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Genetic correlations of young bull reproductive traits and heifer puberty traits with female reproductive performance in two tropical beef genotypes in northern Australia

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Abstract. Genetic correlations of young bull and heifer puberty traits with measures of early and lifetime female reproductive performance were estimated in two tropical beef cattle genotypes. Heifer age at puberty was highly (r_g = –0.71 ± 0.11) and moderately (r_g = –0.40 ± 0.20) genetically correlated with pregnancy rate at first annual mating (mating 1) and lifetime annual calving rate, respectively in Brahman (BRAH). In Tropical Composite (TCOMP), heifer age at puberty was highly correlated with reproductive outcomes from the first re-breed (mating 2), mainly due to its association with lactation anoestrous interval (r_g = 0.72 ± 0.17). Scrotal circumference were correlated with heifer age at puberty (r_g = –0.41 ± 0.11 at 12 months in BRAH; –0.30 ± 0.13 at 6 months in TCOMP) but correlations were lower with later female reproduction traits. Bull insulin-like growth factor-I was correlated with heifer age at puberty (r_g = –0.56 ± 0.11 in BRAH; –0.43 ± 0.11 in TCOMP) and blood luteinising hormone concentration was moderately correlated with lactation anoestrous interval (r_g = 0.59 ± 0.23) in TCOMP. Semen quality traits, including mass activity, motility and percent normal sperm were genetically correlated with lactation anoestrus and female lifetime female reproductive traits in both genotypes, but the magnitudes of the relationships differed with bull age at measurement. Preputial eversion and sheath scores were genetically associated with lifetime calving and weaning rates in both genotypes. Several of the early-in-life male and female measures examined were moderately to highly genetically correlated with early and lifetime female reproduction traits and may be useful as indirect selection criteria for improving female reproduction in tropical breeds in northern Australia.

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Introduction

Genetic improvement using modern breeding techniques such as best linear unbiased prediction estimated breeding values relies on the recording of phenotypes. In some cases, traits are difficult to record or unable to be recorded on the selection candidate, for example when they are expressed late in life or in only one sex. Recent research (Johnston *et al*. 2014) has shown female reproduction traits in tropical genotypes are heritable and that genetic progress can be made through selection. However, the rates of genetic improvement are expected to be low, as recording reproductive traits can only occur later in life in reproductively active females. Indirect selection offers a means of increasing response to selection. Land (1973) proposed the existence of genetic relationships between male and female reproduction in mammals, and several studies in beef cattle have established significant genetic correlations between scrotal circumference and female reproduction (Brinks *et al*. 1978; Meyer *et al*. 1991; Martin *et al*. 1992). The BREEDPLAN multiple-trait evaluation in Australia (Graser *et al*. 2005) applies a genetic correlation between the male trait scrotal circumference and the female reproduction trait days to calving.

Research in two tropically adapted beef genotypes has reported heifer age at puberty to be heritable (Johnston *et al*. 2009), and Corbet *et al*. (2013) showed a range of young male reproduction traits had heritabilities that were moderate to high. These could therefore be considered as candidate genetic indicators to improve female reproduction in tropical breeds, as proposed by Burns *et al*. (2013). The aim of this study was to estimate the genetic associations of young bull reproductive traits and heifer puberty traits with female reproduction, and to identify the genetic indicator traits that could be included in multiple-trait genetic evaluation to increase the rate of genetic improvement in female reproduction.

Materials and methods

Data were from a single large beef breeding experiment in northern Australia that investigated the genetics of whole-

[1]AGBU is a joint venture of NSW Department of Primary Industries and the University of New England.

herd profitability (Burrow *et al*. 2003). The experimental design associated with each aspect of the study are described by Barwick *et al*. (2009*a*, 2009*b*), Burns *et al*. (2013) and Johnston *et al*. (2014). In brief, Brahman (BRAH) and Tropical Composite (TCOMP) steers (n = 2216) and heifers (n = 2174) were generated over 4 years at eight cooperator properties and were the progeny of 54 BRAH and 52 TCOMP sires. At weaning, the heifer calves were allocated to one of four Queensland research stations (Swans Lagoon, Ayr; Toorak, Julia Creek; Belmont, Rockhampton and Brian Pastures, Gayndah) that represented a range of northern Australia breeder cow herd environments (see Barwick *et al*. 2009*b*; for a description of the environment at each research station). Heifers were managed as a year group and from ~10 to 12 months of age were ultrasound scanned every 4–6 weeks to determine age at first *corpus luteum*. All heifers were naturally mated to first calve at ~3 years of age. Subsequently the cows were mated annually and full reproduction data collected, including reproductive tract scanning to determine resumption of cycling after calving. Cows remained in the project until the weaning of calves from their sixth mating when they were ~8.5 years of age, unless they failed to wean a calf in consecutive years or were culled for other management reasons (e.g. poor temperament).

Bulls studied were the male calves generated from the mating of project females with 136 industry-sourced sires, and were born in the first 7 years of the project (2004–10) across five research stations. The bulls were recorded pre-weaning (4 months), at weaning (6 months), and then through to 2 years of age for a range of reproductive traits, including full bull breeding soundness evaluation and sperm morphology assessments at 12, 18 and 24 months of age (Burns *et al*. 2013; Corbet *et al*. 2013). Table 1 presents the traits used in this study and a brief description.

Table 1. Trait description of bull, heifer and female reproduction traits

Code	Trait	Measurement time	Description
		Bulls[A]	
IN	Inhibin (ng/mL)	4 months	Circulating blood inhibin concentration
LH	Luteinising hormone (ng/mL)	4 months	Circulating blood LH concentration following a gonadotrophin releasing hormone (GnRH) challenge
IGF-I	Insulin-like growth factor-I (ng/mL)	6 months	Circulating blood IGF-I concentration
MASS	Sperm mass activity (score)	12, 18, 24 months	Scored from 0 = no activity to 5 = rapid distinct swirls
MOT	Sperm motility (%)	12, 18, 24 months	Percent progressively motile sperm
PNS	Percent normal sperm (%)	12,18, 24 months	Percent morphologically normal sperm
SC	Scrotal circumference (cm)	6, 12, 18, 24 months	Circumference of scrotum
SH	Sheath score (score)	18 months	Sheath structure score from 1 (pendulous) to 9 (very tight)
EV	Preputial eversion (mm)	18 months	Estimated length of everted preputial mucosa
		Heifer puberty[B]	
AGECL	Age at puberty (day)	10–40 months	Age at first *corpus luteum* (CL)
WTCL	Weight at puberty (kg)	At 1st CL	Weight at first CL
FATCL	Fat at puberty (mm)	At 1st CL	P8 fat depth at the first CL
TSIZE	Tract size (mm)	27 months	Reproductive tract size score
CLPROIR	Pubertal before mating	≤27 months	Presence of a CL prior (=1) to start of first mating, or not = 0
CLJOIN	Cycling into mating	27 months	Presence of a CL on the scanning day into first mating = 1, or not = 0
		Female reproduction[C]	
CONC	Conception rate	Mating 1 and 2[D]	Conceived (= 1) or not (= 0)
PREG	Pregnancy rate	Mating 1 and 2	Pregnant (= 1) or not (= 0)
CALV	Calving rate	Mating 1 and 2	Full-term calf born (= 1), or not (= 0)
WEAN	Weaning rate	Mating 1 and 2	Weaned a calf (= 1) or not (= 0)
DTO	Days to cycling (day)	Mating 2	Interval from start of mating to estimated date of first ovulation
LAI	Lactation anoestrous interval (day)	Mating 2	Days to cycling of lactating cows
CYCW	Lactation cyclicity rate	Mating 2	Lactating cows, cycling before weaning (= 1) or not (= 0)
DTC	Days to calving (day)	Mating 1 and 2	Interval from the start of mating to subsequent calving
PW	Pregnant-and-weaned rate	Mating 2	Pregnant and weaned a calf (= 1) or not (= 0)
LACR	Lifetime annual calving rate	≤Mating 6	Total number of calves born divided by number of matings
LAWR	Lifetime annual weaning rate	≤Mating 6	Total number of calves weaned divided by number of matings
ACR6	Average calving rate (retained cows)	Mating 6	Lifetime calving rate of surviving cows at mating 6.
AWR6	Average weaning rate (retained cows)	Mating 6	Lifetime weaning rate of surviving cows at mating 6

[A]Adapted from Corbet *et al*. (2013) and Burns *et al*. (2013).
[B]Adapted from Johnston *et al*. (2009).
[C]Adapted from Johnston *et al*. (2014).
[D]Mating 1 = reproductive traits from the maiden mating as 2 year olds; mating 2 = reproductive traits from first re-breed as 3 year olds; mating 6 = reproductive traits from cows still in the herd at their 6th mating as 7 year olds.

Statistical analyses

Genetic correlations were estimated in a series of bivariate analyses for BRAH and TCOMP separately, using restricted maximum likelihood procedures in ASRemL (Gilmour *et al*. 2009). Fixed and random effects fitted were previously described for each group of traits; heifer puberty (Johnston *et al*. 2009), female reproduction (Johnston *et al*. 2014) and male reproduction (Corbet *et al*. 2013). The female reproduction traits included traits recorded at the first (mating 1) and second matings (mating 2), as well as lifetime reproductive traits up to their sixth mating. Male reproduction traits included traits measured at 4, 6, 12, 18 and 24 months of age, with several recorded over time. To reduce the number of analyses required any bull or heifer puberty traits with heritabilities of 10% or less were not included in bivariate analyses.

All analyses used a relationship matrix constructed for the full population as three generations of pedigree where known. Data used in analyses between bull and female traits, were edited to remove any bull records of dam-offspring pairs where the bull was the resultant progeny of the female trait being analysed. Editing was done to remove any contributions to the genetic covariance generated from an environmental covariance between the dam-offspring for the pairs of traits. For example, when analysing female traits associated with mating 1, records were removed for bulls that were the resultant progeny from this first mating. Analyses involving lifetime female traits, the records were removed for bulls that were the only progeny of a cow.

Results

Heifer puberty and female reproduction

Genetic correlations of heifer puberty traits with female reproduction traits at mating 1, mating 2 and lifetime are presented in Tables 2 and 3. For BRAH moderate to high correlations existed between all heifer puberty traits and mating 1 female reproductive traits. However, the correlations were lower for weaning rate at mating 1 with age at puberty (= –0.39) and weight at puberty (= –0.11), and for calving rate with heifer weight at puberty (–0.27). The negative genetic correlations of weight and fatness at puberty suggested possible antagonisms with reproduction output traits at mating 1. Similar trends were observed for TCOMP but the magnitudes of the correlations were lower. The higher standard errors for TCOMP estimates reflect the greater number of TCOMP heifers pubertal before mating (Johnston *et al*. 2009) and the very low heritabilities of TCOMP reproduction traits at the first mating, as reported by Johnston *et al*. (2014).

For TCOMP, many of the heifer pubertal traits were moderately to highly correlated with female reproduction traits at mating 2. The genetic correlations of lactation anoestrous interval with heifer age at puberty and pubertal rate before mating were 0.72 and –0.89, respectively. For BRAH, the correlations for mating 2 traits were generally in similar directions to TCOMP but were much lower, and not significantly different from zero.

Genetic correlations between heifer puberty traits and female lifetime reproduction had high standard errors. The

Table 2. Genetic correlations between heifer puberty traits and female mating 1, mating 2 and lifetime reproduction in Brahmans

See Table 1 for description of traits, approximate standard errors in parentheses

Female reproduction traits	Heifer puberty traits AGECL	WTCL	FATCL	CLPRIOR	CLJOIN
Mating 1					
Conception rate	–0.70 (0.12)	–0.49 (0.16)	–0.54 (0.17)	0.71 (0.16)	0.87 (0.17)
Pregnancy rate	–0.71 (0.11)	–0.49 (0.15)	–0.55 (0.16)	0.70 (0.16)	0.80 (0.18)
Calving rate	–0.61 (0.16)	–0.27 (0.21)	–0.55 (0.19)	0.70 (0.18)	0.81 (0.20)
Weaning rate	–0.39 (0.26)	–0.11 (0.28)	–0.55 (0.25)	0.69 (0.25)	0.70 (0.29)
Days to calving	0.79 (0.14)	0.52 (0.19)	0.54 (0.20)	–0.91 (0.14)	–1.0[A] (0.16)
Mating 2					
Days to cycling	0.22 (0.18)	0.31 (0.18)	0.23 (0.19)	–0.17 (0.21)	–0.38 (0.24)
Lactation anoestrous interval	0.31 (0.18)	0.32 (0.18)	0.28 (0.20)	–0.19 (0.22)	–0.43 (0.24)
Lactation cyclicity rate	–0.26 (0.18)	–0.24 (0.18)	–0.19 (0.20)	0.17 (0.21)	0.41 (0.23)
Conception rate	–0.21 (0.19)	–0.15 (0.19)	–0.26 (0.20)	0.00 (0.23)	0.11 (0.27)
Pregnancy rate	–0.14 (0.20)	0.00 (0.20)	–0.17 (0.21)	0.03 (0.23)	0.12 (0.28)
Calving rate	–0.12 (0.22)	–0.01 (0.22)	–0.09 (0.23)	–0.02 (0.26)	0.07 (0.30)
Weaning rate	–0.28 (0.23)	–0.07 (0.24)	0.03 (0.25)	0.12 (0.27)	0.20 (0.31)
Days to calving	0.08 (0.24)	–0.06 (0.23)	–0.01 (0.24)	0.13 (0.27)	–0.04 (0.32)
Pregnant-and-weaned	–0.27 (0.17)	–0.16 (0.18)	–0.32 (0.19)	0.27 (0.20)	0.44 (0.24)
Lifetime					
Lifetime annual calving rate	–0.40 (0.20)	–0.39 (0.21)	–0.47 (0.22)	0.22 (0.25)	0.47 (0.27)
Lifetime annual weaning rate	–0.36 (0.21)	–0.03 (0.22)	–0.06 (0.24)	0.25 (0.25)	0.42 (0.27)
Average calving rate (retained cows)	–0.36 (0.24)	–0.22 (0.25)	–0.34 (0.25)	0.25 (0.28)	0.29 (0.33)
Average weaning rate (retained cows)	–0.30 (0.25)	0.02 (0.27)	0.01 (0.28)	0.30 (0.28)	0.27 (0.34)

[A]Estimate exceeded bounds.

Table 3. Genetic correlations between heifer puberty traits and female mating 1, mating 2 and lifetime reproduction in Tropical Composite
See Table 1 for description of traits, approximate standard errors in parentheses

Female reproduction traits	Heifer puberty traits				
	AGECL	WTCL	FATCL	CLPRIOR	TSIZE
		Mating 1			
Conception rate	–0.41 (0.35)	–0.14 (0.36)	0.05 (0.39)	0.58 (0.44)	0.53 (0.48)
Pregnancy rate	–0.23 (0.27)	–0.39 (0.26)	–0.23 (0.29)	0.68 (0.31)	–0.06 (0.37)
Calving rate	–0.17 (0.28)	–0.15 (0.28)	–0.12 (0.29)	0.70 (0.33)	0.20 (0.37)
Weaning rate	–0.49 (0.30)	–0.34 (0.31)	0.03 (0.33)	1.0[A] (0.41)	0.51 (0.40)
Days to calving	0.10 (0.27)	0.12 (0.27)	0.22 (0.27)	–0.80 (0.28)	–0.25 (0.36)
		Mating 2			
Days to cycling	0.78 (0.18)	0.73 (0.19)	0.70 (0.22)	–0.90 (0.25)	–0.57 (0.28)
Lactation anoestrous interval	0.72 (0.17)	0.69 (0.18)	0.61 (0.22)	–0.89 (0.23)	–0.60 (0.26)
Lactation cyclicity rate	–0.64 (0.19)	–0.59 (0.20)	–0.61 (0.22)	0.49 (0.30)	0.27 (0.31)
Conception rate	–0.37 (0.28)	–0.20 (0.29)	–0.38 (0.30)	0.39 (0.36)	0.46 (0.32)
Pregnancy rate	–0.68 (0.40)	–0.19 (0.38)	–0.45 (0.40)	0.47 (0.48)	0.44 (0.43)
Calving rate	–0.58 (0.32)	–0.21 (0.31)	–0.15 (0.32)	0.22 (0.39)	0.37 (0.37)
Weaning rate	–0.63 (0.38)	–0.17 (0.35)	–0.09 (0.36)	0.22 (0.45)	0.36 (0.42)
Days to calving	0.43 (0.26)	0.03 (0.27)	0.25 (0.27)	0.04 (0.35)	–0.28 (0.34)
Pregnant-and-weaned	–0.70 (0.21)	–0.43 (0.25)	–0.27 (0.27)	0.90 (0.28)	0.57 (0.30)
		Lifetime			
Lifetime annual calving rate	–0.33 (0.28)	–0.22 (0.28)	–0.20 (0.32)	0.59 (0.30)	0.63 (0.28)
Lifetime annual weaning rate	–0.29 (0.23)	–0.05 (0.25)	–0.07 (0.27)	0.66 (0.25)	0.77 (0.21)
Average calving rate (retained cows)	–0.49 (0.42)	–0.39 (0.41)	–0.31 (0.44)	0.57 (0.52)	0.08 (0.51)
Average weaning rate (retained cows)	–0.51 (0.31)	–0.33 (0.32)	–0.43 (0.33)	1.0[A] (0.41)	0.43 (0.39)

[A]Estimate exceeded bounds.

directions of the correlations in both genotypes generally reflected the association seen between heifer age at puberty and performance at mating 1 and 2. In both genotypes, younger age at puberty tended to be genetically associated with increased lifetime reproductive performance.

Young bull traits and heifer puberty

Genetic correlations between bull traits and heifer age at puberty traits are presented in Tables 4 and 5. For BRAH, correlations were generally low across the male hormone traits. The exception was insulin-like growth factor-I (IGF-I) with moderate correlations with age at puberty, pubertal rate before mating and cycling into mating (–0.56, 0.42, and 0.53, respectively). Semen quality and scrotal traits were generally moderately correlated, and consistent in sign with heifer puberty traits, with the exception of fatness at puberty. Similar results were observed for TCOMP, although correlations with IGF-I were lower in magnitude. In both genotypes there was a trend for the correlations of semen traits with heifer puberty traits to increase in magnitude with measurement at older ages, whereas for scrotal circumference the reverse trend was observed. For TCOMP, genetic correlations of scrotal circumference with heifer weight at puberty and reproductive tract size were positive. Preputial eversion and sheath score were moderately correlated with weight at puberty in both genotypes, and with heifer age at puberty in BRAH.

Young bull traits and female reproduction (mating 1 and 2)

Genetic correlations of bull traits with female reproduction at mating 1 are presented in Table 6 (BRAH) and Table 7 (TCOMP). Genetic correlations were generally low to moderate for both genotypes and followed a similar pattern as correlations observed for bull traits with heifer puberty traits. Of the bull hormone traits, IGF-I in BRAH displayed the strongest genetic correlations with female reproductive performance at mating 1, with positive correlations ranging from 0.29 to 0.44 and –0.34 with days to calving. For both genotypes the semen trait mass activity at 18 months was lowly to moderately correlated (albeit with large standard error) with female traits at mating 1. Percent normal sperm at 18 and 24 months was genetically correlated with mating 1 female reproduction traits in TCOMP, with the exceptions of conception and pregnancy rates with percent normal sperm at 24 months. Scrotal circumference was lowly to moderately correlated with female reproduction traits at mating 1 in both BRAH and TCOMP.

Genetic correlations between bull and female traits at mating 2 are presented in Tables 8 and 9. For BRAH the genetic correlations with the bull hormone traits were low. For TCOMP, luteinising hormone (LH) was moderately to highly correlated with mating 2 reproduction traits (e.g. 0.59 with lactation anoestrous interval and –0.66 with calving rate). Semen quality traits in BRAH and TCOMP at 18 and 24 months showed consistent correlations with mating 2 traits in both genotypes. Genetic correlations of mass activity and motility at 18 months with mating 2 traits were moderate to high, albeit with high standard errors in TCOMP. Percent normal sperm at 12 and 18 months in TCOMP were also correlated with the mating 2 traits. However, at 24 months the correlations were lower and not significantly different from zero. In BRAH, percent normal sperm at 18 months was lowly

Table 4. Genetic correlations between bull reproduction traits and heifer puberty traits in Brahman
See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Heifer puberty traits				
		AGECL	WTCL	FATCL	CLPRIOR	CLJOIN
				Hormones		
Inhibin	4	–0.28 (0.10)	–0.05 (0.10)	–0.09 (0.10)	0.22 (0.11)	0.26 (0.15)
Luteinising hormone	4	0.00 (0.16)	–0.17 (0.15)	–0.14 (0.16)	–0.10 (0.19)	0.02 (0.25)
IGF-I	6	–0.56 (0.11)	–0.34 (0.12)	0.06 (0.12)	0.42 (0.15)	0.53 (0.20)
				Semen quality		
Mass activity	12	–0.24 (0.12)	–0.31 (0.12)	–0.10 (0.12)	0.44 (0.15)	0.79 (0.20)
	18	–0.51 (0.17)	–0.42 (0.16)	0.15 (0.15)	0.58 (0.19)	0.71 (0.24)
Motility	12	–0.31 (0.13)	–0.36 (0.12)	–0.08 (0.13)	0.54 (0.16)	0.82 (0.22)
	18	–0.49 (0.20)	–0.25 (0.19)	0.29 (0.18)	0.55 (0.21)	0.64 (0.25)
Percent normal sperm	18	–0.48 (0.21)	–0.65 (0.22)	0.11 (0.20)	0.67 (0.25)	0.97 (0.34)
	24	–0.27 (0.20)	–0.15 (0.20)	0.13 (0.21)	0.50 (0.23)	0.44 (0.31)
				Scrotal and sheath		
Scrotal circumference	6	–0.30 (0.11)	0.11 (0.11)	0.05 (0.11)	0.09 (0.14)	0.24 (0.18)
	12	–0.41 (0.11)	–0.09 (0.11)	0.01 (0.11)	0.41 (0.13)	0.60 (0.16)
	18	–0.27 (0.10)	–0.07 (0.10)	0.04 (0.10)	0.30 (0.12)	0.46 (0.16)
	24	–0.15 (0.10)	0.09 (0.09)	–0.02 (0.10)	0.10 (0.12)	0.25 (0.16)
Sheath score	18	–0.38 (0.15)	–0.22 (0.14)	0.15 (0.15)	0.29 (0.17)	–0.08 (0.22)
Preputial eversion	18	0.33 (0.13)	0.43 (0.12)	0.09 (0.13)	–0.25 (0.16)	0.09 (0.20)

Table 5. Genetic correlations between bull reproduction traits and heifer puberty traits in Tropical Composite
See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Heifer puberty traits				
		AGECL	WTCL	FATCL	CLPRIOR	TSIZE
				Hormones		
Inhibin	4	0.01 (0.10)	0.05 (0.10)	0.06 (0.10)	0.19 (0.17)	–0.01 (0.15)
Luteinising hormone	4	0.17 (0.13)	0.15 (0.13)	0.14 (0.13)	–0.34 (0.21)	–0.02 (0.19)
IGF-I	6	–0.43 (0.11)	–0.24 (0.12)	0.09 (0.13)	0.23 (0.21)	–0.10 (0.19)
				Semen quality		
Mass activity	12	–0.29 (0.13)	–0.26 (0.13)	–0.01 (0.13)	0.22 (0.21)	0.06 (0.20)
	18	–0.24 (0.20)	–0.10 (0.19)	0.12 (0.19)	0.50 (0.31)	0.12 (0.28)
Motility	12	–0.26 (0.13)	–0.22 (0.14)	–0.02 (0.13)	0.12 (0.22)	0.05 (0.20)
	18	–0.38 (0.18)	–0.26 (0.17)	0.18 (0.18)	0.36 (0.29)	0.16 (0.25)
Percent normal sperm	12	–0.05 (0.16)	–0.22 (0.16)	0.18 (0.17)	–0.04 (0.26)	0.41 (0.24)
	18	–0.24 (0.17)	–0.28 (0.17)	0.37 (0.17)	0.28 (0.26)	0.40 (0.23)
	24	–0.11 (0.14)	0.05 (0.14)	0.41 (0.16)	0.06 (0.22)	0.05 (0.21)
				Scrotal and sheath		
Scrotal circumference	6	–0.30 (0.13)	0.33 (0.11)	–0.02 (0.12)	0.32 (0.21)	0.55 (0.22)
	12	–0.21 (0.11)	0.23 (0.11)	–0.01 (0.11)	0.15 (0.18)	0.41 (0.21)
	18	–0.17 (0.11)	0.38 (0.11)	0.04 (0.11)	0.07 (0.18)	0.54 (0.22)
	24	–0.06 (0.11)	0.49 (0.11)	0.07 (0.12)	0.07 (0.19)	0.44 (0.21)
Sheath score	18	–0.15 (0.13)	–0.45 (0.12)	–0.21 (0.14)	0.08 (0.21)	–0.07 (0.20)
Preputial eversion	18	–0.05 (0.16)	0.43 (0.16)	0.09 (0.17)	–0.08 (0.27)	–0.12 (0.25)

to moderately to highly correlated with mating 2 traits. At 24 months, the correlations were moderate to high across the mating 2 traits.

Scrotal circumference in BRAH was lowly to moderately correlated with mating 2 traits, with slightly higher correlations when measured at 18 months (Table 8). In TCOMP, correlations with scrotal circumference were low and with no consistent trends in the correlations at the different measurement ages (Table 9). Preputial eversion score and sheath score in TCOMP were correlated with lactation anoestrus traits (e.g. –0.58 and 0.41 correlations with lactation cyclicity rate, respectively), but less with other reproductive

Table 6. Genetic correlations between bull reproduction traits and female mating 1 reproduction traits in Brahman
See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female mating 1 traits CONC	PREG	CALV	WEAN	DTC
		Hormones				
Inhibin	4	0.13 (0.12)	0.14 (0.12)	0.23 (0.15)	0.09 (0.21)	–0.27 (0.15)
Luteinising hormone	4	0.00 (0.17)	–0.01 (0.17)	0.10 (0.21)	0.63 (0.33)	–0.05 (0.21)
IGF-I	6	0.32 (0.17)	0.29 (0.16)	0.44 (0.20)	0.34 (0.26)	–0.34 (0.21)
		Semen quality				
Mass activity	12	0.09 (0.14)	0.14 (0.14)	0.16 (0.18)	0.35 (0.24)	–0.25 (0.18)
	18	0.38 (0.23)	0.42 (0.23)	0.12 (0.26)	0.50 (0.38)	–0.15 (0.27)
Motility	12	0.18 (0.16)	0.25 (0.16)	0.21 (0.19)	0.40 (0.26)	–0.32 (0.20)
	18	0.17 (0.23)	0.18 (0.22)	–0.04 (0.27)	0.26 (0.38)	–0.03 (0.27)
Percent normal sperm	18	0.17 (0.23)	0.26 (0.23)	–0.02 (0.27)	0.08 (0.38)	–0.04 (0.28)
	24	–0.24 (0.28)	–0.08 (0.27)	–0.26 (0.34)	0.26 (0.47)	0.44 (0.34)
		Scrotal and sheath				
Scrotal circumference	6	0.13 (0.14)	0.12 (0.14)	0.35 (0.17)	0.20 (0.23)	–0.36 (0.17)
	12	0.10 (0.14)	0.16 (0.14)	0.25 (0.17)	0.32 (0.23)	–0.30 (0.18)
	18	0.07 (0.13)	0.14 (0.13)	0.24 (0.17)	0.31 (0.24)	–0.34 (0.17)
	24	0.10 (0.13)	0.14 (0.13)	0.25 (0.17)	0.16 (0.23)	–0.25 (0.17)
Sheath score	18	0.35 (0.20)	0.29 (0.19)	0.11 (0.22)	0.16 (0.31)	–0.12 (0.23)
Preputial eversion	18	–0.22 (0.17)	–0.13 (0.17)	0.03 (0.20)	0.04 (0.29)	0.09 (0.20)

Table 7. Genetic correlations between bull reproduction traits and female mating 1 reproduction traits in Tropical Composite
See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female mating 1 traits CONC	PREG	CALV	WEAN	DTC
		Hormones				
Inhibin	4	0.09 (0.31)	0.24 (0.21)	0.24 (0.21)	0.08 (0.22)	–0.13 (0.19)
Luteinising hormone	4	0.32 (0.35)	–0.14 (0.25)	–0.20 (0.25)	0.07 (0.28)	0.51 (0.24)
IGF-I	6	–0.12 (0.38)	0.15 (0.24)	–0.01 (0.25)	–0.35 (0.27)	–0.11 (0.23)
		Semen quality				
Mass activity	12	–0.07 (0.33)	0.12 (0.22)	–0.01 (0.23)	0.14 (0.26)	–0.08 (0.21)
	18	–0.17 (0.50)	0.20 (0.34)	0.42 (0.31)	0.46 (0.37)	–0.38 (0.30)
Motility	12	–0.09 (0.33)	0.12 (0.22)	0.02 (0.23)	0.27 (0.26)	–0.10 (0.21)
	18	0.19 (0.41)	0.21 (0.30)	0.32 (0.29)	0.29 (0.34)	–0.22 (0.28)
Percent normal sperm	12	–0.09 (0.42)	0.01 (0.31)	–0.13 (0.30)	–0.11 (0.35)	0.10 (0.28)
	18	0.43 (0.42)	0.45 (0.30)	0.43 (0.30)	0.71 (0.41)	–0.50 (0.27)
	24	–0.07 (0.36)	0.26 (0.28)	0.50 (0.29)	0.79 (0.41)	–0.43 (0.28)
		Scrotal and sheath				
Scrotal circumference	6	0.19 (0.36)	–0.03 (0.23)	0.07 (0.24)	–0.01 (0.27)	0.00 (0.22)
	12	0.19 (0.32)	0.19 (0.21)	0.11 (0.22)	0.28 (0.26)	–0.18 (0.20)
	18	0.21 (0.34)	0.08 (0.22)	0.18 (0.22)	0.42 (0.27)	–0.15 (0.21)
	24	0.01 (0.31)	–0.06 (0.22)	0.17 (0.23)	0.35 (0.28)	–0.11 (0.21)
Sheath score	18	–0.24 (0.43)	–0.13 (0.31)	–0.57 (0.36)	–0.04 (0.34)	0.48 (0.38)
Preputial eversion	18	0.15 (0.46)	–0.19 (0.31)	0.30 (0.35)	–0.18 (0.37)	0.15 (0.29)

traits, while in BRAH, they were not significantly correlated with female reproduction traits at mating 2.

Young bull traits and lifetime female reproduction

Genetic correlations of bull traits with female lifetime traits are presented in Tables 10 and 11. All estimates had large standard errors but some general trends were apparent. Bull hormone traits were generally lowly correlated with female lifetime traits. Mass activity and motility at 18 months were highly correlated (0.70 and 0.75, respectively), with lifetime annual calving rate. These correlations reduced in the magnitude with lifetime traits recorded only in cows still present at mating 6. Scrotal circumference showed no consistent relationships with lifetime reproduction traits in BRAH, and in TCOMP there was a tendency for the correlations to be negative. Preputial eversion was genetically correlated with lifetime calving rate (–0.59 in BRAH and TCOMP) and weaning rate (–0.71

Table 8. Genetic correlations between bull reproduction traits and female mating 2 reproduction traits in Brahman

See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female mating 2 traits DTO	LAI	CYCW	CONC	PREG	CALV	WEAN	DTC	PW
					Hormones					
Inhibin	4	–0.04 (0.12)	–0.08 (0.13)	0.03 (0.12)	0.04 (0.13)	0.02 (0.14)	0.14 (0.15)	0.13 (0.18)	–0.19 (0.16)	0.07 (0.12)
Luteinising hormone	4	–0.26 (0.17)	–0.29 (0.18)	0.17 (0.17)	0.27 (0.18)	0.26 (0.20)	0.33 (0.21)	0.34 (0.23)	–0.29 (0.23)	0.21 (0.19)
IGF-I	6	–0.21 (0.14)	–0.21 (0.15)	0.11 (0.14)	0.26 (0.15)	0.21 (0.16)	0.20 (0.17)	0.36 (0.19)	–0.24 (0.18)	0.14 (0.14)
					Semen quality					
Mass activity	12	–0.17 (0.14)	–0.17 (0.14)	0.09 (0.13)	0.21 (0.15)	0.19 (0.16)	0.14 (0.17)	0.24 (0.20)	–0.24 (0.18)	0.18 (0.13)
	18	–0.26 (0.17)	–0.27 (0.18)	0.31 (0.17)	0.43 (0.20)	0.49 (0.21)	0.55 (0.23)	0.63 (0.27)	–0.65 (0.24)	0.36 (0.17)
Motility	12	–0.12 (0.14)	–0.12 (0.14)	0.03 (0.13)	0.11 (0.15)	0.08 (0.16)	0.03 (0.17)	0.11 (0.20)	–0.11 (0.19)	0.15 (0.13)
	18	–0.38 (0.21)	–0.37 (0.22)	0.46 (0.20)	0.53 (0.24)	0.58 (0.24)	0.72 (0.26)	0.79 (0.30)	–0.77 (0.28)	0.44 (0.21)
Percent normal sperm	18	–0.56 (0.31)	–0.52 (0.31)	0.49 (0.30)	0.36 (0.31)	0.28 (0.32)	0.29 (0.35)	0.15 (0.40)	–0.21 (0.37)	0.23 (0.28)
	24	–0.72 (0.24)	–0.65 (0.24)	0.60 (0.23)	0.52 (0.25)	0.56 (0.25)	0.63 (0.26)	0.53 (0.30)	–0.69 (0.28)	0.47 (0.23)
					Scrotal and sheath					
Scrotal circumference	6	–0.02 (0.14)	–0.04 (0.14)	–0.01 (0.14)	0.12 (0.15)	0.03 (0.16)	0.01 (0.18)	0.12 (0.20)	0.18 (0.21)	0.12 (0.14)
	12	–0.14 (0.13)	–0.19 (0.13)	0.09 (0.13)	0.15 (0.14)	0.14 (0.15)	0.15 (0.16)	0.17 (0.19)	–0.19 (0.17)	0.11 (0.13)
	18	–0.22 (0.12)	–0.27 (0.13)	0.21 (0.12)	0.29 (0.13)	0.27 (0.14)	0.27 (0.15)	0.40 (0.20)	–0.35 (0.16)	0.19 (0.12)
	24	–0.04 (0.12)	–0.09 (0.12)	0.04 (0.12)	0.09 (0.13)	0.09 (0.14)	0.10 (0.15)	0.15 (0.18)	–0.12 (0.17)	0.05 (0.12)
Sheath score	18	–0.11 (0.15)	–0.12 (0.16)	0.03 (0.15)	0.12 (0.17)	0.10 (0.18)	0.11 (0.20)	0.11 (0.23)	–0.18 (0.22)	0.00 (0.16)
Preputial eversion	18	0.16 (0.15)	0.13 (0.16)	–0.14 (0.15)	–0.11 (0.17)	–0.15 (0.18)	–0.12 (0.20)	–0.18 (0.22)	0.20 (0.22)	–0.04 (0.15)

Table 9. Genetic correlations between bull reproduction traits and female mating 2 reproduction traits in Tropical Composite

See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female mating 2 traits DTO	LAI	CYCW	CONC	PREG	CALV	WEAN	DTC	PW
					Hormones					
Inhibin	4	–0.12 (0.18)	–0.09 (0.16)	–0.08 (0.16)	0.06 (0.21)	0.16 (0.31)	–0.02 (0.22)	0.01 (0.26)	0.08 (0.17)	0.02 (0.18)
Luteinising hormone	4	0.66 (0.27)	0.59 (0.23)	–0.55 (0.22)	–0.60 (0.28)	–0.68 (0.43)	–0.66 (0.30)	–0.68 (0.37)	0.46 (0.23)	–0.44 (0.25)
IGF-I	6	–0.08 (0.20)	–0.10 (0.18)	0.11 (0.18)	–0.03 (0.23)	–0.13 (0.31)	0.14 (0.24)	0.08 (0.29)	0.03 (0.20)	–0.27 (0.20)
					Semen quality					
Mass activity	12	–0.17 (0.21)	–0.12 (0.19)	0.17 (0.19)	0.02 (0.24)	–0.25 (0.35)	0.09 (0.25)	0.28 (0.29)	0.03 (0.21)	0.10 (0.21)
	18	–0.71 (0.39)	–0.68 (0.36)	0.72 (0.38)	0.57 (0.44)	0.90 (0.71)	0.91 (0.53)	0.92 (0.71)	–0.62 (0.40)	0.66 (0.36)
Motility	12	–0.14 (0.22)	–0.11 (0.19)	0.13 (0.20)	–0.02 (0.24)	–0.24 (0.32)	0.00 (0.26)	0.19 (0.32)	0.01 (0.21)	0.02 (0.21)
	18	–0.74 (0.39)	–0.73 (0.35)	0.73 (0.35)	0.72 (0.43)	0.95 (0.72)	1.0[A] (0.58)	1.0[A] (0.98)	–0.64 (0.38)	0.41 (0.35)
Percent normal sperm	12	–0.37 (0.27)	–0.34 (0.25)	0.39 (0.25)	0.33 (0.30)	0.23 (0.41)	0.55 (0.33)	0.63 (0.37)	–0.47 (0.28)	0.31 (0.30)
	18	–0.34 (0.27)	–0.30 (0.25)	0.26 (0.25)	0.26 (0.30)	–0.03 (0.40)	0.31 (0.33)	0.36 (0.39)	–0.16 (0.27)	0.44 (0.29)
	24	0.05 (0.22)	0.05 (0.20)	0.02 (0.20)	0.10 (0.25)	0.04 (0.34)	0.26 (0.29)	0.39 (0.35)	–0.04 (0.23)	0.31 (0.26)
					Scrotal and sheath					
Scrotal circumference	6	0.18 (0.18)	0.15 (0.16)	–0.30 (0.16)	–0.24 (0.22)	–0.26 (0.30)	–0.03 (0.24)	–0.07 (0.28)	–0.06 (0.20)	–0.31 (0.20)
	12	0.11 (0.18)	0.14 (0.16)	–0.10 (0.17)	–0.24 (0.21)	–0.20 (0.29)	0.15 (0.23)	0.20 (0.29)	–0.14 (0.19)	–0.03 (0.19)
	18	0.10 (0.18)	0.13 (0.16)	–0.13 (0.17)	–0.24 (0.19)	–0.17 (0.27)	0.14 (0.24)	0.35 (0.35)	–0.07 (0.20)	0.01 (0.19)
	24	0.22 (0.18)	0.23 (0.16)	–0.28 (0.17)	–0.37 (0.19)	–0.35 (0.26)	–0.04 (0.23)	0.13 (0.30)	0.06 (0.19)	–0.15 (0.19)
Sheath score	18	–0.39 (0.19)	–0.30 (0.19)	0.41 (0.18)	0.21 (0.24)	0.04 (0.34)	0.08 (0.26)	0.18 (0.31)	–0.15 (0.22)	0.09 (0.23)
Preputial eversion	18	0.64 (0.25)	0.52 (0.25)	–0.58 (0.24)	–0.36 (0.30)	–0.26 (0.42)	–0.26 (0.32)	–0.32 (0.37)	0.34 (0.26)	–0.31 (0.27)

[A]Estimate exceeded bounds.

Table 10. Genetic correlations between bull reproduction traits and female lifetime reproduction traits in Brahman
See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female lifetime reproduction traits			
		LACR	LAWR	ACR6	AWR6
		Hormones			
Inhibin	4	0.32 (0.22)	0.26 (0.24)	0.22 (0.15)	0.15 (0.16)
Luteinising hormone	4	0.29 (0.32)	0.42 (0.32)	0.11 (0.23)	0.46 (0.24)
IGF-I	6	–0.14 (0.25)	0.02 (0.26)	0.13 (0.19)	0.20 (0.19)
		Semen quality			
Mass activity	12	–0.34 (0.25)	–0.28 (0.27)	–0.15 (0.18)	–0.31 (0.19)
	18	0.70 (0.34)	0.61 (0.33)	0.45 (0.26)	0.54 (0.26)
Motility	12	–0.07 (0.27)	–0.22 (0.28)	–0.16 (0.19)	–0.41 (0.18)
	18	0.75 (0.36)	0.79 (0.36)	0.41 (0.26)	0.51 (0.28)
Percent normal sperm	18	0.09 (0.41)	–0.12 (0.42)	0.13 (0.30)	–0.01 (0.31)
	24	–0.25 (0.46)	0.13 (0.46)	0.43 (0.32)	0.49 (0.35)
		Scrotal and sheath			
Scrotal circumference	6	–0.25 (0.27)	–0.32 (0.28)	0.05 (0.18)	0.17 (0.19)
	12	0.03 (0.24)	–0.21 (0.24)	0.13 (0.17)	0.12 (0.18)
	18	0.12 (0.22)	0.14 (0.23)	0.06 (0.15)	0.12 (0.17)
	24	0.04 (0.22)	–0.03 (0.23)	0.06 (0.16)	0.14 (0.17)
Sheath score	18	0.33 (0.31)	0.28 (0.33)	0.23 (0.21)	0.35 (0.23)
Preputial eversion	18	–0.59 (0.28)	–0.71 (0.27)	–0.20 (0.21)	–0.17 (0.22)

Table 11. Genetic correlations between bull reproduction traits female lifetime reproduction traits in Tropical Composite
See Table 1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female lifetime reproduction traits			
		LACR	LAWR	ACR6	AWR6
		Hormones			
Inhibin	4	0.49 (0.45)	0.17 (0.27)	–0.02 (0.15)	–0.08 (0.13)
Luteinising hormone	4	–0.64 (0.55)	0.03 (0.33)	–0.39 (0.25)	–0.06 (0.18)
IGF-I	6	0.73 (0.39)	0.18 (0.33)	0.24 (0.20)	–0.02 (0.17)
		Semen quality			
Mass activity	12	–0.15 (0.38)	–0.20 (0.31)	0.01 (0.19)	0.14 (0.17)
	18	0.20 (0.55)	–0.36 (0.44)	0.20 (0.29)	0.21 (0.25)
Motility	12	0.06 (0.38)	0.08 (0.30)	–0.03 (0.20)	0.14 (0.18)
	18	0.37 (0.51)	–0.05 (0.39)	0.27 (0.27)	0.29 (0.24)
Percent normal sperm	12	0.31 (0.44)	–0.07 (0.38)	0.24 (0.25)	0.23 (0.22)
	18	0.37 (0.46)	–0.02 (0.38)	0.43 (0.24)	0.41 (0.22)
	24	0.22 (0.40)	0.24 (0.33)	0.09 (0.21)	0.17 (0.19)
		Scrotal and sheath			
Scrotal circumference	6	–0.62 (0.39)	–0.46 (0.25)	–0.06 (0.18)	–0.06 (0.16)
	12	–0.26 (0.37)	–0.29 (0.29)	0.11 (0.17)	0.16 (0.15)
	18	–0.26 (0.36)	–0.28 (0.27)	0.07 (0.17)	0.14 (0.16)
	24	–0.45 (0.37)	–0.33 (0.27)	–0.15 (0.17)	–0.01 (0.16)
Sheath score	18	0.26 (0.42)	0.57 (0.28)	0.32 (0.19)	0.42 (0.17)
Preputial eversion	18	–0.59 (0.44)	–0.88 (0.33)	–0.56 (0.23)	–0.43 (0.22)

in BRAH; –0.88 in TCOMP). In BRAH, these correlations were reduced in magnitude for lifetime traits recorded only in cows present at mating 6.

Discussion

Earlier work by others suggested male traits were useful genetic predictors of female reproductive performance (Land 1973; Smith *et al*. 1989) including studies in tropical beef genotypes (Mackinnon *et al*. 1990; Meyer *et al*. 1991). Brinks *et al*. (1978) and Martin *et al*. (1992) suggested scrotal circumference at 12 months was effectively the same trait as heifer age at puberty in beef cattle. However, results from the present study showed only low to moderate correlations, ranging from –0.06 to –0.41. Morris *et al*. (2000) reported a similar correlation (–0.25) in Angus cattle and Martinez-Velazquez *et al*. (2003) found genetic correlations of –0.15 and 0.23 for scrotal circumference with heifer age at puberty and first mating weaning rate, respectively in pooled *Bos taurus* breeds. Perry *et al*. (1990), in tropical breeds similar to this study, reported no evidence of a relationship between heifer age at puberty and bull scrotal circumference in small half-sib families. Our results showed the magnitude of relationships was influenced by the age of the bulls at scrotal measurement. In both genotypes, correlations between heifer age at puberty and scrotal circumference were higher at younger ages (i.e. 12 months BRAH; 6 months in TCOMP). They were reduced in magnitude at 18 months, and by 24 months there was no significant association of scrotal circumference with heifer age at puberty in either genotype.

Scrotal circumference was lowly to moderately positively correlated with reproductive outcomes from the maiden mating, generally reflecting the same associations with age at puberty. Eler *et al*. (2004) similarly found a genetic correlation of 0.20 between yearling heifer pregnancy rate and scrotal circumference in Nellore cattle, and Morris *et al*. (2000) a 0.14 correlation (albeit with very large standard error) in first-calving Angus heifers. In Hereford cattle, Toelle and Robison (1985) also reported selecting for testicular size increased female calving rate and decreased age at first breeding, but Evans *et al*. (1999) found no genetic correlation between heifer pregnancy rate and scrotal circumference but provided some evidence of a non-linear association.

The relationships between scrotal circumference and mating 2 and lifetime reproduction traits were generally low. However, the –0.35 genetic correlation of scrotal circumference at 18 months with days to calving in BRAH was similar to the –0.30 correlation reported by Meyer and Johnston (2001) in a large BRAH herd. Forni and Albuquerque (2005) however, reported a lower correlation (–0.10) in Nellore cattle. The low correlations observed in TCOMP are contrary to the results of Meyer *et al.* (1991) who reported a correlation of –0.41 in Belmont Reds between scrotal circumference and days to calving from repeat records. The results are similar to those of Morris *et al*. (2000) who reported a 0.25 correlation between scrotal circumference and second mating pregnancy rate, and only a 0.07 correlation with pregnancy rate in cows beyond mating 2. Morris *et al*. (2000) also reported a –0.36 genetic correlation between heifer age at puberty and lifetime pregnancy rate, but all estimates had large standard errors. Morris and Cullen (1994), in mixed British breeds of cattle, reported a genetic correlation between heifer age at puberty and maiden pregnancy rate of –0.30, and a correlation with lifetime pregnancy rate of –0.29. Their estimates of correlations with scrotal circumference also had large standard errors but tended to be higher with maiden pregnancy rate than with lifetime pregnancy rate. They observed no trend in the estimates for scrotal circumference measured at different ages.

Semen quality traits had similar, or higher, correlations than scrotal circumference with heifer age at puberty and moderate correlations with mating 1 traits. For mating 2 traits, in particular lactation anoestrus traits, the correlations with semen quality traits were consistently higher than the correlations with scrotal circumference. Semen mass activity and motility were genetically related to female mating 2 traits, particularly when measured at 18 months. These two measures can be recorded crush-side but requires a trained technician. The semen morphology trait, percent normal sperm, was also moderately to highly correlated with mating 2 traits, though differences in the magnitudes of the correlations were observed across genotypes for different measurement times. Recording of percent normal sperm is a more costly measure than crush-side semen trait requiring a sample sent for analysis by an accredited morphologist. Percent normal sperm at 24 months was identified as a genetic predictor of all female traits at mating 2 in BRAH, whereas for TCOMP, by this age, the correlations were close to zero. Lifetime female reproduction traits were also correlated with semen quality traits. In BRAH, measures at 18 months, particularly mass activity and motility, were highly correlated with the lifetime traits. In TCOMP, estimates for measures at 18 month had large standard errors but tended to show moderate correlations with lifetime calving rate. No literature estimates were found for genetic correlations between these groups of traits. Phenotypic associations have been reported (Holroyd *et al*. 2002) between semen quality traits and a bull's calf output under multiple-sire mating in tropical beef cattle breeds. Holroyd *et al*. (2002) found significant associations between a bull's percent normal sperm and subsequent calf output but no association with motility from a multiple regression analysis. However, the bulls used were considerably older (2–4 years) than those in the present study.

Of the hormone traits studied, bull IGF-I measured at weaning, was most correlated with heifer age at puberty, particularly in BRAH, supporting the strong genetic correlation between heifer IGF-I and heifer age at puberty (Johnston *et al*. 2009). The concentration of LH deriving from gonadotrophin releasing hormone stimulation was also predictive of reproductive performance in TCOMP; however, the direction of the correlations appeared to be counterintuitive suggesting high LH response in young bulls was genetically correlated with decreased female reproductive performance, particularly at mating 2. Haley *et al*. (1989) concluded from selection lines in sheep that the genes controlling LH response to gonadotrophin releasing hormone are common between the sexes. In other hormone studies, Mackinnon *et al*. (1991) measured testosterone response to gonadotrophin releasing hormone challenge at 9 and 18 months in a beef tropical composite and proposed it was potentially a better measure than scrotal circumference as a genetic indicator of female fertility. Inhibin was also viewed as a potential indicator trait given its role in spermatogenesis (see Burns *et al*. 2010, 2013) but did not show any significant correlations with female reproduction traits in either genotype.

No published estimates of relationships of sheath and preputial eversion with female reproduction were found. There are publications (e.g. Anon. 2005) that described the physiological basis of a protruding prepuce (i.e. eversion) and its associated increased risk of prolapsed. It is also reported to have increased occurrence in polled bulls (Anon. 2005). Our result suggests that bulls with greater preputial eversion (and more pendulous sheaths) were genetically related to lower female reproductive performance. Further, the reduction in the magnitude of the correlations in the subset of cows still present at the sixth mating for BRAH suggests that these traits may be related to an increased chance of culling due to consecutive reproductive failures. Burns *et al*. (2010) in a review postulated that cervix shape and size may affect pregnancy rate in cattle; and Finch *et al*. (2003) reported a high heritability estimate for cervical size in a small sample of Santa Gertrudis. The possibility of there being a genetic link between sheath and preputial eversion and structural aspects of the female reproductive tract warrants further investigation.

The observed correlations of female reproduction with bull traits are supported by relationships between heifer age at puberty and female reproduction. In BRAH, almost half the heifers were not observed to be pubertal at the time of first mating (Johnston *et al*. 2009), compared with almost 80% in TCOMP. This clearly contributed to the genotype difference in the genetic relationships between heifer age at puberty and mating 1 traits. Morris *et al*. (2000) similarly observed a greater correlation between age at puberty and pregnancy rates in heifers under restricted joining (–0.87) than in cows (–0.21). The genetic relationship between age at puberty and lactation anoestrous interval was positive but much stronger in TCOMP compared with BRAH. Mialon *et al*. (2000) reported a 0.50 genetic correlation between heifer age at puberty and postpartum anoestrous interval in Charolais. Martin *et al*. (1992) argued heifer age at puberty may be the best measure of female reproduction because it is free of the effects of lactation. The present results and those of Johnston *et al*. (2014) showed mating 1 and 2 reproductive outcomes were more highly correlated measures of lifetime reproduction than was heifer age at puberty. While there was no evidence of age at puberty being antagonistic to lifetime reproductive performance, age at puberty was mainly predictive of early female reproductive traits.

Age of measurement of the bull traits (i.e. 6, 12, 18, 24 months) influenced the magnitude of many of the correlations of bull traits with female puberty and reproduction. Genetic correlations with scrotal circumference at 6 months of age in BRAH were not consistent, and may reflect difficulty in obtaining the measure in very young animals. Scrotal circumference measured after 6 months of age the genetic correlations in both genotypes tended to decrease in with increasing age. Burrow (2001) observed no difference in the correlations (all very low and negative) with average pregnancy rate (first three matings) for scrotal circumference measured at 6, 12 and 18 months in Belmont Red cattle, they noted some differences with days to calving. Gargantini *et al*. (2005) reported lower correlations with heifer age at puberty and pregnancy rate for scrotal circumference at 12 versus 15 months but standard errors for the estimates were not given.

For the semen quality traits, Corbet *et al*. (2013) showed heritabilities for mass activity and motility declined as age of measurement increased (i.e. 12, 18–24 months) in both genotypes. This most likely reflected the percentage of bulls producing a fertile ejaculate (i.e. were pubertal) increased over this period. Percent normal sperm was observed to have a moderate heritability when measured at 24 months in TCOMP, but was not predictive of female reproduction. These differences need to be considered when implementing strategies for industry performance recording. The genetic correlations with weaning rate also often differed from those with calving rate, in these data, which may indicate that a focus on calf losses will need to be maintained in both performance recording and management (see Bunter *et al*. 2013).

Conclusions

The results generally support the early hypothesis of Land (1973) for a range of additional bull and female measures in tropical beef cattle. Scrotal circumference at younger ages is a modest genetic predictor of heifer age at puberty but not of female reproduction. Semen quality, sheath traits, and some hormones, were highly correlated with female reproduction, particularly of the anoestrus traits in first-lactation cows. These bull measures are potentially useful as indirect selection criteria for improving female reproduction in tropical breeds.

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