**CSIRO** PUBLISHING

*Animal Production Science*, 2013, **53**, 101–113
http://dx.doi.org/10.1071/AN12163

# Male traits and herd reproductive capability in tropical beef cattle. 2. Genetic parameters of bull traits

*N. J. Corbet*[A,B,H], *B. M. Burns*[A,C], *D. J. Johnston*[A,D], *M. L. Wolcott*[A,D], *D. H. Corbet*[A,E], *B. K. Venus*[A,F], *Y. Li*[A,B], *M. R. McGowan*[A,G] *and R. G. Holroyd*[A,E]

[A]Cooperative Research Centre for Beef Genetic Technologies, University of New England, Armidale, NSW 2351, Australia.
[B]CSIRO Livestock Industries, Rockhampton, Qld 4701, Australia.
[C]The University of Queensland, Centre for Animal Science, Queensland Alliance for Agriculture and Food Innovation, Rockhampton, Qld 4701, Australia.
[D]Animal Genetics and Breeding Unit, University of New England, Armidale, NSW 2351, Australia.
[E]Department of Employment Economic Development and Innovation, Rockhampton, Qld 4701, Australia.
[F]Department of Employment Economic Development and Innovation, St Lucia, Qld 4701, Australia.
[G]School of Veterinary Science, The University of Queensland, St Lucia, Qld 4072, Australia.
[H]Corresponding author. Email: Nick.Corbet@daff.qld.gov.au

**Abstract.** A total of 4063 young bulls of two tropical genotypes (1639 Brahman and 2424 Tropical Composite) raised in northern Australia were evaluated for a comprehensive range of production and reproduction traits up to 24 months of age. Prior to weaning, peripheral blood concentrations of luteinising hormone (LH) and inhibin were measured at 4 months of age. At weaning (6 months) blood insulin-like growth factor-1 (IGF-I) and flight time were recorded. Body composition traits of fat depth and eye-muscle area were determined by ultrasonography at 15 months of age when additional measurements of liveweight, hip height and body condition score were recorded. Bull breeding soundness was evaluated at ~12, 18 and 24 months of age when measurements of scrotal circumference, sheath score, semen mass activity, progressive motility of individual sperm and percent morphologically normal sperm were recorded. Magnitude of heritability and genetic correlations changed across time for some traits. Heritability of LH, inhibin, IGF-I and of 18-month scrotal circumference, mass activity, progressive motility and percent normal sperm was 0.31, 0.74, 0.44, 0.75, 0.24, 0.15 and 0.25, respectively, for Brahmans and 0.48, 0.72, 0.36, 0.43, 0.13, 0.15 and 0.20, respectively, for Tropical Composites. Inhibin and IGF-I had moderate genetic association with percent normal sperm at 24 months in Brahmans but low to negligible associations in Tropical Composites. Body condition score in Brahmans and sperm motility (mass and individual) traits in both genotypes had moderate to strong genetic correlation with percent normal sperm and may prove useful candidates for indirect selection. There is scope to increase scrotal circumference by selection and this will be associated with favourable correlated responses of improved semen quality in both genotypes. The lack of genetic antagonism among bull traits indicates that selection for improved semen quality will not adversely affect other production traits.

Received 14 May 2012, accepted 25 July 2012, published online 13 December 2012

## Introduction

Young replacement bulls are the major source of new genetics for beef herds and their inherent fertility contributes to herd reproduction rate. The most practical means of assessing bull fertility is a bull breeding soundness evaluation (BBSE; Chenoweth 1980; Hopkins and Spitzer 1997; Fordyce *et al*. 2006), which incorporates a physical examination, scrotal circumference (SC) measurement and semen evaluation. The BBSE traits measured are used as indicators of inherent bull fertility (Holroyd *et al*. 2002; Parkinson 2004; Kastelic and Thundathil 2008). Other traits linked to reproductive function and measureable before puberty in young bulls include circulating blood hormones [e.g. inhibin, luteinising hormone (LH) and insulin-like growth factor-1 (IGF-I)], these may potentially predict the reproductive capability of bulls (Parkinson 2004; Burns *et al*. 2011).

Inhibin is produced in the testes and linked to the regulation of spermatogenesis (Phillips 2005) while LH, secreted by the pituitary, is linked to testosterone secretion and influences the onset of puberty (Evans *et al*. 1995; Bagu *et al*. 2006). Preliminary estimates suggest a heritable basis for inhibin and LH in beef cattle (Corbet *et al*. 2011). IGF-I is produced primarily by the liver and recognised for its role in early growth stimulus in humans but has also been related to bull SC and sperm motility (Yilmaz *et al*. 2004) and to heifer age at puberty (Johnston *et al*. 2009). IGF-I has been reported to be moderately heritable (0.30–0.50) in cattle of various breeds, sexes and ages (Moore *et al*. 2005; Davis and Simmen 2006; Barwick *et al*. 2009*a*, 2009*b*).

Reported heritability estimates for SC were generally moderate to high (Meyer *et al*. 1990; Burrow 2001; Cammack *et al*. 2009) and genetic correlation with herd reproductive performance generally favourable (Meyer *et al*. 1991; Morris and Cullen 1994; Evans *et al*. 1999; Eler *et al*. 2006; Palomares and Wolfe 2011), which warrant the inclusion of SC in genetic improvement programs (Hammond and Graser 1987; Graser *et al*. 2005). The BBSE semen appraisal includes crush-side estimates of sperm motility (mass activity and percent progressively motile sperm) and laboratory assessment of percent morphologically normal sperm (PNS) in a sample of the ejaculate. Phenotypically, PNS has been reported to be one of the better predictors of calf output by bulls in multiple sire mating groups (Holroyd *et al*. 2002). Heritability of PNS has generally been estimated in the range of 0.10–0.35 in North American and European *Bos taurus* breeds (Ducrocq and Humblot 1995; Kealy *et al*. 2006; Gredler *et al*. 2007) although Yilmaz *et al*. (2004) report a heritability of 0.47 in North American Angus. Heritability of percent abnormal sperm has been reported to be 0.25 in Angus (Garmyn *et al*. 2011) and 0.15 in Nellore cattle (Silva *et al*. 2011). Heritability of sperm motility parameters in *B. taurus* bulls varied from 0.04 (Gredler *et al*. 2007) to 0.22 (Kealy *et al*. 2006). Dias *et al*. (2008) estimated the genetic correlation of SC with mass activity, individual sperm motility and overall BBSE score in Nellore bulls to be 0.60, 0.72 and 0.64, respectively.

With the exception of SC, none of the traits measured at BBSE or concentration of blood hormones have been measured for the purpose of genetic evaluation within breeds with a view to genetic improvement of herd reproduction. To our knowledge there are no published reports of the heritability of semen quality traits and their genetic relationship with hormone concentrations or other BBSE traits in Australian beef herds. The objective of this study was to estimate genetic parameters for a range of traits measured in Australian Brahman (BRAH) and Tropical Composite (TCOMP) bulls from 4 to 24 months of age with a view to ascertaining the potential value of male traits measured early in life as genetic predictors of herd reproductive capability.

## Materials and methods

### *Animals*

A comprehensive account of herd management and data collection protocols is provided by Burns *et al*. (2013). In summary, data were obtained from bulls of two genotypes (BRAH and TCOMP), which were progeny of cows bred for the Beef CRC northern Australia breeding project (Johnston *et al*. 2009). TCOMP were developed with combinations of Belmont Red, Charbray, Santa Gertrudis and Senepol breeds and represent a genotype with 50% tropically adapted and 50% unadapted genetics (Barwick *et al*. 2009*a*). Progeny were bred on five properties across central, northern and western Queensland over 7 years using sires selected to ensure representation of industry populations and genetic linkage across years and properties within genotype. At weaning, bull calves (average of 392 per year) were relocated from birth locations by road transport to Brigalow Research Station (170 km SW of Rockhampton). Additionally, an average of 189 bulls per year were born at Belmont Research Station (25 km NW of Rockhampton) and remained there post-weaning (see Table 1).

**Table 1. Numbers of bulls allocated to each post-weaning location by genotype and year**

| Location | Year | Genotype | |
|---|---|---|---|
| | | Brahman | Tropical Composite |
| Belmont | 2004 | 47 | 42 |
| | 2005 | 103 | 105 |
| | 2006 | 124 | 101 |
| | 2007 | 110 | 110 |
| | 2008 | 117 | 96 |
| | 2009 | 99 | 119 |
| | 2010 | 74 | 74 |
| Brigalow | 2004 | 63 | 130 |
| | 2005 | 133 | 255 |
| | 2006 | 142 | 278 |
| | 2007 | 221 | 321 |
| | 2008 | 197 | 286 |
| | 2009 | 147 | 302 |
| | 2010 | 62 | 205 |
| Total | | 1639 | 2424 |

At Brigalow and Belmont all bulls weaned in the same year were managed as a single group until completion of data collection at 24 months of age. Animals born at Belmont included 250 crossbreds resulting from mixed mating of the two genotypes at that location. Data from the crossbreds were grouped by sire genotype and information on all young bulls by BRAH sires was analysed separately to those by TCOMP sires.

### *Measurements*

A full description of bull traits and how they were measured is provided by Burns *et al*. (2013). In brief, circulating blood hormones, LH and inhibin, were measured at branding (~4 months of age) and IGF-I and flight time were measured at weaning (~6 months of age). BBSE were conducted on the young bulls at three time points when the birth-year contemporary groups were on average 12, 18 and 24 months of age. Actual mean age in days (±s.d.) of the bulls on each occasion was 374 ± 28.2, 526 ± 27.7 and 704 ± 25.5 for BRAH and 398 ± 28.7, 551 ± 29.5 and 728 ± 24.4 for TCOMP, respectively. Traits measured at BBSE included weight, sheath and eversion score, SC, semen mass activity, sperm progressive motility and PNS in a sample of the ejaculate. Body composition and conformation traits were measured at ~15 months of age. Fat depth and EMA measurements (Upton *et al*. 2001) were made using ultrasound imagery by an accredited technician with a commercially available ultrasound machine (Esaote/Pie Medical Aquila, Maastricht, The Netherlands; with a 3.5-MHz ASP-18 transducer). Rectal temperature was recorded on the 2008 and 2009 birth-year cohorts ($n$ = 1296) at the time of their 12-month BBSE. All measurements and scores were determined by experienced cattle veterinarians and technicians. Table 2 lists the traits included in the analyses, the abbreviated codes used in the text and a brief description of trait measurement.

### *Statistical analyses*

#### *Fixed-effect modelling*

Significant fixed effects were identified separately for each genotype using linear mixed model procedures of SAS (SAS

**Table 2. Description of bull traits measured**

| Code | Trait | Description |
|---|---|---|
| LH4 | Luteinising hormone (ng/mL) | Circulating blood LH measured at 4 months of age following GnRH challenge |
| IN4 | Inhibin (ng/mL) | Circulating blood inhibin measured at 4 months of age |
| IGF6 | Insulin-like growth factor-I (ng/mL) | Circulating blood IGF-I measured at 6 months of age |
| FT6 | Flight time (seconds) | Time taken to cover a distance of ~2 m upon leaving weigh scales using electronic sensors |
| RT12 | Rectal temperature (°C) | Body temperature measured at 12 months of age using an integrated thermometer and rectal probe |
| WT | Body mass (kg) | Liveweights were recorded between 12 and 24 months of age using electronic weigh cells; WT12–WT24 |
| CS15 | Body condition (score) | Body condition at 15 months of age scored on the 1 (emaciated) to 5 (excessively fat) scale in one-third score increments (converted numerically to 1.0, 1.3, 1.7, 2.0,. . .5.0) |
| RIB15 | Rib fat thickness (mm) | Subcutaneous fat thickness at the 12th/13th rib site measured using ultrasonography at 15 months of age |
| P815 | Rump fat thickness (mm) | Subcutaneous fat thickness at the rump P8 site measured using ultrasonography at 15 months of age |
| EMA15 | Eye-muscle area ($cm^2$) | Area of the eye muscle (*M. longissimus thoracis et lumborum*) at the 12th/13th rib site determined by ultrasonography at 15 months of age |
| HH15 | Hip height (cm) | Vertical distance from the top of the highest sacral vertebrae to the ground at 15 months of age |
| SH18 | Sheath (score) | Sheath scored from 9 (tight against the underline) to 1 (grossly pendulous) at 18 months of age |
| EV18 | Preputial eversion (mm) | Length of everted preputial mucosa was visually estimated at 18 months of age |
| SC | Scrotal circumference (cm) | Circumference measured at the widest point of the scrotum with both testes fully distended at 6, 12, 18 and 24 months of age; SC6–SC24 |
| MASS | Mass activity (score) | Sperm mass activity was scored from 0 = no activity to 5 = rapid distinct swirls at 12, 18 and 24 months of age; MASS12–MASS24; animals failing to provide an ejaculate with sperm present were assigned a zero score |
| MOT | Progressive motility (%) | Percent progressively motile sperm was estimated at 12, 18 and 24 months of age; MOT12–MOT24; animals failing to provide an ejaculate with sperm present were assigned a zero value |
| PNS | Percent normal sperm (%) | Percent morphologically normal sperm was determined by an accredited morphologist at 12, 18 and 24 months of age; PNS12–PNS24 |

Institute, Cary, NC, USA) or GENSTAT (13th Edition, VSN International, Hemel Hempstead, UK). Models included the fixed effects of year (2004–10), birth location (five properties), birth month (Sept. to Jan.), post-weaning location (Brigalow or Belmont), dam age (3–9 years) and previous lactation status (wet or dry), dam management group, their interactions and sire as a random effect. The effect of assay or sample group was included for blood hormone traits and age nested within birth month was included as a covariate for all traits. Ambient temperature was included as a covariate for rectal temperature records. Terms for sire group and dam group and their interaction were included to account for additive and possible non-additive breed and composite genotype effects in TCOMP and crossbreds. Non-significant terms were sequentially removed from the model to yield the final model for each trait.

### *Variance component estimation*

Additive genetic variance and heritability for each trait was estimated in univariate analyses separately for each genotype using ASReml (version 3.0). The animal models used included the final fixed effects identified above for each trait with an additional random common environmental effect of the dam when significant using log-likelihood ratio tests. SC at various ages was analysed with and without bodyweight as a covariate in the model. Genetic and phenotypic correlations between traits were estimated in a series of bivariate analyses with ASReml. For all analyses a relationship matrix was derived from a pedigree of 17 020 animals spanning several generations. A total of 60 BRAH and 76 TCOMP sires were represented in the dataset with an average of 30 bull progeny per sire. Of these sires, 66 produced 20 or more sons with semen morphology records at 24 months of age.

## Results and discussion

Summary statistics for the hormonal traits, flight time, rectal temperature and body composition traits are presented for BRAH and TCOMP bulls in Table 3. Summary statistics for SC measured from 6 to 24 months and semen quality traits measured at ~12, 18 and 24 months of age are presented in Table 4. These summary statistics are not adjusted for fixed effects and show the unadjusted means and variation in the traits recorded for each genotype.

### *Heritability of bull traits*

Estimates of heritability made from univariate analyses are presented in Tables 5, 6 and 7. Traits with low number of observations or zero heritability were not considered for further analyses. For brevity not all recorded weight and fat traits are presented but WT15 and P815, representing body mass and fatness respectively, are included for further evaluation and discussion. Heritability of the traits recorded was generally moderate indicating that genetic change could, in most cases, be readily made by selection.

### *Heritability of hormone traits*

The heritability estimate for LH4 was moderate but for IN4 was high and consistently so for both genotypes (Table 5). Although no previously published estimates of the heritability of LH or inhibin concentrations were found for other cattle populations, high heritability in humans (0.68 and 0.80, respectively), has been reported (Kuijper *et al*. 2007). Mackinnon *et al*. (1991) reported the heritability of GnRH-stimulated testosterone secretion to be 0.42 and 0.55 at 9 and 18 months of age, respectively, in a genotype similar to the TCOMP studied here. The heritability of IGF6 and FT6 in

**Table 3. Unadjusted means ± s.d. and ranges for hormone and production traits measured on Brahman and Tropical Composite bulls**
See Table 2 for trait description, *n* = number of bulls measured for each trait

| Trait | *n* | Mean ± s.d. | Min. | Max. |
|---|---|---|---|---|
| | | *Brahman* | | |
| LH4 (ng/mL) | 1025 | 5.2 ± 4.46 | 0.2 | 29.3 |
| IN4 (ng/mL) | 1288 | 7.4 ± 1.82 | 3.2 | 16.2 |
| IGF6 (ng/mL) | 1626 | 517 ± 302.1 | 56 | 1765 |
| FT6 (seconds) | 1607 | 1.20 ± 0.634 | 0.27 | 5.40 |
| RT12 (°C) | 540 | 39.2 ± 0.49 | 37.0 | 40.7 |
| WT12 (kg) | 1469 | 247 ± 35.3 | 125 | 360 |
| WT15 (kg) | 1462 | 297 ± 38.4 | 144 | 430 |
| WT18 (kg) | 1436 | 353 ± 38.4 | 214 | 488 |
| WT24 (kg) | 1430 | 384 ± 44.4 | 222 | 570 |
| CS15 (score) | 1415 | 2.5 ± 0.28 | 1.0 | 3.3 |
| RIB15 (mm) | 1458 | 1.1 ± 0.24 | 0.5 | 3.0 |
| P815 (mm) | 1458 | 1.4 ± 0.56 | 0.5 | 5.0 |
| EMA15 ($cm^2$) | 1458 | 47 ± 7.9 | 21 | 71 |
| HH15 (cm) | 1457 | 128 ± 4.9 | 110 | 144 |
| SH18 (score) | 1437 | 4 ± 1.2 | 1 | 8 |
| EV18 (mm) | 1438 | 18 ± 21.0 | 0 | 100 |
| | | *Tropical Composite* | | |
| LH4 (ng/mL) | 1520 | 7.1 ± 5.16 | 0.2 | 31.8 |
| IN4 (ng/mL) | 1895 | 7.8 ± 1.92 | 2.7 | 15.1 |
| IGF6 (ng/mL | 2415 | 532 ± 299.4 | 47 | 1838 |
| FT6 (seconds) | 2274 | 1.23 ± 0.553 | 0.39 | 5.40 |
| RT12 (°C) | 792 | 39.2 ± 0.50 | 37.3 | 41.0 |
| WT12 (kg) | 2106 | 275 ± 40.8 | 133 | 420 |
| WT15 (kg) | 2099 | 319 ± 44.1 | 186 | 456 |
| WT18 (kg) | 2097 | 369 ± 45.1 | 228 | 510 |
| WT24 (kg) | 2087 | 392 ± 50.7 | 236 | 580 |
| CS15 (score) | 2099 | 2.4 ± 0.28 | 1.7 | 3.3 |
| RIB15 (mm) | 2099 | 1.0 ± 0.14 | 0.5 | 3.0 |
| P815 (mm) | 2099 | 1.1 ± 0.30 | 0.5 | 4.0 |
| EMA15 ($cm^2$) | 2097 | 51 ± 8.1 | 21 | 77 |
| HH15 (cm) | 2099 | 125 ± 4.9 | 105 | 139 |
| SH18 (score) | 2104 | 7 ± 1.7 | 1 | 9 |
| EV18 (mm) | 2104 | 10 ± 20.9 | 0 | 120 |

young bulls reported in the present study have similar magnitude to estimates reported for other breeds and classes of cattle (Davis and Simmen 2006; Kadel *et al*. 2006; Barwick *et al*. 2009*a*, 2009*b*; Prayaga *et al*. 2009).

### *Heritability of production traits*

The estimate of heritability for RT12 (Table 5) was higher in BRAH (0.27) than in TCOMP (0.17). The estimate for TCOMP was consistent with the report of Burrow (2001) from a study of TCOMP with genetic links to the current TCOMP population. Prayaga *et al*. (2009) reported a heritability of 0.22 for rectal temperature in a study of the dams of the current BRAH bulls when at a similar age. Riley *et al*. (2012) report a heritability estimate of 0.19 for rectal temperature measured in a combined herd of Angus, BRAH and Romosinuano breeds and crossbreeds in subtropical Florida, USA.

With the exception of P8 fat depth (P815) in TCOMP the heritability of body growth traits (WT15, EMA15 and HH15) and sheath traits (SH18 and EV18) was generally moderate indicating that the traits are under substantial genetic control. Heritability

**Table 4. Unadjusted means ± s.d. and ranges for scrotal circumference and semen quality traits measured on Brahman and Tropical Composite bulls**
See Table 2 for trait description, *n* = number of bulls measured for each trait

| Trait | *n* | Mean ± s.d. | Min. | Max. |
|---|---|---|---|---|
| | | *Brahman* | | |
| SC6 (cm) | 1608 | 17.1 ± 1.71 | 12 | 25 |
| SC12 (cm) | 1447 | 21.2 ± 3.13 | 13 | 35 |
| SC18 (cm) | 1409 | 26.4 ± 3.49 | 16 | 42 |
| SC24 (cm) | 1403 | 30.2 ± 3.21 | 19 | 42 |
| MASS12 (score) | 1333 | 0.2 ± 0.59 | 0.0 | 4.0 |
| MOT12 (%) | 1333 | 9 ± 21.2 | 0 | 90 |
| PNS12 (%) | 103 | 24 ± 20.1 | 2 | 87 |
| MASS18 (score) | 1398 | 1.3 ± 1.12 | 0.0 | 4.5 |
| MOT18 (%) | 1398 | 39 ± 31.5 | 0 | 98 |
| PNS18 (%) | 826 | 49 ± 29.1 | 0 | 98 |
| MASS24 (score) | 1394 | 2.5 ± 1.14 | 0.0 | 5.0 |
| MOT24 (%) | 1394 | 67 ± 25.6 | 0 | 98 |
| PNS24 (%) | 1234 | 71 ± 23.1 | 1 | 98 |
| | | *Tropical Composite* | | |
| SC6 (cm) | 2388 | 19.3 ± 2.55 | 11 | 31 |
| SC12 (cm) | 2092 | 26.5 ± 3.36 | 15 | 37 |
| SC18 (cm) | 2081 | 29.9 ± 3.00 | 19 | 40 |
| SC24 (cm) | 2067 | 31.6 ± 2.85 | 21 | 42 |
| MASS12 (score) | 1919 | 1.4 ± 1.35 | 0.0 | 4.5 |
| MOT12 (%) | 1919 | 44 ± 34.6 | 0 | 95 |
| PNS12 (%) | 970 | 55 ± 27.9 | 1 | 96 |
| MASS18 (score) | 2080 | 2.2 ± 1.25 | 0.0 | 5.0 |
| MOT18 (%) | 2080 | 56 ± 28.4 | 0 | 100 |
| PNS18 (%) | 1794 | 67 ± 22.6 | 0 | 97 |
| MASS24 (score) | 2063 | 2.8 ± 1.07 | 0 | 5 |
| MOT24 (%) | 2063 | 70 ± 24.5 | 0 | 98 |
| PNS24 (%) | 1912 | 75 ± 19.1 | 0 | 99 |

estimates for WT15 and P815 suggest genotype differences between BRAH and TCOMP in the genetic control of weight and fatness. Barwick *et al*. (2009*b*) report a like difference in heritability of weight in the dams of these bulls when at a similar age. They also report an advantage to BRAH in mean P8 fat thickness but no genotype difference in heritability of P8 fat depth (0.42 for BRAH and 0.44 for TCOMP) in the females. The low estimates of variance for P8 fat depth in TCOMP bulls may simply be explained by the very low levels of subcutaneous fat measured on these bulls grazed at pasture (Table 3).

### *Heritability of scrotal circumference*

The heritability of SC in both genotypes was moderate to high and tended to be of higher magnitude in BRAH (Table 6). Including bodyweight as a covariate in the models tended to reduce the magnitude of additive and phenotypic variance but had little effect on the heritability of SC at the various ages, except for SC6 in BRAH where heritability was lower when adjusted for weight. Similar reports of negligible effects of weight adjustment on SC heritability estimates have been documented across breeds (Quirino and Bergmann 1998; Burrow 2001). Within genotype there was little difference in heritability of SC measured from 6 to 24 months of age, except in BRAH where the measurement at 6 months was lower than at all other ages. The lower variance for

**Table 5. Additive variance ($\sigma^2_a$), phenotypic variance ($\sigma^2_p$) and heritability ($h^2$) of blood hormone levels and production traits of Brahman and Tropical Composite bulls**

See Table 2 for trait description; approximate standard error shown in parentheses

| Trait | Brahman | | | Tropical Composite | | |
|---|---|---|---|---|---|---|
| | $\sigma^2_a$ | $\sigma^2_p$ | $h^2$ | $\sigma^2_a$ | $\sigma^2_p$ | $h^2$ |
| LH4 | 4.15 | 13.29 | 0.31 (0.10) | 7.50 | 15.50 | 0.48 (0.08) |
| IN4 | 2.09 | 2.84 | 0.74 (0.09) | 2.15 | 2.97 | 0.72 (0.10) |
| IGF6 | 7237 | 16 579 | 0.44 (0.08) | 6266 | 17 533 | 0.36 (0.07) |
| FT6 | 0.078 | 0.277 | 0.28 (0.07) | 0.078 | 0.254 | 0.31 (0.07) |
| RT12 | 0.051 | 0.174 | 0.29 (0.13) | 0.028 | 0.166 | 0.17 (0.09) |
| WT15 | 244.6 | 626.1 | 0.39 (0.10) | 542.7 | 876.6 | 0.62 (0.10) |
| CS15 | 0.010 | 0.048 | 0.21 (0.07) | 0.012 | 0.051 | 0.23 (0.06) |
| P815 | 0.114 | 0.289 | 0.39 (0.09) | 0.008 | 0.083 | 0.10 (0.04) |
| EMA15 | 10.1 | 27.7 | 0.37 (0.08) | 16.6 | 32.2 | 0.52 (0.07) |
| HH15 | 5.97 | 13.11 | 0.46 (0.09) | 8.46 | 15.24 | 0.56 (0.07) |
| SH18 | 0.293 | 0.986 | 0.30 (0.08) | 0.807 | 2.327 | 0.35 (0.08) |
| EV18 | 126.3 | 419.0 | 0.30 (0.08) | 100.3 | 428.8 | 0.23 (0.06) |

**Table 6. Additive variance ($\sigma^2_a$), phenotypic variance ($\sigma^2_p$) and heritability ($h^2$) of scrotal circumference of Brahman and Tropical Composite bulls**

See Table 2 for trait description. Measurements were made from weaning to 24 months of age; variance components are shown with (*Wt. adj.*) and without bodyweight as a covariate for each trait; approximate standard error shown in parentheses

| Trait | Brahman | | | Tropical Composite | | |
|---|---|---|---|---|---|---|
| | $\sigma^2_a$ | $\sigma^2_p$ | $h^2$ | $\sigma^2_a$ | $\sigma^2_p$ | $h^2$ |
| SC6 | 0.81 | 1.75 | 0.46 (0.08) | 1.44 | 3.50 | 0.41 (0.08) |
| SC6 (*wt adj.*) | 0.51 | 1.45 | 0.35 (0.07) | 1.16 | 2.78 | 0.42 (0.07) |
| SC12 | 3.07 | 4.72 | 0.65 (0.08) | 3.42 | 7.47 | 0.46 (0.09) |
| SC12 (*wt adj.*) | 2.52 | 3.86 | 0.65 (0.08) | 2.77 | 6.24 | 0.44 (0.08) |
| SC18 | 5.06 | 6.76 | 0.75 (0.09) | 3.10 | 7.25 | 0.43 (0.09) |
| SC18 (*wt adj.*) | 4.40 | 5.89 | 0.75 (0.08) | 2.63 | 6.25 | 0.42 (0.08) |
| SC24 | 4.71 | 6.31 | 0.75 (0.09) | 2.98 | 6.73 | 0.44 (0.09) |
| SC24 (*wt adj.*) | 3.81 | 5.18 | 0.74 (0.09) | 2.74 | 5.86 | 0.47 (0.09) |

**Table 7. Additive variance ($\sigma^2_a$), phenotypic variance ($\sigma^2_p$) and heritability ($h^2$) of semen quality traits of Brahman and Tropical Composite bulls**

See Table 2 for trait description. Measurements were made at 12, 18 and 24 months of age; approximate standard error shown in parentheses

| Trait | Brahman | | | Tropical Composite | | |
|---|---|---|---|---|---|---|
| | $\sigma^2_a$ | $\sigma^2_p$ | $h^2$ | $\sigma^2_a$ | $\sigma^2_p$ | $h^2$ |
| | | | *12 months* | | | |
| MASS12 | 0.147 | 0.217 | 0.68 (0.10) | 0.511 | 1.528 | 0.33 (0.06) |
| MOT12 | 149.3 | 335.9 | 0.44 (0.09) | 346.3 | 1073.0 | 0.32 (0.06) |
| PNS12 | 0.001 | 379.4 | 0.00 (0.00) | 296.7 | 720.5 | 0.41 (0.10) |
| | | | *18 months* | | | |
| MASS18 | 0.265 | 1.115 | 0.24 (0.07) | 0.190 | 1.431 | 0.13 (0.05) |
| MOT18 | 123.9 | 804.9 | 0.15 (0.06) | 116.4 | 768.3 | 0.15 (0.05) |
| PNS18 | 198.5 | 800.9 | 0.25 (0.09) | 96.7 | 480.5 | 0.20 (0.06) |
| | | | *24 months* | | | |
| MASS24 | 0.106 | 1.140 | 0.09 (0.05) | 0.050 | 1.009 | 0.05 (0.03) |
| MOT24 | 30.3 | 608.4 | 0.05 (0.04) | 53.4 | 558.6 | 0.10 (0.04) |
| PNS24 | 75.0 | 496.8 | 0.15 (0.06) | 96.8 | 360.4 | 0.27 (0.06) |

SC6 in both genotypes may reflect the difficulty in accurately measuring SC at weaning when testes are still developing and in some cases difficult to clasp. Additive genetic variance and heritability of SC tended to be highest ~18 months of age in BRAH and 12 months of age in TCOMP. The results suggest that measurement and selection of young bulls (particularly BRAH) for SC would best be made at ages later than 6 months. Many published estimates for heritability of SC across breeds were in the range of 0.40–0.70 for bulls between 12 and 18 months of age (Cammack *et al*. 2009; Burns *et al*. 2011). The high heritability of SC in BRAH reported here is not dissimilar to estimates (0.64 ± 0.06) provided by Eler *et al*. (2006) for SC18 in their study of young Nellore bulls. Burrow (2001), in a study of TCOMP, reported heritability estimates of 0.44, 0.37 and 0.46, respectively, for SC6, SC12 and SC18, which are similar to those reported in Table 6 for TCOMP.

### *Heritability of semen traits*

Estimates of heritability of sperm motility traits (MASS and MOT) were moderate in TCOMP and moderate to high in BRAH when measured at 12 months of age (Table 7). However, heritability of sperm motility traits declined over time from 12 to 24 months of age. The measurements of MASS and MOT at 12 months included high proportions of zero values assigned to peri-pubertal bulls producing no sperm (80% in BRAH and 30% in TCOMP). Preliminary analyses examined the binary trait defined as whether or not the bull produced an ejaculate with spermatozoa present at 12 months of age and provided heritabilities of 0.37 ± 0.06 and 0.18 ± 0.05 for BRAH and TCOMP, respectively (Corbet *et al*. 2011). The measurements of MASS and MOT at 12 months of age likely include an element of sexual maturation as the bulls reach pubertal age and later measures at 18 and 24 months of age may be more indicative of the true heritability of post-pubertal sperm motility. The estimates of heritability of MASS24 and MOT24 were low, ranging from 0.05 to 0.10 across both genotypes, and were comparable with estimates reported for other cattle breeds (Kealy *et al*. 2006; Gredler *et al*. 2007).

In BRAH, additive variance of PNS was zero at 12 months of age when only a small number of bulls (12%) provided an ejaculate with sufficient sperm to allow evaluation of 100 spermatozoa for morphological assessment of PNS. At the same stage 52% of the TCOMP had sufficient sperm for PNS evaluation suggesting an advantage to TCOMP in earlier sexual development. However, by 24 months of age 88% of BRAH and 92% of TCOMP produced ejaculates with sufficient sperm for morphological assessment. The estimates of heritability of PNS in ejaculates from 24-month-old bulls were moderate for TCOMP (0.27 ± 0.06) and low for BRAH (0.15 ± 0.06), these estimates were comparable with those reported by previous studies in other cattle breeds across the world (Kealy *et al*. 2006; Gredler *et al*. 2007; Garmyn *et al*. 2011; Silva *et al*. 2011).

### *Genetic and phenotypic correlations between hormone and production traits*

Bull traits were measured from 4 to 24 months of age spanning pre-pubertal, peri-pubertal and post-pubertal developmental stages. Genetic and phenotypic correlations among the hormone and production-type traits measured to 18 months of age are presented in Tables 8 and 9 for BRAH and TCOMP, respectively. Phenotypic correlations were generally low or close to zero, exceptions were between growth traits (e.g. among WT15, EMA15, HH15 and for CS15 with WT15, P815 and EMA15) and between sheath traits (SH18 and EV18). The moderate to strong phenotypic correlations among growth traits were mirrored by generally strong genetic correlations. The strong negative phenotypic and genetic correlations between SH18 and EV18 in both genotypes indicate that animals with more pendulous sheaths are prone to eversion of more preputial mucosa and that selection for less pendulous sheaths will also reduce the amount of mucosa everted.

Hormones, LH4 and IN4, had a low positive genetic correlation with each other and mostly low or negligible genetic association with other production traits in both genotypes. The exception was a strong negative genetic correlation between IN4 and RT12 in TCOMP bulls suggesting that those able to maintain lower body temperature secreted more inhibin. The reason for a genetic association between blood inhibin concentration and heat tolerance is not clear but the association was not evident at the phenotypic level nor was it evident in BRAH, a genotype considered to be inherently better adapted to high ambient temperatures (Prayaga 2003). The high standard error associated with the estimate suggests caution in interpretation. In TCOMP the genetic correlations between hormone and sheath traits suggested that animals with high LH and low inhibin levels at 4 months of age were prone to have less pendulous sheaths and less everted preputial mucosa. The suggested genetic link between circulating hormones and sheath traits was not evident in BRAH.

Blood concentration of IGF-I measured at weaning in BRAH had moderate positive genetic correlations with IN4, WT15, EMA15 and HH15 and a moderate negative genetic correlation with P815. The same genetic correlations in TCOMP were low with the exception of a moderate genetic correlation (0.34 ± 0.10) between IGF6 and EMA15. In BRAH the genetic correlations suggest that selection for increased IGF-I at 6 months will be associated with correlated responses of increased growth of muscle and frame but less subcutaneous fat. These results are contrary to those reported by Moore *et al*. (2005) where higher IGF-I concentrations (at 240 days) were found to be genetically associated with lower WT (at 400 days) and higher P8 fat in a population of Australian Angus bulls and heifers. Davis *et al*. (2003) reported genetic association of serum IGF-I concentration with fat thickness to be low and positive and with EMA to be low and negative in American Angus bulls and heifers during a post-weaning feedlot period. However, the mean fat thickness of the animals studied by Davis *et al*. (2003) was 6 times that of the bulls in the present study and twice that of the animals described by Moore *et al*. (2005). Variation in estimates of genetic correlation among IGF-I, growth and fatness traits between studies is likely affected not only by breed, sex and age but additionally by weight and fatness of the animals at the time of trait measurement.

**Table 8. Genetic and phenotypic correlations among hormone and production traits for Brahman bulls**

See Table 2 for trait description. Genetic correlations above the diagonal, phenotypic below; all estimates from bivariate analyses; approximate standard errors in parentheses; standard errors for phenotypic correlations ranged from 0.02 to 0.04; traits were measured between 4 and 18 months of age

| Trait | LH4 | IN4 | IGF6 | FT6 | RT12 | WT15 | CS15 | P815 | EMA15 | HH15 | SH18 | EV18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LH4 | – | 0.06 (0.17) | 0.31 (0.18) | –0.24 (0.20) | –0.29 (0.26) | 0.18 (0.19) | 0.03 (0.24) | 0.12 (0.19) | –0.15 (0.20) | –0.14 (0.18) | 0.09 (0.22) | –0.02 (0.21) |
| IN4 | 0.00 | – | 0.36 (0.11) | –0.08 (0.15) | 0.07 (0.22) | 0.24 (0.13) | –0.12 (0.17) | 0.13 (0.14) | 0.19 (0.14) | 0.13 (0.13) | –0.06 (0.15) | 0.07 (0.14) |
| IGF6 | 0.11 | 0.15 | – | –0.06 (0.16) | –0.33 (0.22) | 0.53 (0.11) | 0.24 (0.19) | –0.42 (0.14) | 0.46 (0.13) | 0.31 (0.13) | –0.30 (0.16) | 0.23 (0.16) |
| FT6 | 0.00 | 0.01 | 0.02 | – | –0.27 (0.25) | 0.24 (0.17) | 0.31 (0.19) | 0.25 (0.17) | –0.04 (0.18) | –0.02 (0.17) | –0.05 (0.19) | 0.10 (0.18) |
| RT12 | –0.06 | 0.03 | –0.09 | –0.06 | – | –0.47 (0.22) | 0.19 (0.30) | 0.10 (0.25) | –0.08 (0.25) | –0.12 (0.23) | 0.05 (0.28) | 0.24 (0.27) |
| WT15 | 0.05 | 0.06 | 0.16 | 0.06 | –0.10 | – | –0.10 (0.20) | –0.16 (0.16) | 0.51 (0.12) | 0.72 (0.08) | –0.20 (0.17) | 0.08 (0.17) |
| CS15 | 0.00 | –0.03 | 0.08 | 0.07 | 0.00 | 0.20 | – | 0.37 (0.17) | 0.57 (0.16) | –0.48 (0.15) | –0.22 (0.20) | 0.30 (0.21) |
| P815 | –0.05 | 0.00 | –0.08 | 0.04 | –0.06 | 0.10 | 0.25 | – | –0.11 (0.16) | –0.30 (0.14) | 0.17 (0.17) | –0.08 (0.17) |
| EMA15 | 0.06 | 0.04 | 0.19 | 0.00 | 0.02 | 0.52 | 0.31 | 0.08 | – | 0.31 (0.14) | –0.42 (0.16) | 0.20 (0.17) |
| HH15 | –0.01 | 0.06 | 0.09 | 0.00 | –0.04 | 0.64 | –0.06 | –0.03 | 0.27 | – | –0.28 (0.16) | 0.13 (0.16) |
| SH18 | 0.09 | 0.03 | 0.03 | 0.00 | –0.01 | –0.05 | 0.01 | 0.04 | –0.02 | –0.05 | – | –0.67 (0.11) |
| EV18 | –0.01 | 0.02 | 0.03 | –0.05 | 0.02 | 0.05 | –0.01 | –0.03 | 0.03 | 0.07 | –0.37 | – |

**Table 9. Genetic and phenotypic correlations among hormone and production traits for Tropical Composite bulls**

See Table 2 for trait description. Genetic correlations above the diagonal, phenotypic below; all estimates from bivariate analyses; approximate standard errors in parentheses; standard errors for phenotypic correlations ranged from 0.02 to 0.04; traits were measured between 4 and 18 months of age

| Trait | LH4 | IN4 | IGF6 | FT6 | RT12 | WT15 | CS15 | P815 | EMA15 | HH15 | SH18 | EV18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LH4 | – | 0.14 (0.12) | 0.23 (0.14) | 0.14 (0.15) | –0.02 (0.29) | 0.13 (0.13) | 0.01 (0.17) | –0.29 (0.21) | 0.17 (0.13) | –0.33 (0.20) | 0.36 (0.14) | –0.34 (0.16) |
| IN4 | 0.01 | – | 0.12 (0.11) | 0.09 (0.12) | –0.97 (0.34) | 0.17 (0.10) | 0.12 (0.14) | 0.25 (0.18) | 0.12 (0.11) | 0.13 (0.13) | –0.28 (0.12) | 0.28 (0.13) |
| IGF6 | 0.08 | 0.02 | – | 0.07 (0.14) | 0.22 (0.22) | 0.19 (0.09) | –0.04 (0.14) | –0.18 (0.18) | 0.34 (0.10) | 0.08 (0.09) | –0.04 (0.10) | 0.00 (0.11) |
| FT6 | –0.02 | 0.01 | –0.04 | – | 0.06 (0.26) | 0.15 (0.13) | 0.19 (0.16) | –0.21 (0.21) | 0.11 (0.13) | 0.02 (0.17) | –0.08 (0.15) | 0.25 (0.16) |
| RT12 | –0.03 | –0.08 | 0.01 | –0.04 | – | 0.11 (0.26) | –0.34 (0.32) | –0.46 (0.34) | 0.00 (0.26) | –0.08 (0.24) | 0.08 (0.31) | 0.03 (0.31) |
| WT15 | 0.00 | 0.08 | 0.11 | 0.00 | 0.05 | – | 0.20 (0.14) | –0.14 (0.18) | 0.59 (0.07) | 0.72 (0.08) | –0.27 (0.12) | 0.34 (0.13) |
| CS15 | –0.03 | –0.02 | 0.04 | –0.02 | 0.01 | 0.17 | – | 0.30 (0.20) | 0.35 (0.13) | –0.46 (0.15) | 0.17 (0.16) | 0.00 (0.17) |
| P815 | –0.06 | 0.00 | –0.02 | –0.01 | –0.06 | 0.08 | 0.21 | – | –0.24 (0.18) | –0.29 (0.15) | –0.07 (0.21) | 0.32 (0.21) |
| EMA15 | 0.06 | 0.00 | 0.20 | –0.04 | 0.03 | 0.48 | 0.26 | 0.02 | – | 0.34 (0.14) | 0.21 (0.13) | –0.06 (0.14) |
| HH15 | –0.02 | 0.06 | –0.01 | 0.00 | 0.00 | 0.64 | –0.07 | –0.03 | 0.27 | – | –0.29 (0.16) | 0.11 (0.16) |
| SH18 | 0.13 | –0.16 | 0.09 | –0.02 | –0.03 | –0.11 | 0.06 | –0.02 | 0.10 | –0.05 | – | –0.93 (0.03) |
| EV18 | –0.10 | 0.12 | –0.06 | 0.02 | 0.02 | 0.10 | –0.04 | 0.03 | –0.03 | 0.07 | –0.55 | – |

### *Genetic and phenotypic correlations among scrotal circumference and semen quality traits*

Phenotypic and genetic correlations between SC traits measured at different ages were generally moderate to high (Tables 10 and 11). With the exception of SC6 in BRAH, SC measured between weaning and 24 months age had strong genetic correlation (ranged from 0.55 to 0.88) with crush-side scores of sperm motility (MASS and MOT) in ejaculates collected at 12, 18 and 24 months age in both genotypes. Genetic correlation between SC and PNS was strongest at 18 months in BRAH ($0.50 \pm 0.13$) and at 12 months in TCOMP ($0.55 \pm 0.13$). The low or negative genetic association between SC6 and semen quality traits in BRAH may reflect the difficulty in accurately measuring SC at weaning as previously discussed. Otherwise, genetic correlations between SC and PNS24 were generally low in BRAH and moderate and positive in TCOMP. The trends in genetic correlation between SC and semen quality traits of these bulls suggest that selection for SC was best made at ~18 months of age for BRAH and 12 or 18 months for TCOMP to optimise correlated responses in sperm motility and PNS at 24 months of age. Genetic correlations of similar magnitude to those presented here between SC and semen quality traits have been reported across a range of other cattle breeds (Gipson *et al*. 1987; Dias *et al*. 2008). Most recently, Siqueira *et al*. (2012) in their study of Nellore bulls, report a strong negative genetic correlation between SC18 and total sperm defects (–0.82) suggesting that selection for increased SC would reduce sperm defects.

Crush-side scores of sperm motility (both MASS and MOT) at 12, 18 and 24 months of age had low phenotypic but moderate to strong genetic correlations with each other and with PNS in both genotypes. Additionally, PNS at 12 and 18 months of age had strong genetic correlation with each other and with PNS24 in both genotypes suggesting that many of the same genes are responsible for MASS, MOT and PNS regardless of measurement age. Dias *et al*. (2008) and Siqueira *et al*. (2012), in their studies of Nellore bulls, also report strong genetic correlation for mass activity (–0.86 to –1.00) and sperm motility (–0.71 to –0.81) with total number of defective sperm. The results indicate that indirect selection to improve PNS could be made using crush-side scores of sperm motility and the measurements could be made as early as 12 months of age in TCOMP but may need to be delayed until 18 months in BRAH when more bulls are sexually mature and can provide an ejaculate with spermatozoa present. However, low heritability of MASS and MOT traits recorded at 24 months (Table 7) may need to be considered before promoting them as potential selection criteria.

### *Genetic correlation between early measured traits and scrotal circumference*

Scrotal circumference was recorded at 6-monthly intervals from weaning to 24 months of age. The genetic correlations for SC with hormone and production traits measured from 4 to 18 months of age are presented in Table 12 for BRAH and Table 13 for TCOMP. The genetic correlation between LH4 and measures of SC in BRAH and TCOMP were low and not significantly different from zero. Genetic correlations between IN4 and SC were generally moderate and positive (0.28–0.54) indicating that higher concentrations of inhibin are genetically associated with

**Table 10. Genetic and phenotypic correlations among scrotal circumference and semen quality traits for Brahman bulls**

See Table 2 for trait description. Genetic correlations above the diagonal, phenotypic below; all estimates from bivariate analyses; approximate standard errors in parentheses; standard errors for phenotypic correlations ranged from 0.02 to 0.04; semen quality was evaluated at 12, 18 and 24 months of age

| Trait | SC6 | SC12 | MASS12 | MOT12 | PNS12[A] | SC18 | MASS18 | MOT18 | PNS18 | SC24 | MASS24 | MOT24 | PNS24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SC6 | – | 0.69 (0.08) | 0.16 (0.13) | 0.13 (0.15) | – | 0.57 (0.09) | –0.08 (0.18) | –0.09 (0.20) | –0.30 (0.19) | 0.66 (0.08) | –0.24 (0.24) | 0.00 (0.31) | –0.26 (0.22) |
| SC12 | 0.42 | – | 0.66 (0.08) | 0.70 (0.08) | – | 0.92 (0.03) | 0.69 (0.11) | 0.65 (0.13) | 0.31 (0.17) | 0.83 (0.05) | 0.51 (0.22) | 0.71 (0.37) | 0.23 (0.18) |
| MASS12 | 0.06 | 0.43 | – | 0.99 (0.01) | – | 0.52 (0.10) | 0.79 (0.09) | 0.73 (0.12) | 0.43 (0.17) | 0.30 (0.12) | 0.66 (0.21) | 0.58 (0.29) | 0.45 (0.18) |
| MOT12 | 0.06 | 0.47 | 0.76 | – | – | 0.55 (0.10) | 0.74 (0.11) | 0.73 (0.13) | 0.48 (0.16) | 0.36 (0.12) | 0.69 (0.20) | 0.62 (0.29) | 0.44 (0.18) |
| PNS12 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| SC18 | 0.37 | 0.77 | 0.31 | 0.35 | – | – | 0.82 (0.08) | 0.79 (0.10) | 0.50 (0.13) | 0.97 (0.01) | 0.75 (0.18) | 0.88 (0.35) | 0.32 (0.18) |
| MASS18 | 0.02 | 0.36 | 0.28 | 0.31 | – | 0.48 | – | 0.97 (0.04) | 0.91 (0.09) | 0.70 (0.11) | 1.00 (0.13) | 1.00 (0.40) | 0.60 (0.19) |
| MOT18 | 0.01 | 0.27 | 0.20 | 0.22 | – | 0.38 | 0.78 | – | 0.86 (0.13) | 0.66 (0.13) | 0.99 (0.16) | 1.00 (0.29) | 0.76 (0.13) |
| PNS18 | 0.05 | 0.23 | 0.19 | 0.25 | – | 0.31 | 0.40 | 0.28 | – | 0.31 (0.17) | 0.73 (0.22) | 0.84 (0.37) | 0.93 (0.13) |
| SC24 | 0.39 | 0.62 | 0.13 | 0.18 | – | 0.83 | 0.33 | 0.27 | 0.14 | – | 0.76 (0.17) | 0.86 (0.31) | 0.22 (0.19) |
| MASS24 | 0.00 | 0.16 | 0.11 | 0.12 | – | 0.25 | 0.30 | 0.27 | 0.20 | 0.24 | – | 1.00 (0.13) | 0.42 (0.30) |
| MOT24 | 0.02 | 0.10 | 0.06 | 0.07 | – | 0.19 | 0.21 | 0.24 | 0.12 | 0.20 | 0.77 | – | 0.29 (0.40) |
| PNS24 | –0.01 | 0.06 | 0.07 | 0.08 | – | 0.15 | 0.27 | 0.33 | 0.32 | 0.12 | 0.31 | 0.32 | – |

[A]Correlations with percent normal sperm at 12 months in Brahmans were not estimable due to a small number of observations ($n = 103$) and no residual variance.

**Table 11. Genetic and phenotypic correlations among scrotal circumference and semen quality traits for Tropical Composite bulls**

See Table 2 for trait description. Genetic correlations above the diagonal, phenotypic below; all estimates from bivariate analyses; approximate standard errors in parentheses; standard errors for phenotypic correlations ranged from 0.02 to 0.04; semen quality was evaluated at 12, 18 and 24 months of age

| Trait | SC6 | SC12 | MASS12 | MOT12 | PNS12 | SC18 | MASS18 | MOT18 | PNS18 | SC24 | MASS24 | MOT24 | PNS24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SC6 | – | 0.87 (0.04) | 0.18 (0.13) | 0.16 (0.13) | 0.30 (0.15) | 0.87 (0.04) | 0.43 (0.17) | 0.30 (0.16) | 0.32 (0.16) | 0.86 (0.04) | 0.33 (0.23) | 0.29 (0.19) | 0.38 (0.14) |
| SC12 | 0.54 | – | 0.60 (0.10) | 0.56 (0.10) | 0.55 (0.13) | 0.97 (0.01) | 0.85 (0.12) | 0.55 (0.13) | 0.35 (0.15) | 0.92 (0.02) | 0.62 (0.21) | 0.42 (0.18) | 0.35 (0.14) |
| MASS12 | 0.14 | 0.43 | – | 0.98 (0.01) | 0.87 (0.08) | 0.38 (0.12) | 1.00 (0.08) | 0.79 (0.10) | 0.79 (0.11) | 0.10 (0.14) | 0.76 (0.20) | 0.53 (0.17) | 0.54 (0.13) |
| MOT12 | 0.14 | 0.42 | 0.84 | – | 0.77 (0.09) | 0.35 (0.13) | 1.00 (0.07) | 0.85 (0.09) | 0.79 (0.10) | 0.10 (0.14) | 0.78 (0.20) | 0.55 (0.18) | 0.47 (0.14) |
| PNS12 | 0.12 | 0.31 | 0.52 | 0.56 | – | 0.25 (0.15) | 0.43 (0.20) | 0.29 (0.19) | 0.85 (0.10) | 0.14 (0.16) | 0.14 (0.29) | 0.21 (0.23) | 0.60 (0.14) |
| SC18 | 0.54 | 0.85 | 0.28 | 0.28 | 0.13 | – | 0.65 (0.14) | 0.44 (0.15) | 0.21 (0.16) | 0.99 (0.01) | 0.66 (0.18) | 0.46 (0.17) | 0.34 (0.14) |
| MASS18 | 0.10 | 0.29 | 0.28 | 0.30 | 0.17 | 0.29 | – | 0.89 (0.06) | 0.74 (0.14) | 0.31 (0.17) | 0.98 (0.16) | 0.84 (0.14) | 0.54 (0.16) |
| MOT18 | 0.08 | 0.23 | 0.23 | 0.26 | 0.16 | 0.24 | 0.78 | – | 0.80 (0.12) | 0.24 (0.16) | 0.97 (0.17) | 0.95 (0.12) | 0.61 (0.14) |
| PNS18 | 0.08 | 0.23 | 0.28 | 0.31 | 0.44 | 0.22 | 0.32 | 0.40 | – | 0.04 (0.16) | 0.80 (0.23) | 0.83 (0.15) | 0.98 (0.05) |
| SC24 | 0.53 | 0.76 | 0.17 | 0.17 | 0.04 | 0.90 | 0.19 | 0.17 | 0.10 | – | 0.55 (0.20) | 0.33 (0.18) | 0.20 (0.14) |
| MASS24 | 0.11 | 0.20 | 0.23 | 0.23 | 0.11 | 0.23 | 0.27 | 0.29 | 0.21 | 0.22 | – | 0.98 (0.08) | 0.80 (0.18) |
| MOT24 | 0.08 | 0.15 | 0.19 | 0.20 | 0.14 | 0.17 | 0.25 | 0.29 | 0.28 | 0.17 | 0.80 | – | 0.76 (0.12) |
| PNS24 | 0.09 | 0.19 | 0.20 | 0.21 | 0.35 | 0.16 | 0.25 | 0.27 | 0.55 | 0.13 | 0.34 | 0.47 | – |

**Table 12. Genetic correlations of hormone and production traits with scrotal circumference and semen quality traits for Brahman bulls**

See Table 2 for trait description. All estimates from bivariate analyses; approximate standard errors in parentheses; semen quality was evaluated at 12, 18 and 24 months of age

| Trait | SC6 | SC12 | MASS12 | MOT12 | PNS12[A] | SC18 | MASS18 | MOT18 | PNS18 | SC24 | MASS24 | MOT24 | PNS24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LH4 | –0.11 (0.18) | 0.02 (0.17) | 0.25 (0.17) | 0.26 (0.19) | – | 0.03 (0.17) | 0.23 (0.23) | 0.08 (0.26) | –0.01 (0.26) | –0.11 (0.17) | 0.39 (0.30) | 0.12 (0.40) | 0.27 (0.27) |
| IN4 | 0.54 (0.10) | 0.37 (0.11) | 0.11 (0.12) | 0.13 (0.14) | – | 0.39 (0.10) | 0.12 (0.17) | 0.23 (0.18) | –0.09 (0.20) | 0.39 (0.10) | 0.16 (0.23) | 0.00 (0.29) | –0.37 (0.18) |
| IGF6 | 0.51 (0.11) | 0.56 (0.09) | 0.34 (0.13) | 0.37 (0.13) | – | 0.49 (0.10) | 0.48 (0.15) | 0.35 (0.19) | 0.10 (0.21) | 0.46 (0.11) | 0.18 (0.24) | –0.01 (0.31) | 0.44 (0.20) |
| FT6 | 0.07 (0.16) | 0.10 (0.15) | –0.30 (0.15) | –0.20 (0.17) | – | 0.22 (0.14) | 0.43 (0.18) | 0.44 (0.21) | 0.14 (0.23) | 0.21 (0.14) | 0.27 (0.28) | 0.69 (0.36) | –0.26 (0.23) |
| RT12 | –0.10 (0.25) | –0.32 (0.20) | –0.24 (0.21) | –0.23 (0.23) | – | –0.40 (0.19) | –0.61 (0.24) | –0.31 (0.30) | –0.73 (0.23) | –0.30 (0.21) | –0.30 (0.38) | –0.32 (0.50) | 0.04 (0.35) |
| WT15 | 0.64 (0.09) | 0.43 (0.11) | 0.02 (0.15) | 0.02 (0.16) | – | 0.35 (0.11) | 0.03 (0.19) | –0.06 (0.21) | –0.16 (0.22) | 0.43 (0.11) | 0.17 (0.25) | 0.26 (0.32) | 0.05 (0.23) |
| CS15 | –0.21 (0.18) | –0.03 (0.17) | –0.03 (0.18) | –0.16 (0.19) | – | –0.01 (0.16) | 0.56 (0.18) | 0.46 (0.23) | 0.36 (0.23) | –0.02 (0.17) | 0.04 (0.30) | 0.21 (0.37) | 0.69 (0.20) |
| P815 | –0.13 (0.15) | –0.21 (0.13) | –0.03 (0.15) | –0.18 (0.16) | – | –0.05 (0.13) | 0.25 (0.18) | 0.24 (0.20) | 0.25 (0.20) | –0.07 (0.13) | 0.32 (0.24) | 0.48 (0.28) | 0.27 (0.21) |
| EMA15 | 0.20 (0.15) | 0.16 (0.14) | –0.05 (0.15) | –0.08 (0.17) | – | 0.14 (0.13) | 0.13 (0.19) | –0.01 (0.22) | 0.24 (0.21) | 0.07 (0.14) | 0.00 (0.26) | 0.04 (0.32) | 0.16 (0.23) |
| HH15 | 0.51 (0.10) | 0.18 (0.12) | –0.01 (0.13) | 0.02 (0.14) | – | 0.14 (0.11) | –0.30 (0.17) | –0.32 (0.19) | –0.04 (0.20) | 0.25 (0.11) | –0.04 (0.24) | 0.08 (0.30) | –0.14 (0.21) |
| SH18 | –0.12 (0.16) | 0.23 (0.14) | 0.33 (0.15) | 0.37 (0.17) | – | 0.14 (0.14) | 0.29 (0.20) | 0.56 (0.21) | 0.12 (0.23) | –0.02 (0.15) | 0.12 (0.27) | –0.05 (0.33) | 0.18 (0.23) |
| EV18 | 0.03 (0.15) | 0.00 (0.14) | –0.15 (0.15) | –0.15 (0.16) | – | –0.03 (0.14) | –0.06 (0.19) | 0.03 (0.21) | 0.17 (0.23) | 0.03 (0.14) | 0.08 (0.26) | 0.10 (0.32) | 0.20 (0.22) |

[A]Correlations with percent normal sperm at 12 months in Brahmans were not estimable due to a small number of observations ($n$ = 103) and no residual variance.

**Table 13. Genetic correlations of hormone and production traits with scrotal circumference and semen quality traits for Tropical Composite bulls**

See Table 2 for trait description. All estimates from bivariate analyses; approximate standard errors in parentheses; semen quality was evaluated at 12, 18 and 24 months of age

| Trait | SC6 | SC12 | MASS12 | MOT12 | PNS12 | SC18 | MASS18 | MOT18 | PNS18 | SC24 | MASS24 | MOT24 | PNS24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LH4 | 0.20 (0.14) | 0.28 (0.14) | 0.04 (0.16) | 0.20 (0.15) | –0.40 (0.16) | 0.18 (0.15) | 0.44 (0.19) | 0.34 (0.18) | –0.20 (0.18) | 0.17 (0.15) | 0.52 (0.29) | 0.37 (0.22) | –0.10 (0.17) |
| IN4 | 0.18 (0.11) | 0.28 (0.11) | –0.33 (0.12) | –0.31 (0.12) | –0.03 (0.15) | 0.35 (0.10) | –0.18 (0.17) | –0.15 (0.16) | –0.20 (0.15) | 0.40 (0.10) | –0.17 (0.25) | –0.17 (0.19) | –0.26 (0.13) |
| IGF6 | 0.38 (0.11) | 0.42 (0.11) | 0.23 (0.14) | 0.15 (0.14) | 0.11 (0.16) | 0.28 (0.12) | 0.37 (0.18) | 0.21 (0.17) | 0.04 (0.17) | 0.19 (0.13) | 0.28 (0.24) | 0.09 (0.20) | –0.01 (0.15) |
| FT6 | 0.30 (0.13) | 0.39 (0.13) | –0.03 (0.15) | –0.11 (0.15) | 0.01 (0.17) | 0.34 (0.14) | 0.32 (0.19) | 0.10 (0.18) | –0.12 (0.17) | 0.38 (0.13) | –0.15 (0.27) | 0.06 (0.22) | –0.02 (0.16) |
| RT12 | –0.25 (0.27) | –0.37 (0.26) | 0.10 (0.29) | 0.11 (0.30) | –0.16 (0.32) | –0.24 (0.27) | 0.01 (0.38) | –0.14 (0.35) | –0.39 (0.30) | –0.17 (0.29) | –0.46 (0.53) | –0.35 (0.40) | –0.15 (0.31) |
| WT15 | 0.68 (0.06) | 0.57 (0.07) | –0.11 (0.13) | 0.00 (0.13) | –0.06 (0.14) | 0.66 (0.06) | 0.01 (0.17) | 0.04 (0.16) | –0.14 (0.15) | 0.68 (0.06) | 0.40 (0.22) | 0.38 (0.17) | –0.05 (0.14) |
| CS15 | –0.03 (0.14) | 0.07 (0.15) | –0.04 (0.16) | 0.00 (0.16) | –0.07 (0.18) | 0.09 (0.15) | –0.04 (0.21) | –0.13 (0.20) | 0.12 (0.18) | 0.08 (0.15) | –0.14 (0.28) | 0.03 (0.22) | 0.03 (0.17) |
| P815 | –0.26 (0.18) | –0.13 (0.19) | –0.19 (0.21) | –0.21 (0.21) | 0.08 (0.22) | –0.01 (0.19) | –0.05 (0.26) | 0.14 (0.24) | 0.04 (0.23) | 0.08 (0.19) | 0.17 (0.35) | 0.15 (0.27) | 0.13 (0.21) |
| EMA15 | 0.32 (0.11) | 0.09 (0.12) | –0.03 (0.13) | –0.04 (0.13) | –0.07 (0.15) | 0.25 (0.12) | –0.14 (0.17) | –0.17 (0.16) | –0.02 (0.15) | 0.24 (0.12) | 0.16 (0.23) | 0.13 (0.19) | –0.04 (0.14) |
| HH15 | 0.51 (0.11) | 0.20 (0.12) | –0.05 (0.14) | –0.01 (0.15) | –0.12 (0.15) | 0.14 (0.12) | –0.31 (0.17) | –0.33 (0.19) | –0.03 (0.21) | 0.29 (0.11) | –0.03 (0.25) | 0.08 (0.31) | –0.17 (0.21) |
| SH18 | –0.46 (0.11) | –0.29 (0.13) | 0.39 (0.14) | 0.37 (0.14) | 0.11 (0.17) | –0.47 (0.10) | 0.24 (0.20) | 0.10 (0.19) | 0.12 (0.18) | –0.56 (0.09) | 0.01 (0.28) | –0.10 (0.22) | –0.16 (0.16) |
| EV18 | 0.40 (0.12) | 0.08 (0.15) | –0.42 (0.14) | –0.38 (0.15) | –0.17 (0.18) | 0.25 (0.14) | –0.42 (0.19) | –0.34 (0.19) | –0.32 (0.18) | 0.41 (0.12) | –0.20 (0.28) | –0.16 (0.22) | –0.05 (0.17) |

larger SC. This positive genetic association between IN4 and SC is juxtaposed to the negative genetic association between IN4 and PNS24 in both genotypes (–0.37 ± 0.18 and –0.26 ± 0.13, respectively, for BRAH and TCOMP) and may mitigate correlated responses in PNS24 if selecting for increased SC. IGF6 was also positively correlated with SC in both genotypes and with greater magnitude in BRAH (0.46–0.56). Yilmaz *et al*. (2004) report a genetic correlation of 0.35 (±0.11) between IGF-I and SC in 12–14-month-old Angus bulls, not dissimilar to the genetic correlation of 0.42 (±0.11) recorded here for TCOMP at 12 months.

Genetic correlations between FT6 and SC across various ages were low for BRAH and moderate and positive for TCOMP indicating that bulls selected for larger SC would generally be slower (less flighty). Genetic correlations between RT12 and SC were moderate and negative (albeit with high standard error) indicating a trend of lower body temperature to be genetically associated with larger SC. Burrow (2001) reported genetic correlations for flight time and rectal temperature with SC at various ages to be in the same direction as those reported here but of lower magnitude. The results indicate no antagonistic responses in heat tolerance or temperament (as measured by flight time) if selecting for increased SC.

SC at various ages had moderate to strong genetic correlation with weight (WT15) and low to moderate genetic correlation with height (HH15) in both genotypes. Estimates of genetic correlation of SC with muscling (EMA15) were low but positive in TCOMP and with body condition (CS15) and fatness (P815) the genetic correlations were low or close to zero in both BRAH and TCOMP. Burrow (2001) reported moderate to strong genetic correlation estimates between bodyweights and SC at various ages in young TCOMP cattle, similar to those reported here. The results suggest that selection for larger SC will engender correlated responses of larger body size and muscling but little change in body condition or fatness.

Estimates of genetic correlation between sheath traits (SH18 and EV18) and SC in BRAH were low, but in TCOMP were moderate and negative for SH18 and low to moderate and positive for EV18. These estimates indicate that selection for larger SC will likely be associated with more pendulous sheath and greater length of everted prepuce in TCOMP. This possible antagonism may need to be monitored and sheath score included when selecting young bulls to avert any genetic trends towards more pendulous sheaths and risk of physical injury or infection.

### *Genetic correlation between early measured traits and semen quality*

The genetic association between the bull traits measured from 4 to 18 months of age and semen quality traits (MASS, MOT and PNS) measured at 12, 18 and 24 months of age are presented in Tables 12 and 13. PNS is considered here as the bench-marking bull fertility trait due to its reported phenotypic association with calf output (Holroyd *et al*. 2002).

Inhibin had negative genetic associations with sperm motility (MASS12 and MOT12) at 12 months in TCOMP and with PNS24 in both genotypes suggesting that lower concentrations of inhibin in 4-month-old bulls would be genetically associated with slightly higher PNS at 24 months of age. However, the moderate positive

genetic correlations between inhibin and SC, discussed previously, suggest that selection to reduce IN4 will likely be associated with reduction in SC. The suggested antagonism among inhibin, SC and PNS traits may need to be heeded when identifying potential alternative selection criteria.

Genetic correlation between LH4 and sperm motility traits in BRAH was low or close to zero. LH4 tended to be positively associated with MASS and MOT in TCOMP but because of high standard error the association was only significantly different from zero for MASS18 (0.44 ± 0.19). Estimates of genetic correlation between LH4 and PNS were generally low or close to zero except for a moderate negative association with PNS12 in TCOMP (–0.40 ± 0.16). Similar inconsistent genetic correlation with semen quality traits is suggested for IGF6. In BRAH, genetic correlation of IGF6 with MASS and MOT at 12 and 18 months (0.34 ± 0.13 to 0.48 ± 0.15) and with PNS24 (0.44 ± 0.20) were moderate and positive. However, in TCOMP genetic correlation between IGF6 and PNS was zero and the only significant genetic correlation between IGF6 and semen quality was that with MASS18 (0.37 ± 0.18). Yilmaz *et al*. (2004) also reported zero genetic correlation between IGF-I and PNS but a moderate genetic correlation (0.43 ± 0.32) with sperm motility in Angus, similar to the present results for TCOMP at 18 months. The generally inconsistent nature of these genetic associations between circulating blood hormones and semen quality traits suggest that the former might not be useful predictors of the latter across breeds.

Flight time measured at weaning in BRAH tended to have positive genetic association with MASS18 and MOT18 but not with PNS, indicating that selection for less fearful BRAH bulls (high FT6) is likely to be associated with better sperm motility but not better percent normal. Genetic association between flight time and semen quality in TCOMP was negligible. Published studies of genetic association between temperament and fertility traits are sparse and generally reported low or zero estimates for male and female reproductive traits (Burrow 2001; Phocas *et al*. 2006) indicating that selection for less flighty animals would at least be unlikely to be antagonistic to herd reproduction. This trend was supported by the results of Cooke *et al*. (2011) who report that excitable temperament was detrimental to pregnancy rates to fixed time AI in Nellore cows.

Sheath score (SH18) tended to have positive genetic correlation with semen quality (MASS and MOT) measured at 12 and 18 months of age in both breeds. Preputial eversion (EV18) tended to have a negative genetic correlation with semen quality, particularly at 12 and 18 months of age in TCOMP. The associations suggest that bulls with less pendulous sheaths and less preputial eversion tend to produce better quality ejaculates. At 24 months of age, however, the associations between sheath scores and semen quality were less evident or negligible. Holroyd *et al*. (2002) reported that sheath area in Brahman bulls was negatively related to calf output.

Estimates of genetic correlation for body growth and composition traits with semen quality traits were generally low or close to zero. The exceptions were those of body condition (CS15) and rump fat thickness (P815) measured at 15 months of age in BRAH. The estimated genetic correlations suggest that increased body condition score and thicker rump fat of BRAH at 15 months was genetically associated with improved PNS and more motile sperm at 18 and 24 months age. These genetic associations were not evident in TCOMP suggesting that selection for increased body condition (or fatness) would have a correlated response in semen quality in BRAH but little effect in TCOMP. Similar genotype differences were found for the genetic correlations between body fatness and age at puberty in heifers (Johnston *et al*. 2009). Dias *et al*. (2008) reported low positive genetic correlation between bodyweight and semen quality in Nellore cattle. In general estimates of genetic correlation between growth traits and semen quality were not antagonistic indicating that selection for traits in either category will not adversely affect traits in the other.

## Conclusions

Genetics play a role in determining reproductive traits measured in young bulls up to 24 months of age and, while expression of the traits is affected by environmental influences, most could be improved by selection. Scrotal circumference was among the most heritable of the bull traits studied but the magnitude of positive genetic association with semen quality traits varied with genotype and age at measurement. Semen quality is recognised as a major determinant of bull fertility and the most heritable measure amongst the semen quality traits studied was PNS. The lack of consistent strong genetic correlation between PNS and other heritable bull traits suggests that the existence of a single reliable indicator of bull fertility across breeds is not among those measured. However, aside from SC, the possible exceptions to this generalisation are IGF-I and body condition score in BRAH and sperm motility traits in both BRAH and TCOMP genotypes. If PNS is identified as the breeding objective, these moderately correlated traits measured on younger bulls may prove useful criteria to define reasonably accurate indexes for indirect selection. Additionally, the lack of genetic antagonism among bull traits indicates that selection for improved semen quality will not adversely affect other production traits.

Logically, the usefulness of bull traits as indicators of whole herd fertility should be tested. This could be gauged by estimates of genetic correlation of bull traits with female lifetime reproductive performance traits. Such genetic parameters are required to determine the utility of measuring traits such as PNS and including them in genetic selection programs.

## Acknowledgements

The authors acknowledge the Cooperative Research Centre for Beef Genetic Technologies and its core partners and the generous financial support of Meat and Livestock Australia. We acknowledge the tremendous contributions of the Australian Agricultural Co., C. and R. Briggs, Consolidated Pastoral Co., North Australian Pastoral Co., MDH Pty Ltd, J. and S. Halberstater, G. and J. McCamley, P. MacGibbon, Collins Belah Valley, N. and D. Daley, E. and D. Streeter, Roxborough Brahman Stud, Simon Cattle Co., Tremere Pastoral, T. and C. Hore, P. and F. Anderson, G. M. and J. Seifert, G. E. and A. Maynard and the research stations of AgForce Queensland and DEEDI. We also gratefully acknowledge the scientists and technical staff of the Beef CRC partner organisations (CSIRO, DEEDI, AGBU and The University of Queensland) who contributed to or supported the work. We especially thank Tim Grant, Karl Enchelmeier, Jo Campbell, Brett Ward, Rob Young, Warren Sim, Paul Williams, Jessica Crisp and Jim Cook for their contributions to cattle management, data collection, laboratory analyses and data handling.

## References


Bagu ET, Cook SJ, Honaramooz A, Aravindakshan JP, Huchkowsky S, Rawlings NC (2006) Changes in serum luteinizing hormone (LH) concentrations in response to luteinizing hormone releasing hormone (LHRH) in bull calves that attained puberty early or late. *Theriogenology* **66**, 937–944. doi:10.1016/j.theriogenology.2006.02.034

Barwick SA, Wolcott ML, Johnston DJ, Burrow HM, Sullivan MT (2009*a*) Genetics of steer daily and residual feed intake in two tropical beef genotypes, and relationships among intake, body composition, growth and other post-weaning measures. *Animal Production Science* **49**, 351–366. doi:10.1071/EA08249

Barwick SA, Johnston DJ, Burrow HM, Holroyd RG, Fordyce G, Wolcott ML, Sim WD, Sullivan MT (2009*b*) Genetics of heifer performance in 'wet' and 'dry' seasons and their relationships with steer performance in two tropical beef genotypes. *Animal Production Science* **49**, 367–382. doi:10.1071/EA08273

Burns BM, Gazzola C, Holroyd RG, Crisp J, McGowan MR (2011) Male reproductive traits and their relationship to reproductive traits in their female progeny: a systematic review. *Reproduction in Domestic Animals* **46**, 534–553. doi:10.1111/j.1439-0531.2011.01748.x

Burns BM, Corbet NJ, Corbet DH, Li Y, Crisp JM, Venus BK, Johnston DJ, McGowan MR, Holroyd RG (2013) Male traits and herd reproductive capability in tropical beef cattle. 1. Experimental design and animal measures. *Animal Production Science* **53**, 87–100. doi:10.1071/AN12162

Burrow HM (2001) Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. *Livestock Production Science* **70**, 213–233. doi:10.1016/S0301-6226(01)00178-6

Cammack KM, Thomas MG, Enns RM (2009) Review of reproductive traits and their heritabilities in beef cattle. *The Professional Animal Scientist* **25**, 517–528.

Chenoweth PJ (1980) Bull fertility. *Modern Veterinary Practice* **61**, 987–991.

Cooke RF, Bohnert DW, Meneghetti M, Losi TC, Vasconcelos JLM (2011) Effects of temperament on pregnancy rates to fixed time AI in *Bos indicus* beef cows. *Livestock Science* **142**, 108–113. doi:10.1016/j.livsci.2011.06.024

Corbet NJ, Burns BM, Corbet DH, Crisp JM, Johnston DJ, McGowan MR, Venus BK, Holroyd RG (2011) Bull traits measured early in life as indicators of herd fertility. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **19**, 55–58.

Davis ME, Simmen RCM (2006) Genetic parameter estimates for serum insulin-like growth factor I concentrations, and body weight and weight gains in Angus beef cattle divergently selected for serum insulin-like growth factor I concentration. *Journal of Animal Science* **84**, 2299–2308. doi:10.2527/jas.2005-567

Davis ME, Boyles SL, Moeller SJ, Simmen RCM (2003) Genetic parameter estimates for serum insulin-like growth factor I concentration and ultrasound measurements of backfat thickness and longissimus muscle area in Angus beef cattle. *Journal of Animal Science* **81**, 2164–2170.

Dias JC, Andrade VJ, Martins JAM, Emerick LL, Vale Filho VR (2008) Genetic and phenotypic correlations among reproductive and productive traits of Nelore bulls. *Pesquisa Agropecuaria Brasileira* **43**, 53–59.

Ducrocq V, Humblot P (1995) Genetic characteristics and evolution of semen production of young Normande bulls. *Livestock Production Science* **41**, 1–10. doi:10.1016/0301-6226(94)00029-7

Eler JP, Ferraz JBS, Balieiro JCC, Mattos EC, Mourao GB (2006) Genetic correlation between heifer pregnancy and scrotal circumference measured at 15 and 18 months of age in Nellore cattle. *Genetics and Molecular Research* **5**, 569–580.

Evans ACO, Davies FJ, Nasser LF, Bowman P, Rawlings NC (1995) Differences in early patterns of gonadotrophin secretion between early and late maturing bulls, and changes in semen characteristic at puberty. *Theriogenology* **43**, 569–578. doi:10.1016/0093-691X(94)00062-Y

Evans JL, Golden BL, Bourdon RM, Long HL (1999) Additive genetic relationships between heifer pregnancy and scrotal circumference in Hereford cattle. *Journal of Animal Science* **77**, 2621–2628.

Fordyce G, Entwistle K, Norman S, Perry V, Gardiner B, Fordyce P (2006) Standardising bull breeding soundness evaluations and reporting in Australia. *Theriogenology* **66**, 1140–1148. doi:10.1016/j.theriogenology.2006.03.009

Garmyn AJ, Moser DW, Christmas RA, Bormann JM (2011) Estimation of genetic parameters and effects of cytoplasmic line on scrotal circumference and semen quality traits in Angus bulls. *Journal of Animal Science* **89**, 693–698. doi:10.2527/jas.2010-3534

Gipson TA, Vogt DW, Ellersieck MR, Massey JW (1987) Genetic and phenotypic parameter estimates for scrotal circumference and semen traits in young beef bulls. *Theriogenology* **28**, 547–555. doi:10.1016/0093-691X(87)90272-X

Graser HU, Tier B, Johnston DJ, Barwick SA (2005) Genetic evaluation for the beef industry in Australia. *Australian Journal of Experimental Agriculture* **45**, 913–921. doi:10.1071/EA05075

Gredler B, Fuerst C, Fuerst-Waltl B, Schwarzenbacher H, Sölkner J (2007) Genetic parameters for semen production traits in Austrian dual-purpose Simmental bulls. *Reproduction in Domestic Animals* **42**, 326–328. doi:10.1111/j.1439-0531.2006.00778.x

Hammond K, Graser HU (1987) The value of indirect selection for female reproduction in beef cattle using scrotal circumference. *Proceedings of the Australian Association of Animal Breeding and Genetics* **6**, 232–236.

Holroyd RG, Doogan VJ, DeFaveri J, Fordyce G, McGowan MR, Bertram JD, Vankan DM, Fitzpatrick LA, Jayawardhana GA, Miller RG (2002) Bull selection and use in northern Australia 4. Calf output and predictors of fertility of bulls in multiple-sire herds. *Animal Reproduction Science* **71**, 67–79. doi:10.1016/S0378-4320(02)00026-X

Hopkins FM, Spitzer JC (1997) The new Society for Theriogenology breeding soundness evaluation system. *Veterinary Clinics of North America: Food Animal Science* **13**, 283–293.

Johnston DJ, Barwick SA, Corbet NJ, Fordyce G, Holroyd RG, Williams PJ, Burrow HM (2009) Genetics of heifer puberty in two tropical beef genotypes in northern Australia and associations with heifer- and steer-production traits. *Animal Production Science* **49**, 399–412. doi:10.1071/EA08276

Kadel MJ, Johnston DJ, Burrow HM, Graser HU, Ferguson DM (2006) Genetics of flight time and other measures of temperament and their value as selection criteria for improving meat quality traits in tropically adapted breeds of beef cattle. *Australian Journal of Agricultural Research* **57**, 1029–1035. doi:10.1071/AR05082

Kastelic JP, Thundathil JC (2008) Breeding soundness evaluation and semen analysis for predicting bull fertility. *Reproduction in Domestic Animals* **43**, 368–373. doi:10.1111/j.1439-0531.2008.01186.x

Kealy CG, MacNeil MD, Tess MW, Geary TW, Bellows RA (2006) Genetic parameter estimates for scrotal circumference and semen characteristics of line 1 Hereford bulls. *Journal of Animal Science* **84**, 283–290.

Kuijper EAM, Lambalk CB, Boomsma DI, Van der Sluis S, Blankenstein MA, De Geus EJC, Posthuma D (2007) Heritability of reproductive hormones in adult male twins. *Human Reproduction (Oxford, England)* **22**, 2153–2159. doi:10.1093/humrep/dem145

Mackinnon MJ, Corbet NJ, Meyer K, Burrow HM, Bryan RP, Hetzel DJS (1991) Genetic parameters for testosterone response to GnRH stimulation and scrotal circumference in tropical beef bulls. *Livestock Production Science* **29**, 297–309. doi:10.1016/0301-6226(91)90105-Y

Meyer K, Hammond K, Parnell PF, Mackinnon MJ, Sivarajasingham S (1990) Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. *Livestock Production Science* **25**, 15–30. doi:10.1016/0301-6226(90)90038-8

Meyer K, Hammond K, Mackinnon MJ, Parnell PF (1991) Estimates of covariances between reproduction and growth in Australian beef cattle. *Journal of Animal Science* **69**, 3533–3543.

Moore KL, Johnston DJ, Graser HU, Herd R (2005) Genetic and phenotypic relationships between insulin-like growth factor-I (IGF-I) and net feed intake, fat, and growth traits in Angus beef cattle. *Australian Journal of Agricultural Research* **56**, 211–218. doi:10.1071/AR04248

Morris CA, Cullen NG (1994) A note on genetic correlations between pubertal traits of males and females and lifetime pregnancy rate in beef cattle. *Livestock Production Science* **39**, 291–297. doi:10.1016/0301-6226(94)90291-7

Palomares RA, Wolfe DF (2011) Factors that affect scrotal circumference of the bull and its impact on herd reproductive performance. A review. *Clinical Theriogenology* **3**, 115–127.

Parkinson TJ (2004) Evaluation of fertility and infertility in natural service bulls. *Veterinary Journal (London, England)* **168**, 215–229. doi:10.1016/j.tvjl.2003.10.017

Phillips DJ (2005) Activins, inhibins and follistatins in the large domestic species. *Domestic Animal Endocrinology* **28**, 1–16. doi:10.1016/j.domaniend.2004.05.006

Phocas F, Boivin X, Sapa J, Trillat G, Boissy A, Le Neindre P (2006) Genetic correlations between temperament and breeding traits in Limousin heifers. *Animal Science (Penicuik, Scotland)* **82**, 805–811. doi:10.1017/ASC200696

Prayaga KC (2003) Evaluation of cattle genotypes and estimation of direct and maternal effects in a tropical environment. 2. Adaptive and temperament traits. *Australian Journal of Agricultural Research* **54**, 1027–1038. doi:10.1071/AR03072

Prayaga KC, Corbet NJ, Johnston DJ, Wolcott ML, Fordyce G, Burrow HM (2009) Genetics of adaptive traits in heifers and their relationship to growth, pubertal and carcass traits in two tropical beef genotypes. *Animal Production Science* **49**, 413–425. doi:10.1071/EA08247

Quirino CR, Bergmann JAG (1998) Heritability of scrotal circumference adjusted and unadjusted for body weight in Nellore bulls, using univariate and bivariate animal models. *Theriogenology* **49**, 1389–1396. doi:10.1016/S0093-691X(98)00085-5

Riley DG, Chase CC Jr, Coleman SW, Olson TA (2012) Genetic assessment of rectal temperature and coat score in Brahman, British and Criollo crossbred and straightbred cows and calves under subtropical summer conditions. *Livestock Science* **148**, 109–118. doi:10.1016/j.livsci.2012.05.017

Silva MR, Pedrosa VB, Silva JCB, Eler JP, Guimarães JD, Albuquerque LG (2011) Testicular traits as selection criteria for young Nellore bulls. *Journal of Animal Science* **89**, 2061–2067. doi:10.2527/jas.2010-3525

Siqueira JB, Oba E, Pinho RO, Quintino HP, Eler JP, Miranda Neto T, Guimarães SEF, Guimarães JD (2012) Heritability estimates and genetic correlations of reproductive features in Nellore bulls, offspring of super precocious, precocious and normal cows under extensive farming conditions. *Reproduction in Domestic Animals* **47**, 313–318. doi:10.1111/j.1439-0531.2011.01874.x

Upton WH, Burrow HM, Dundon A, Robinson DL, Farrell EB (2001) CRC breeding program design, measurements and database: methods that underpin CRC research results. *Australian Journal of Experimental Agriculture* **41**, 943–952. doi:10.1071/EA00064

Yilmaz A, Davis ME, Simmen RCM (2004) Estimation of (co)variance components for reproductive traits in Angus beef cattle divergently selected for blood serum IGF-I concentration. *Journal of Animal Science* **82**, 2285–2292.