409 ± 14	1.35 ± 0.03	121.0 ± 1.0	32.0 ± 0.5	10.8 ± 0.2	442 ± 19
Brahman	47	398 ± 8	469 ± 10	1.09 ± 0.03	131.8 ± 0.8	32.4 ± 0.3	11.0 ± 0.1	464 ± 14
Boran	43	381 ± 11	434 ± 14	1.00 ± 0.04	124.9 ± 1.1	31.9 ± 0.5	10.9 ± 0.2	442 ± 22
Tuli	44	362 ± 10	400 ± 13	0.98 ± 0.03	123.1 ± 1.0	30.4 ± 0.5	10.4 ± 0.2	384 ± 19
Belgian Blue	44	325 ± 8	407 ± 11	1.26 ± 0.03	122.6 ± 0.8	30.8 ± 0.4	10.8 ± 0.1	410 ± 15
All F ₁ bulls	234	350 ± 4	423 ± 5	1.16 ± 0.01	124.3 ± 0.4	31.5 ± 0.2	10.8 ± 0.1	429 ± 8
Average sire breed								
LSD 0.05 ^b		24.5	30.4	0.07	2.28	1.03	0.41	41.7
	df	Probability levels						
Sire breed (SB)	5	<0.001	<0.001	0.001	<0.001	0.001	0.059	0.003
Sire/sire breed	97	0.028	0.022	0.005	0.017	0.001	0.008	<0.001
Dam breed (DB)	2	0.198	0.609	0.015	0.527	0.304	0.013	0.115
Dam age	3	0.867	0.211	0.006	0.209	0.320	0.057	0.126
Year (Y)	2	0.002	0.009	<0.001	0.174	0.064	<0.001	<0.001
SB × DB	8	0.472	0.786	0.423	0.664	0.877	0.759	0.818
SB × Y	10	—	—	0.001	—	—	—	—
Dam age × Y	6	—	—	0.006	—	—	—	—
Birth date linear	1	0.026	0.868	0.234	0.094	0.348	0.177	0.129

^aPuberty occurred when a bull first produced an ejaculate containing at least 50×10^6 sperm with 10% progressive motility.

^bSC = scrotal circumference, Avg TL = average testis length, PTR = paired testicular volume, ADG = average daily gain.

^cBreed group differences larger than the sire breed least significant difference (LSD 0.05) are significant ($P < 0.05$).

ford-, and Belgian Blue-sired breeds through 12 mo of age ($P < 0.05$; Figure 1). The proportion of Belgian Blue-sired bulls reaching puberty was somewhat lower than that of Angus- and Hereford-sired bulls through 11 mo of age, but the proportion pubescent was more similar to that of Angus- and Hereford-sired bulls than to other breeds. The pattern of pubertal development in Tuli-sired bulls (*Sanga* bulls) appeared to be intermediate to the two patterns displayed by *Bos taurus*- and *Bos indicus*-sired bulls.

Characteristics at First Freezable Semen

At first freezable semen, as at puberty, large breed differences in age, body weight, and hip height were observed (Table 8). Angus-sired bulls were 24 to 87 d younger at freezable semen, which was earlier ($P < 0.001$) than other breeds except Hereford- ($P = 0.32$) and Belgian Blue-sired bulls ($P = 0.30$). Brahman-sired bulls were older at freezable semen ($P < 0.01$) than were bulls of all other sire breeds except Boran ($P = 0.16$). With their older age at freezable semen, Brahman-sired bulls were taller and heavier at freezable semen ($P < 0.02$ to 0.001) than were bulls of all other sire breeds. Boran-sired bulls were taller at freezable semen ($P < 0.04$ to 0.001) than were breeds other than Brahman (Table 8), but body weight at freezable semen in Boran-sired bulls did not differ from that of Hereford- ($P = 0.35$) and Angus-sired bulls ($P = 0.15$). Hereford- and Belgian Blue-sired bulls were similar in age, body weight, and hip height at freezable semen (Table 8).

Boran- and Tuli-sired bulls had lower ADG from weaning to freezable semen than did Brahman- ($P < 0.01$) and other breeds ($P < 0.001$), while the ADG of Hereford-, Angus-, and Belgian Blue-sired bulls were similar and higher than that of other breeds ($P < 0.001$; Table 8). Sire breed, sire within breed, and year had significant effects on age and body weight at freezable semen in F₁ bulls (Table 8), while only sire breed and sire within sire breed had significant effects on hip height at freezable semen.

At first freezable semen, defined as the age when a bull first produced an ejaculate containing at least 500×10^6 sperm with $>50\%$ progressive motility, several fixed effects influenced testis size in F₁ bulls. Sire breed, sire within sire breed, and year all had significant effects on mean SC, AvgTL, and PTV at freezable semen (Table 8). Mean SC, AvgTL, and PTV at freezable semen each were very similar among Angus-, Brahman-, and Boran-sired bulls ($P > 0.30$), slightly smaller in Hereford- and Belgian Blue-sired bulls, and smallest in Tuli-sired bulls (Table 8). Scrotal circumference, AvgTL, and PTV at freezable semen were not influenced significantly by any interactions (Table 8).

Discussion

In the U.S. beef cattle industry, sources of tropically adapted germplasm have been generally limited to Zebu breeds (*Bos indicus*, cattle with a prominent thoracic hump that originally evolved in southern Asia), primarily to the American Brahman (Chase et al.,

2001). Currently, about 37% of all beef cows in the United States are maintained in stressful subtropical environments where 25 to 50% *Bos indicus* inheritance (primarily Brahman) is required to provide for efficient production (Cundiff et al., 1986, 2000). *Bos indicus* × *Bos taurus* cross cattle excel in weaning weight per cow exposed (Cundiff et al., 1986) and in cow efficiency (Green et al., 1991), because of higher heterosis relative to *Bos indicus* × *Bos taurus* crosses. However, as the proportion of *Bos indicus* inheritance increases, the advantages of Brahman influence on heterosis and components of cow efficiency are tempered by older age at puberty (Gregory et al., 1979b; Chenoweth et al., 1996; Cundiff et al., 2000), discounts for reduced marbling of beef (Wheeler et al., 1994; Franke, 1997), and reduced meat tenderness (Wheeler et al., 1994; 2001; Franke, 1997; O'Connor et al., 1997). Toward this end, further germplasm evaluation is needed to identify new breeds that maintain production advantages while reducing these problems. Thus, we thought it was appropriate to investigate male reproductive development in *Bos taurus* breeds that may provide increased marbling and muscling and to determine if additional *Bos indicus* and *Sanga* breeds (cattle with a prominent cervical hump) that evolved under tropical conditions in Africa share the same male reproductive characteristics as those which have evolved in southern Asia. The sires from the sire breeds used in this study (Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli) were selected to represent the predominant genetics of each breed. Thus, the results provide a current comparison of male reproductive development in bulls representing these diverse breeds.

At birth, Brahman-sired bull calves weighed 5.3 to 6.7 kg more, Boran-sired calves weighed 1.7 to 3.1 kg more, and Tuli-sired calves weighed 4.1 to 5.5 kg less, than did Hereford-, Angus-, and Belgian Blue-sired bull calves. The heavier birth weights of Zebu-sired compared to *Bos taurus*-sired bull calves agrees well with published data. Others have reported that progeny of Brahman sires are 3 to 6 kg heavier, progeny of Boran sires are slightly heavier, and progeny of Tuli sires are 2 to 4 kg lighter in birth weight than are progeny of *Bos taurus* sires (Browning et al., 1995; Herring et al., 1996; Thrift, 1997). The relationships between these sire breed differences in birth weight were maintained at weaning. At weaning, Brahman-sired bulls weighed 6 to 16 kg more, Boran-sired bulls weighed 0 to 10 kg more, and Tuli-sired bulls weighed 2 to 12 kg less, than did Hereford-, Angus-, and Belgian Blue-sired bulls. Again, these breed differences in weaning weight agree well with data in previous reports (Browning et al., 1995; Herring et al., 1996; Thrift, 1997; Cundiff et al., 1998; Chase et al., 2000). Bulls from Hereford cows (42.8 ± 1.1) tended to have lower birth weights ($P = 0.13$) than did bulls from Angus (44.5 ± 0.9) and MARC III (45.9 ± 0.9 kg) cows, and bulls from Hereford (1.00 ± 0.02) and MARC III (1.02 ± 0.02) cows had lower rates of gain from birth to weaning ($P < 0.05$) than did bulls

from Angus cows (1.09 ± 0.02 kg). Thus, there was an interaction between sire breed and dam breed ($P = 0.04$) for ADG from birth to weaning, but this interaction exhibited no other apparent or meaningful trend.

By 230 d of age, body weight did not differ between Angus-, Hereford-, Brahman-, Boran-, and Belgian Blue-sired F1 bulls, but body weight in Tuli-sired bulls remained significantly lower than in other breeds. Despite their lower body weight, Tuli-sired bulls did not differ in hip height from Angus-, Hereford-, and Belgian Blue-sired bulls at 230 d of age. However, Brahman-sired bulls were substantially taller (5 to 7 cm) than other breeds at 230 d of age, and Boran-sired bulls were significantly taller (~2 cm) than Tuli-sired bulls. Others have reported that hip heights of Tuli-sired calves are 7 to 9 cm shorter than Brahman-sired calves at weaning but are similar to or less than hip heights of *Bos taurus*-sired calves (Herring et al., 1996; Browning et al., 1997; Chase et al., 2000).

Dramatic differences in testis size were present among sire breeds at initial measurement. Scrotal circumference in Brahman- and Boran-sired bulls was 2 to 4 cm smaller than in Tuli-, Belgian Blue-, and Hereford-sired bulls and 4 to 6 cm smaller than in Angus-sired bulls at 230 d of age. Testicular length and PTV exhibited sire breed effects similar to differences in scrotal circumference, and PTV in Zebu-sired bulls was approximately one-half that of Angus-sired bulls, while PTV was intermediate in Tuli-, Belgian Blue-, and Hereford-sired bulls. When castrated at 205 to 223 d of age in Texas, paired testes weight in Angus-sired bulls (73 ± 4 g) was twice that of Brahman-sired bulls (37 ± 4 g), and that of Tuli-sired bulls was intermediate (43 ± 3 g; Browning et al., 1997). Bulls in their study had Brahman dams and had substantially smaller testes than did bulls in our study at similar ages. In Florida, scrotal circumference at 249 d of age in Brahman × Angus bulls was smaller (20 cm) than in Tuli × Angus bulls (22 cm; Chase et al., 2001) and agrees well with data obtained in our study for Brahman-sired bulls (22 cm) at initial measurement. Bulls in Texas (Browning et al., 1997) also weighed 70 to 130 kg less than bulls in our study and weighed 33 to 74 kg less than bulls in Florida (Chase et al., 2000). In another study in Texas (Herring et al., 1996), body weight at weaning (7 mo) of F1 calves (both sexes) sired by Brahman, Boran, and Tuli bulls and born to Hereford and Angus cows was similar to that reported in Florida but remained 74 to 82 kg lower than that of comparable breed types in our study. Tropical adaptation (heat-tolerance) is associated with reduced testis size in *Bos indicus* cattle (Fields et al., 1979, 1982; Godfrey et al., 1990; Randel, 1994; Chase et al., 1997) and may be part of the explanation for the smaller testis size of bulls in Texas. In addition, climate may have had a detrimental effect on growth and testis development of Zebu-cross bulls in Texas.

As evidenced by sire breed differences in body weight at yearling age and at final measurement (454 d of age), *Bos taurus*-sired bulls grew more rapidly after weaning

than did Brahman-, Boran-, and Tuli-sired bulls. This is best reflected by comparison of sire breed differences in ADG from weaning to yearling age; the ADG of all three *Bos taurus*-sired bull groups were relatively similar and significantly higher than the ADG of Brahman-, Boran-, and Tuli-sired bulls. These results are consistent with other reports on growth rates and body weights for these breed types (Herring et al., 1996; Freetly and Cundiff, 1997; Chase et al., 2001) and substantiate the hypothesis that offspring of heat-adapted sire breeds have lower rates of gain and feed efficiencies than do offspring of nonheat adapted sire breeds (Freetly and Cundiff, 1997). These differences in growth patterns through yearling age may be partially attributable to seasonal effects that favor heat-adapted breeds during the preweaning period (predominantly summer months; April to September) but favoring cold-tolerant breeds during the post weaning period (predominantly winter months; October to March). Previous comparisons of breeds that evolved in temperate vs tropical climates have shown a similar effect of season on growth of steers (Cundiff et al., 1984) and heifers (Gregory et al., 1979a, 1979b; Freetly and Cundiff, 1997; Thallman et al., 1999) born in spring months.

Testis size was smaller in offspring of heat-adapted sire breeds through yearling age but had become similar among Hereford-, Brahman-, Boran-, and Belgian Blue-sired bulls by 454 d of age. However, testis size in Tuli-sired bulls remained smaller than in bulls of other sire breeds through 454 d of age, and testis size and TDSP in Tuli-sired bulls remained smaller at slaughter. Thus, offspring of heat-adapted sire breeds have substantially smaller testes at 7 mo of age and exhibit delayed testicular development compared to offspring of nonheat adapted sire breeds at least through yearling age. Relatively rapid testicular growth occurred in offspring of heat-adapted sire breeds between 12 and 15 mo of age. While differences in yearling testis size primarily reflect breed differences in age at puberty, postpubertal testis growth appears to be more rapid in offspring of heat-adapted sire breeds. Accelerated postpubertal testis growth in heat-adapted breeds may be related to seasonal effects on body growth that favor heat-adapted breeds during the postyearling period (predominantly summer months; April to July). Alternatively, the high level of heterosis in *Bos indicus* × *Bos taurus* offspring (Koger, 1980; Green et al., 1991; Gregory et al., 1991, 1997a,b; Cundiff et al., 1986, 2000) may have improved testicular growth (Gregory et al., 1991) enough in Brahman- and Boran-sired offspring to offset the detrimental effect of heat-tolerance. Further research is needed to clarify the potential effects of these factors on testicular development.

In the current study, bulls from heat-adapted sire breeds reached puberty 11 to 82 d later and produced freezable semen 36 to 87 d later than did bulls from nonheat adapted sire breeds. Breed differences for age at puberty in genetically related Angus-, Hereford-, Belgian Blue-, Brahman-, Boran-, and Tuli-sired heifers

at Clay Center (Freetly and Cundiff, 1997) were very similar to the relative breed differences in bull age at puberty. Also, the older age at puberty in bulls and heifers sired by heat-adapted breeds compared to non-adapted breeds agrees with the older pubertal age reported for Brahman- and Sahiwal-sired heifers (Gregory et al., 1979b) and Brahman- and Sahiwal-sired bulls (Lunstra et al., 1993). Thus, data in the current study support the concept that breed differences in age at puberty appear to be of similar magnitude in both males and females, even in widely divergent beef breeds (Lunstra et al., 1988; Gregory et al., 1991; Freetly and Cundiff, 1997). However, Tuli- and Boran-sired bulls reached puberty earlier than did Brahman-sired bulls, suggesting that earlier puberty can be achieved in some heat-adapted breeds of cattle.

At puberty, testis size was quite similar among breeds of bulls, despite the large breed differences in age, body weight, and hip height that were present at puberty. Regardless of sire breed, bulls reached puberty when scrotal circumference reached approximately 28 cm, and PTV reached approximately 300 cm³. We have shown previously that Zebu × *Bos taurus* bulls and bulls of *Bos taurus* beef breeds reach puberty at 28 cm scrotal circumference (Lunstra et al., 1978, 1988, 1993; Godfrey et al., 1992). Consistent with the present results, other researchers have reported that Brahman-, Romosinuano-, Nellore-, Senepol-, and Tuli-sired bulls reach puberty at 27 to 31 cm scrotal circumference (Chase et al., 1997, 2001). Since testis size at puberty does not vary among breed types of bulls that exhibit marked differences in age at puberty, and scrotal circumference in yearling beef bulls is highly heritable ($h^2 = 0.41$ to 0.43 ± 0.06 ; Latimer et al., 1982; Lunstra et al., 1988; Gregory et al., 1991) and is strongly correlated with age at onset of puberty in beef bulls ($r = 0.64$ to 0.80 ; Lunstra et al., 1978; 1988; Lunstra and Echternkamp, 1982) and in genetically related females (Lunstra et al., 1988; Gregory et al., 1991; Freetly and Cundiff, 1997), measurement of yearling scrotal circumference is recommended as a useful tool for assessing and predicting age at puberty among and within bulls of widely divergent breed types.

Implications

Consistent with previous reports characterizing growth and pubertal development in females of these breeds, results of this study demonstrated that male offspring of diverse heat-adapted sire breeds had lower postweaning growth rates and were slower to reach puberty than were offspring of European sire breeds. In addition, measurement of yearling testis size was a reliable indicator of age at puberty among widely divergent breeds of bulls. Thus, producers using heat-adapted breeds need to emphasize growth rate and earlier pubertal development in genetic improvement programs for heat-tolerant breeds and may need to place added emphasis on these traits in selection of breeds

for use in crossbreeding programs or in development of composite populations adapted to subtropical climatic environments in the United States.

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