CSIRO PUBLISHING
Animal Production Science, 2013, **53**, 87–100
http://dx.doi.org/10.1071/AN12162

Male traits and herd reproductive capability in tropical beef cattle. 1. Experimental design and animal measures

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

[A]Cooperative Research Centre for Beef Genetic Technologies, Armidale, NSW 2351, Australia.
[B]The University of Queensland, Centre for Animal Science, Queensland Alliance for Agriculture and Food Innovation, Rockhampton, Qld 4701, Australia.
[C]CSIRO Livestock Industries, Rockhampton, Qld 4701, Australia.
[D]Animal Science, Agri-Science Queensland, Department of Employment, Economic Development and Innovation (DEEDI), Rockhampton, Qld 4701, Australia.
[E]The University of Queensland, School of Veterinary Science, Gatton Campus, Gatton, Qld 4343, Australia.
[F]Animal Science, Agri-Science Queensland, DEEDI, Qld Biosciences Precinct, St Lucia, Qld 4072, Australia.
[G]Animal Genetics and Breeding Unit (AGBU), University of New England, Armidale, NSW 2351, Australia.
[H]CSIRO Livestock Industries, St Lucia, Qld 4067, Australia.
[I]Corresponding author. Email: b.burns@uq.edu.au

Abstract. Research into the genetics of whole herd profitability has been a focus of the Beef Cooperative Research Centre for Beef Genetic Technologies over the past decade and it has been identified that measures of male reproduction may offer a potential indirect means of selecting for improved female reproduction. This paper describes the experimental design and provides a descriptive analysis of an array of male traits in Brahman and Tropical Composite genotypes managed under the medium to high stress, semi-extensive to extensive production systems of northern Australia. A total of 1639 Brahman and 2424 Tropical Composite bulls with known pedigrees, bred and raised in northern Australia, were evaluated for a comprehensive range of productive and reproductive traits. These included blood hormonal traits (luteinising hormone, inhibin and insulin-like growth factor-I); growth and carcass traits (liveweight, body condition score, ultrasound scanned 12–13th rib fat, rump P8 fat, eye muscle area and hip height); adaptation traits (flight time and rectal temperature); and a bull breeding soundness evaluation (leg and hoof conformation, sheath score, length of everted prepuce, penile anatomy, scrotal circumference, semen mass activity, sperm motility and sperm morphology). Large phenotypic variation was evident for most traits, with complete overlap between genotypes, indicating that there is likely to be a significant opportunity to improve bull fertility traits through management and bull selection.

Received 14 May 2012, accepted 23 July 2012, published online 4 December 2012

Introduction

Beef is Australia's most valuable agricultural export commodity. However, with only 2.5% of the world's cattle numbers and 23% of the world's beef trade there is a need for Australia to embrace a greatly increased and smarter use of new technologies if the industry is to remain globally competitive and profitable.

In an analysis of the northern Australian beef status, McCosker *et al*. (2009) reported that weaning rates of less than 50% were commonplace in many northern Australian beef cattle herds. Weaning rates of this magnitude in *Bos indicus* and *Bos indicus* crossbred cattle were subsequently supported by a review of factors that impact on reproduction in beef cattle females (Burns *et al*. 2010) and by a recent survey of herds in northern Australia (McCosker *et al*. 2011). Herd reproductive performance could be improved if traits in males could be identified that were genetically correlated with female reproductive traits and these male traits were able to be measured early in life and at low cost. Prior to the commencement of the current Cooperative Research Centre for Beef Genetic Technologies (Beef CRC) research projects in Australia, little genetic information on bovine male reproductive traits and their associations with components of female reproduction rate was available apart from scrotal size (Burns *et al*. 2011).

While some favourable relationships have been reported between scrotal circumference (SC) and sperm morphology traits (Dias *et al*. 2008) and SC and female reproductive traits (Meyer *et al*. 1991; Eler *et al*. 2006), apart from the studies of Holroyd *et al*. (2002*a*), Schatz *et al*. (2010) and Siqueira *et al*. (2012), research to identify relationships between semen quality traits and female reproductive performance in tropical genotypes is limited. The identification of new traits in tropically adapted males to indirectly improve reproductive performance of both male and female relatives has both genetic and economic advantages for the northern Australian beef industry. A reduction in the number of bulls required for breeding throughout northern Australia by up to 50% has been estimated if early-in-life predictors of an individual's future reproductive performance can be identified (Holroyd *et al.* 2002*a*). Therefore, the successful evaluation and identification of relationships between bulls' reproductive traits and the reproductive performance of the herd, coupled with a higher selection pressure on the bulls, will enable increased rates of genetic improvement in herd reproductive performance and subsequent herd profitability.

The objective of the Beef CRC research was to define the genetic control of traditional and novel measures of male reproductive performance and their genetic correlation with critically important female traits, including age at puberty, lactation anoestrous and traits associated with female lifetime reproductive performance. This paper describes the design of the longitudinal genetic study, the methodology used and presents descriptive statistics for the male reproductive traits measured in two tropically adapted genotypes. Subsequent papers in this series will examine the environmental effects responsible for trait variation and provide genetic parameter estimates.

Research project details

Ethics approval

Conduct of Male Traits to Improve Female Fertility Project was approved for 2005–06 and 2006–11 by the J. M. Rendel Laboratory Animal Experimental Ethics Committee (CSIRO, Queensland) as approvals RH198/04 and RH219/06, respectively.

Design

The initial design of this study aimed to generate ~3500 male progeny across the two genotypes to allow the estimation of genotype-specific [Brahman (BRAH) and Tropical Composite (TCOMP)] heritabilities and genetic correlations for the male reproduction traits and subsequently to estimate genetic correlations with female reproduction traits using dam/son relationships. The progeny were generated by natural mating from the cows involved in the female reproduction experiment described by Barwick *et al*. (2009*a*) and Johnston *et al*. (2009). Approximately 80–100 sires per genotype were initially planned to be used to generate ~20 male progeny per sire. However, the actual numbers of progeny generated and sires used differed to those forecast due to variation created by the bull to cow mating ratios used, the multiple sire natural mating practice, differences in sex ratios and differences in weaning rates across pre-weaning locations and genotypes. Table 1 summarises the actual sire and bull progeny distributions in the dataset for those young bulls with a known sire and at least a weaning weight record. In summary, 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, 40 were used across years at more than one location to form genetic links.

Animals

Male progeny were generated from tropically adapted BRAH and TCOMP cow herds at DEEDI and CSIRO research stations located throughout central, north-east and north-west Queensland in tropical and subtropical northern Australia. Brian Pastures Research Station (BP), latitude 25.66°S, longitude 151.75°E, is located near Gayndah (TCOMP); Swans Lagoon Beef Cattle Research Station (SL), latitude 19.62°S, longitude 147.38°E, is located near Millaroo via Ayr (BRAH); Toorak Research Station (TK), latitude 21.03°S, longitude 141.80°E, is located near Julia Creek (both BRAH and TCOMP); Brigalow Research Station (BRG), latitude 24.84°S, longitude 149.80°E, is located near Theodore (TCOMP) and was used as a temporary site to manage a proportion of the BP and TK breeding female herds during severe drought conditions; and the CSIRO Belmont Research Station (BEL), latitude 23.22°S, longitude 150.38°E, is located near Rockhampton (both BRAH and TCOMP). The breeding females (generation 1) located at these sites were intensively measured for early growth (Barwick *et al*. 2009*b*), age at puberty (Johnston *et al*. 2009) and adaptation (Prayaga *et al*. 2009). In brief, the cows consisted of two genotypes, BRAH ($n = 1027$) and TCOMP ($n = 1132$). The TCOMP encompasses genotypes derived 50% from tropically adapted (50% *B. indicus*, African Sanga or other tropically adapted *B. taurus* genotypes) and 50% from non-tropically adapted *B. taurus* genotypes (Barwick *et al*. 2009*a*). Records on the cows across six mating opportunities included key reproductive traits such as age at puberty, pregnancy rate, days from bull-in to calving, interval from calving to first postpartum oestrus (determined by ultrasonography) and number of calves weaned. The animals used in the present study were the male progeny (generation 2) of the cows described above. The generation 2 calves were born from 2004 to 2010 and were sired by industry sires. Sires were chosen that were not closely related to the genetics of the cows and preferably had BREEDPLAN estimated breeding

Table 1. Numbers of male progeny and progeny per sire distributions
Includes bull progeny with at least a weaning liveweight record

Sire genotype	Number of progeny	Number of sires	Average progeny per sire (range)	Number of sires ≥20 progeny	Number of link sires[A]	% Progeny by link sires
BRAH	1639	60	27 (3–75)	37	13	36
TCOMP	2424	76	32 (2–85)	47	27	48
Total	4063	136	30 (2–85)	84	40	43

[A]Sires with male progeny at more than one pre-weaning location.

values for reproduction traits (e.g. scrotal size and days to calving).

Sires were mated in large multiple sire groups of 150–250 females with ~3% bulls for 12 weeks. Mating times at the research sites were generally late November to late February at BP; mid December to mid March at BEL, TK and BRG (when required); and early January to early April at SL. Sire parentage was determined by DNA fingerprinting (Vankan 2005) after DNA was extracted from a blood or a tail hair sample collected at branding (~3–4 months of age). DNA collected at this time was also stored for future genome-wide association studies. A total of 4063 bull progeny were generated in seven birth-year cohorts from the five breeding locations. At weaning each year, the bull calves from SL, TK, and BP were relocated to BRG and those born at BEL remained at BEL except for 42 BRAH (2007) and 19 BRAH and 20 TCOMP (2008) calves that were transferred to BRG after weaning (Table 2). Animals born at BEL included 250 crossbreds resulting from the mixed mating of the BRAH and TCOMP genotypes at that location. Data from the crossbreds were grouped by sire genotype and information on all young bulls sired by BRAH sires was summarised separately to those sired by TCOMP sires. The number of male progeny by year, genotype, birth location and post-weaning location are reported in Table 2.

Environments

The post-weaning production system environments of BRG and BEL, where the bulls in this study were evaluated, have previously been described in detail (Anon. 1976; Burns *et al*. 1997; Turner 1982; Barwick *et al*. 2009*a*, 2009*b*).

The long-term climatic parameters measured at BRG and BEL are presented in Table 3. BRG is located 190 km south-west of Rockhampton in the Brigalow belt of central Queensland. On average, ~56% of annual rainfall falls during November–February (Table 3). Generally, this rainfall sustains pasture growth allowing cattle to achieve liveweight gains of 0.5–0.75 kg/day over a 7–8-month period (October–November to April–May). Liveweight can generally be maintained during winter, except under extremely dry conditions following lower than average summer rainfall. The experimental animals in this study grazed mainly improved pastures sown on cleared Brigalow scrub soils. These improved pastures include green panic (*Panicum maximum* var. *trichoglume*), buffel (*Cenchrus*

Table 2. Distribution of young bulls by pre- and post-weaning location, genotype and birth year

Pre-weaning location	Post-weaning location	2004	2005	2006	2007	2008	2009	2010	Total
				Brahman					
Belmont	Belmont	47	103	124	68	84	74	47	547
Belmont	Brigalow	0	0	0	42	19	0	0	61
Swan's Lagoon	Brigalow	44	109	96	150	127	114	49	689
Toorak	Brigalow	19	24	46	29	51	33	13	215
				Tropical Composite					
Belmont	Belmont	42	105	101	83	61	84	48	524
Belmont	Brigalow	0	0	0	0	20	0	0	20
Brigalow	Brigalow	0	0	57	62	72	0	0	191
Brian Pastures	Brigalow	72	176	149	195	84	189	147	1012
Toorak	Brigalow	58	79	72	64	110	113	58	554
				Crossbred					
Belmont	Belmont	0	0	0	69	68	60	53	250
Total		282	596	645	762	696	667	415	4063

Table 3. Long-term climatic parameters for bull post-weaning evaluation sites
Source: Bureau of Meteorology (www.bom.gov.au)

Location	Average maximum temperature (°C)	Average minimum temperature (°C)	Mean rainfall (mm)	Relative humidity (% at 0900 hours)
Brigalow Research Station				
1968–2011				
November–February	33	20	395	64
March–June	27	13	165	66
July–October	26	10	155	62
Belmont Research Station				
1939–2012				
November–February	32	21	433	68
March–June	27	16	213	72
July–October	26	13	114	49

ciliaris) and rhodes (*Chloris gayana*) grasses growing on cracking clays and duplex soils in the Highworth land system (Speck *et al*. 1968). While some Fitzroy stylo (*Stylosanthes scabra* cv. Fitzroy) is evident, Seca stylo (*Stylosanthes scabra* cv. Seca) is the predominant species. The stocking rate at this location was 0.45 AE/ha (450 kg per adult equivalent).

BRG is moderately stressful for cattle due to the high temperatures and parasite burdens experienced in the wet summer months and poorer pasture quality in the dry winter months. The main constraints to animal production at BRG include the cattle tick (*Boophilus microplus*), which is endemic, gastro-intestinal helminths (*Haemonchus placei*, *Cooperia* spp., *Trichostrongylus axei* and *Oesphagostomum radiatum*), high ambient temperatures (Burns *et al*. 1986) and bovine infectious keratoconjunctivitis (Burns *et al*. 1988). Buffalo fly (*Haematobia irritans exigua*) has not been considered a problem, as large population numbers are evident for only a few weeks of each year (Burns *et al*. 1997). Occasional severe outbreaks of bovine ephemeral fever occur (Burns *et al*. 1997). Supplementation with a protein meal or a urea and protein meal based dry lick was supplied if required during the dry winter months.

BEL is located 25 km north of Rockhampton and 40 km from the east coast in central Queensland. An average of 61% of mean annual rainfall falls between November and February (Table 3). The stocking rate at BEL was 0.36 AE/ha supporting similar annual liveweight gains to those recorded at BRG. The environment at BEL is also moderately stressful for cattle due to the high temperatures and parasite burdens experienced in the wet summer months and poor pasture quality in the dry winter months. Parasites include the cattle tick (*Boophilus microplus*), which is endemic, gastro-intestinal helminths (*Haemonchus placei*, *Cooperia* spp., *Trichostrongylus axei* and *Oesphagostomum radiatum*), buffalo fly (*Haematobia irritans exigua*), which has not been considered a major parasite problem, high ambient temperatures and humidity and exposure to diseases such as bovine infectious keratoconjunctivitis and occasional outbreaks of bovine ephemeral fever occur (Anon. 1976; Turner 1982). During the period of low nutrition in winter, cattle are maintained on a mixture of improved and native pastures. A dry lick urea-based supplement or whole cottonseed was provided when required.

Husbandry and management

At each site, date of birth, calf sex and dam identification number were recorded. After a 2-week weaner training period each year, the bull calves were allocated to a rearing site and transported as required (Table 2). From weaning to the conclusion of data recording at 24 months of age, all animals in the same birth-year cohort were managed as a single group at BRG and BEL. Bulls were mustered for measurements at 3-monthly intervals between weaning and when cohort average age was ~24 months of age.

Management of progeny followed accepted industry husbandry practices and included:

(1) Branding at ~3–4 months of age in January–March. All progeny were scored for horned, scurred or polled status and those that were not polled were dehorned using either a dehorning knife or a scoop dehorning device, which was dependent on the size of the horn growth, and all animals were fire-branded.
(2) Weaning at ~6 months of age in April–June.
(3) Vaccination with initial 5 in 1 vaccine against clostridial diseases (*Clostridium tetani*, *Cl. perfringens* type D, *Cl. novyi* type B, *Cl. chauvoei* and *Cl. septicum*) at branding with boosters at weaning and annually; long-acting botulism vaccination (*Cl. botulinum* types C and D) at branding; Trivalent (3-germ) tick fever vaccine to protect against tick fever organisms (*Babesia bovis*, *Babesia bigemina* and *Anaplasma marginale*) carried by the cattle tick *Boophilus microplus*; bovine ephemeral fever (3-day sickness) vaccine 4 weeks apart in August–September of weaning year with a booster in August of the following year.
(4) Supplementation with protein meal or a urea-based dry lick delivering ~200 g crude protein equivalent daily per bull during the dry winter months.

Measurements

A comprehensive array of measurements was recorded on each bull as described in Table 4. Blood hormonal levels of gonadotrophin-releasing hormone, stimulated luteinising hormone (LH) and inhibin were recorded at 3–4 months of age while insulin-like growth factor-I (IGF-I) was recorded at weaning (~6 months of age) (Table 4). LH and inhibin and IGF-I were all evaluated in the experimental animals at their birth location [BP, TK, SL, BEL and BRG (during drought years)] before their transfer to BRG post-weaning. As a consequence of the different mating times at the breeding locations described previously, calves at BP were on average older than BEL, TK and BRG calves, which were older than SL calves. To ensure that calves at each site were evaluated for LH and inhibin and then IGF-I at approximately the same age, a blood sampling strategy was implemented to fit in with mating, branding and weaning times across birth location. LH and inhibin hormonal measurements coincided with branding and a cohort mean age ranging from 3.7 to 4.4 months and IGF-I measurement coincided with weaning and a mean age ranging from 6.1 to 6.7 months across sites and years. This strategy minimised any age influence on the evaluation of these hormones at the respective sites.

A full complement of other measurements was recorded from weaning to 24 months of age, with growth and scrotal measurements recorded at 3-monthly intervals. Central to this study was the implementation of a standardised bull breeding soundness evaluation (BBSE) developed by the Australian Cattle Veterinarians (ACV) (Entwistle and Fordyce 2003; Fordyce *et al*. 2006). A physical examination (conformation and scrotal traits) and collection of semen for motility and morphology examination were the key components of the BBSE conducted on the young bulls at ~12, 18 and 24 months of age.

Semen was collected using a CGS Electrojector (N2794, CGS Products Pty Ltd, Trafalgar, Vic., Australia). Attempts to collect an ejaculate were only made if SC was $\geq$20 cm. If an animal did not produce an ejaculate following electro-

Table 4. Detailed description of traits measured on tropical breed bulls

Component traits	Code	Description
		Growth and carcass traits
Liveweight (kg)	LWT	Unfasted liveweight using electronic weigh scales on the morning of the data collection date. Birthweight (LWT0) was recorded within 48 h of parturition. Liveweights were recorded at 6, 9, 12, 15, 18, 21 and 24 months of age.
Body condition score (1–5)	CS	Five-point scale with one-third score increments adapted from the scale below reported by Upton *et al*. (2001) and developed by Lowman *et al*. (1976) to describe body reserves of fat and muscling. 1 (poor) = the individual short ribs are sharp to touch and no tail head tissue can be felt. 2 (backward) = the individual short ribs can still be felt, but feel rounded rather than sharp. There is some tissue cover around the tail head. 3 (moderate) = the short ribs can only be felt with very firm thumb pressure. Areas either side of the tail head have some tissue cover that can be easily felt. 4 (prime) = the short ribs cannot be felt and tissue cover around the tail head is easily seen as slight mounds; folds of tissue are beginning to develop over the ribs and thighs of the animal. 5 (fat) = the bone structure of the animal is no longer noticeable and the tail head is almost completely buried in body tissue. Folds of tissue are apparent over the ribs and thigh.
Hip height (cm)	HH	Vertical distance from a fixed point to the top of the highest sacral vertebrae subtracted from the vertical distance from the fixed point to the ground at 15 months of age.
Rump fat (mm)	SP8	Real-time ultrasound-scanned subcutaneous fat depth at the P8 site (after 'position 8' from the original research to define the optimum site for carcass fat measurement) on the rump (at the intersection of a line parallel to the spine from the *tuber ischium* and a line perpendicular to it from the spinous process of the third sacral vertebra); adapted from Upton *et al*. (1999, 2001).
Rib fat (mm)	SRIB	Real-time ultrasound-scanned subcutaneous fat depth between the 12th and 13th ribs; adapted from Upton *et al*. (1999, 2001).
Eye muscle area (cm^2)	SEMA	Real-time ultrasound-scanned cross-sectional area of the eye muscle (*M. longissimus thoracis et lumborum*) between the 12th and 13th ribs; adapted from Upton *et al*. (1999, 2001).
		Adaptation traits
Flight time (s)	FT	Flight time was an electronically recorded time taken for an animal to cover a distance of ~2 m after exiting a weigh crush (Burrow *et al*. 1988). Flight times were recorded twice at weaning (FT6a and FT6b) at ~7 days apart (Burrow and Corbet 2000) and at 12, 18 and 24 months of age. Recorded by an experienced operator.
Rectal temperature (°C)	RT	Rectal temperature measured with an Anritherm integrated thermometer (Anritherm HL600, Anritsu Meter Co. Ltd, Tokyo, Japan) and a rectal probe. Recorded by an experienced operator.
Time of rectal temperature (based on 24 h)	TRT	Time of the day when rectal temperature and BBSE were recorded.
		Hormonal traits
Inhibin (ng/mL)	IN4	A whole blood sample (minimum 5 mL) was collected by venipuncture from the jugular vein of restrained calves (3–4 months of age – coincided with branding) into 10-mL Serum BD Vacutainer tubes (Becton, Dickinson and Co.) using a 20 G × 1′ (0.9 × 25 mm) BD Vacutainer Precision Glide needle (Becton, Dickinson and Co.). Blood samples were centrifuged crush side at 2500*g* for 20 min and the sera frozen at −20°C until assayed for concentrations of inhibin. Sera were assayed by Monash University using established protocols (Phillips 2005).
GnRH-stimulated LH (ng/mL)	LH4	At Time 0, a basal whole blood sample (minimum 5 mL) was collected by venipuncture from the jugular vein of restrained calves (3–4 months of age – basal blood LH4) into 10-mL Lithium Heparin BD Vacutainer tubes (Becton, Dickinson and Co.) using a 20 G × 1′ (0.9 × 25 mm) BD Vacutainer Precision Glide needle. Calves were treated immediately post-sampling with 0.5 µg/kg (intramuscular) injection of a gonadotrophin-releasing hormone (GnRH) (gonadorelin; Fertagyl, Intervet Australia Pty Limited). At 20 min post-GnRH injection, the calves were restrained for a second time and a second whole blood sample (minimum 5 mL) was collected by venipuncture from the jugular vein to establish the GnRH-stimulated LH blood level (stimulated blood LH4 level). This dose rate of 0.5 µg/kg of GnRH was considered sufficient to elicit a significant LH response when captured 20 min post-GnRH treatment. Calf crush order was identified/recorded by paint markings at the first sampling and the sampling order was maintained at the second blood sample. Blood samples were centrifuged crush side at 2500*g* for 20 min and the plasma frozen at −20°C until assayed for concentrations of LH. Plasma LH concentrations in all samples were measured by a double-antibody radioimmunoassay procedure (Martin *et al*. 1980) that was modified by Hotzel *et al*. (1998) and Hawken *et al*. (2009) and conducted by Ms M. Blackberry, University of Western Australia.
Insulin-like growth factor-I (ng/mL)	IGF6	At weaning (~6 months of age), whole blood was collected by venipuncture from the coccygeal vein of restrained calves, using a 20 G × 1′ (0.9 × 25 mm) BD Vacutainer Precision Glide needle, onto bloodspot collection cards supplied by PrimeGRO to determine blood IGF-I levels. IGF-I was assayed using a commercially available [Rivalea (Australia) Pty Ltd] enzyme-linked immunosorbent assay (Moore *et al*. 2005).
		Conformation traits[A]
Leg structure (1–9)	LStruct	A numeric score of hind leg angularity on a scale of 1–9, with 9 being normal and 1 being an animal with markedly straight or angled hind legs and a grossly abnormal gait (Anon. 1994).

(*Continued next page*)

Table 4. (*continued*)

Component traits	Code	Description
	LCode	Accompanying α code to define the hind leg abnormality. P (pastern) = excessive angle at the pastern. T (straight hocks) = insufficient angle at the hock when viewed from the side. S (sickle hocks) = excessive angle at the hock when viewed from the side. B (bowed legs) = bowed out at the hocks when viewed from behind. H (cow hocks) = cow hocked or too close at the hocks when viewed from behind. C (stringhalt) = upward fixation of the patella.
Foot structure (1–9)	FStruct	A numeric score of feet structure on a scale of 1–9, with 9 being normal conformation and 1 being severely abnormal causing gross lameness and a crippled gait (Anon. 1994).
	FCode	Accompanying α code to define the hoof abnormality. L (length) = excessively long claws when viewed from the side. C (curve) = excessive curvature of the claws when viewed from the front, i.e. scissored claws. H (heel) = heel very close to the ground.
Sheath score (1–9)	SH	A numeric score (1–9) based on the angle of the prepuce, the vertical distance from the abdominal wall to the prepucial orifice and the size of the umbilical area (Anon. 1994). 9 (tight) = prepuce hangs at less than 45° angle, sheath depth less than 10 cm, umbilical area is normal size. 7–8 (small) = prepuce hangs at 45° angle, sheath depth up to ~15 cm, moderate sized umbilicus. 5–6 (moderate) = prepuce hangs at 45° angle, sheath depth ~20 cm, large umbilicus. 3–4 (large) = prepuce hangs at up to 90° angle, sheath depth just above hock-knee horizontal line, excessive looseness of umbilical area. 1–2 (very large) = prepuce hangs at up to 90° angle, sheath depth at or below hock-knee horizontal line, excessive looseness and length of umbilicus.
Prepuce eversion (mm)	EV	An estimate of the length of preputial mucosa everted while the bull stands freely (Holroyd *et al*. 2002*b*).
Erection (yes/no)	PE	During electro-stimulation occurrence of protrusion of the penis was recorded.
Penis anatomy	PS	When the penis was observed it was scored as either anatomically normal or abnormal (e.g. penile frenulum papillomatosis).
Horn status	HSt	Scored at branding time (~3–4 months of age). Each animal, where possible, was scored for the presence or absence of horns and also if the horn material was a scur (horn bud not attached), with a reassessment at 12–18 months of age, P = Polled, S = Scurred, H = Horned.
		Scrotal traits[A]
Scrotal circumference (cm)	SC	ACV recommended SC measurement procedure with a standard metal tape (see Holroyd *et al*. 2002*b*; Entwistle and Fordyce 2003).
Testicular tone (1–5)	TT	Testicular tone was scored on a scale of 1–5 with 1 = very soft, 3–4 = ideal, 5 = very hard; as described by Holroyd *et al.* (2002*b*) and based on an ACV classification described by Entwistle and Fordyce (2003).
		Semen collection traits[A]
Density (1–5)	DENS	Density of ejaculate scored immediately after collection on a scale of 1–5 with 1 = clear to cloudy, 2 = cloudy to milky, 3 = milky, 4 = creamy, 5 = thick creamy or dense. Density recorded crush side immediately after semen collection.
Mass activity (1–5)	MASS	Mass activity (or wave motion) recorded crush side immediately after semen collection scored at ×40 magnification on a scale of 1–5 with 1 = no swirl, 2–3 = slow distinct swirl, 4 = moderate swirl and 5 = swirl is in continuous dark waves.
Motility (%)	MOT	Motility recorded crush side immediately after semen collection estimated as percentage of sperm viewed at ×400 magnification that were progressively motile by their own propulsion.
Sperm morphology traits[A]		Immediately after each crush side evaluation of an ejaculate, up to 5 × 50-uL aliquots of ejaculate, dependent on the density of sperm cells in the ejaculate, were taken with a micropipette and placed into 2.95 mL of phosphate-buffered formal saline for sperm morphology assessment. Morphological assessment involved systematic evaluation of 100 sperm cells at ×1000 magnification. A count of the normal cells allowed per cent morphologically normal sperm to be derived. Abnormalities were counted and grouped into categories described below.
Morphologically normal sperm (%)	PNS	Percentage of sperm that have no morphological attributes known to be indicative of subfertility.
Knobbed acrosomes (%)	KA	The KA defect can be heritable due to a disturbance in testes thermoregulation (Entwistle and Fordyce 2003). If knobbed acrosomes are the only abnormality observed in an ejaculate where motility, volume and density are normal, the condition is probably genetic and will not improve. However, if motility, volume and density are poor and many other abnormalities are present, the condition is probably a sign of disturbed spermatogenesis caused by some stressor and the bull may recover.
Pyriform heads (%)	PH	The presence of a moderate number of PH in the absence of other signs of disturbed spermatogenesis is considered normal for some bulls (Entwistle and Fordyce 2003). However, when pronounced forms of pyriformity are observed, they usually are responsible for a decrease in fertility and are believed to result from a disturbance in spermatogenesis. Young bulls ≤2 years of age are more likely to recover from this condition than older bulls.
Abnormal mid pieces (%)	MP	The abnormal sperm MP defect is the most common condition observed in bull ejaculates (Entwistle and Fordyce 2003). This defect may occur as an artefact due to prolonged contact with a hypotonic solution (Negrosin-Eosin stain), cold-shock or other environmental stressors. This type of abnormality can be common in some bulls and fluctuations in the percentage of affected spermatozoa can occur throughout the year. The prognosis of this condition varies with the circumstances and the presence of other types of abnormalities. If this defect is present in the absence of other abnormalities, this condition is usually transient in nature and recovery can occur within 16 days.

(*Continued next page*)

Table 4. (*continued*)

Component traits	Code	Description
Proximal droplets (%)	PD	Entwistle and Fordyce (2003) reported that PD are normal in the pubertal bull and their incidence decreases with age. However, in the mature bull, these droplets can indicate abnormal spermiogenesis and/or epididymal function. These droplets can often be observed in conjunction with other abnormalities of the head and mitochondrial sheath.
Swollen acrosomes (%)	SA	The SA defect can be associated with a 'rusty load'/accumulated sperm condition (Entwistle and Fordyce 2003) (Table 3). The aging of sperm causes the acrosome to undergo a similar reaction to capacitation, which results in the lifting of the acrosome and the failure of the sperm to attach to the oocyte. This condition is often observed in conjunction with other head abnormalities such as knobbed acrosomes.
Abnormal tails and loose heads (%)	TH	The TH defect may occur as a result of temperature shock to the epididymis (Entwistle and Fordyce 2003). This condition is usually transient and the level of defects may decrease after 8–11 days.
Vacuoles and teratoids (%)	VT	The VT defect can occur during spermiogenesis and may be a result of extreme temperatures or stress (Entwistle and Fordyce 2003). Bulls can recover from this condition within 6 weeks of exposure to the insult; however, some bulls can be more susceptible to this condition and may not recover.

[A]Each trait was measured according to the standards prescribed by the Australian Cattle Veterinarians (Entwistle and Fordyce 2003). Traits were measured or scored by experienced technicians trained and supervised by an Australian Cattle Veterinarian (ACV) Accredited Examiner for Bull Breeding Soundness Evaluation (BBSE).

stimulation, rectal massage was applied to the ampullae to determine if an ejaculate could be collected (Entwistle and Fordyce 2003). If an animal lay down in the crush during the collection procedure, an attempt was made to get the animal to its feet to continue the procedure, if this was not successful the animal was released from the crush and given a missing value for the semen traits. All crush side semen assessments were conducted using a PRO 2300 Binocular Phase Contrast Microscope (Prism Optical, Kelvin Grove, Qld, Australia) with an LEC warm stage.

The measurements and samples collected were based on the findings of a systematic review of male reproductive traits and their relationship to reproductive traits in their female progeny (Burns *et al*. 2011). A specific focus of this review was to give consideration to reducing some of the traditional bull reproductive measurements and replacing them with novel parameters that might be more valuable as predictors of male reproductive performance. Subsequently, potential predictors of male reproductive performance were identified, in particular those that could be measured in the younger (<2 years of age) animal. Therefore, at branding (3–4 months of age), weaning (~6 months of age) and during the BBSE, blood and semen samples were collected and stored for future novel assessments. Ambient temperature was recorded at each BBSE to investigate effects on semen quality.

Rationale for traits measured

A total of 108 separate measurements were made spanning blood hormonal, scrotal, growth, carcass, adaptation and semen quality traits recorded from branding to 24 months of age to enable an evaluation of the relationships between the productive and reproductive performance of young bulls. The rationale for taking these measures is described in further detail.

Blood hormonal traits

Because of the associations between LH (Post *et al*. 1987; Perry *et al*. 1990*a*, 1990*b*) and testosterone (Mackinnon *et al*. 1991) and aspects of reproductive performance in post-pubertal tropically adapted genotypes; LH and age of puberty in pre-pubertal *B. taurus* bulls (Evans *et al*. 1995; Moura and Erickson 1997; Bagu *et al*. 2006) and as a useful early-in-life predictor of fertility (Aravindakshan *et al*. 2000), Burns *et al*. (2011) recommended that the concentration of LH in blood be recorded at 3–4 months of age in pre-pubertal BRAH and TCOMP bulls (Table 4).

Inhibin is exclusively produced by Sertoli cells in the testes (Kaneko *et al*. 2001; Sharpe *et al*. 2003; Phillips 2005); is linked to the regulation of spermatogenesis (Phillips 2005); increases fertility-associated characteristics before puberty (Wheaton and Godfrey 2003); has no antagonisms between it, follicle stimulating hormone, LH and testosterone during pre-pubertal and post-pubertal stages of testicular development and function (Matsuzaki *et al*. 2000); and its pre-pubertal serum level is directly related to SC and sperm production in mature bulls (Sharpe *et al*. 2003). As a consequence of these results, Burns *et al*. (2011) recommended that the relationship between serum inhibin concentration and testes development and function should be further investigated and evaluated in pre-pubertal bulls at 3–4 months of age (Table 4).

Yilmaz *et al*. (2004) reported that the serum concentration of IGF-I in pre-pubertal *B. taurus* bulls was positively correlated with adult SC and sperm motility and genetically correlated with the age at first calf of female progeny and calving rate. In addition, Johnston *et al*. (2009) also reported that IGF-I was the best genetic predictor of age at first *corpus luteum* (age at puberty) in BRAH and TCOMP heifers in northern Australia. Therefore, Burns *et al*. (2011) recommended that as blood serum IGF-I appeared to be a promising predictor of fertility in *B. taurus* cattle, it should be evaluated in BRAH and TCOMP bull calves at weaning (Table 4).

Growth and carcass traits

The description of the collection of birthweights and further liveweights from weaning (~6 months of age) to the final collection of trait data at 24 months of age is presented in Table 4. The collection liveweights during this period allowed a growth rate profile to be developed. Growth is related to SC in males (Bourdon and Brinks 1986) and to attainment of puberty in female cattle (Johnston *et al*. 2009; Burns *et al*. 2010).

Body condition score (CS) in this study was based on a 5-point scale as reported by Upton *et al*. (2001) (Table 4). For this Beef CRC Program, this 5-point scale was modified to include one-third score increments. Therefore, body condition was visually assessed on a 1–5 scale to the nearest one-third of a point, using '+' and '–' subcategories, where 1 is poor, 2 is backward, 3 is forward, 4 is prime, 5 is fat; and re-coded to a numeric variable, e.g. 1– (0.7), 1 to 5+ (5.3). CS was recorded at 9, 12, 15, 18, 21 and 24 months of age. Body condition and fatness are affected by nutrition and can have a profound influence on reproductive measures (Barr and Burns 1972).

Hip height was measured at 15 months of age and similarly ultrasound scanned rump fat, rib fat and eye muscle area measurements all recorded at 15 months of age using ultrasound imagery. An accredited scanner used an accredited real-time ultrasound-scanning machine (Esaote/Pie Medical Aquila with a 3.5-MHz ASP-18 transducer), as described by Upton *et al*. (1999, 2001), to record these traits as measures of growth and carcass merit (Table 4).

Adaptation traits

Temperament can have a substantial influence on the productivity of beef enterprises through increases in production costs and possibly through relationships between temperament and traits such as growth (Fordyce *et al*. 1985, 1988*a*), and carcass and meat quality (Fordyce *et al*. 1988*b*; Burrow 1997; Kadel *et al*. 2006). To provide a reliable objective measure of temperament, Burrow and Corbet (2000) recommended a repeat measure of flight time of weaned calves (FT6a and FT6b; Table 4). Measurements were also taken at 12, 18 and 24 months of age.

Rectal temperatures were recorded using an Anritherm integrated thermometer (Anritherm HL600, Anritsu Meter Co. Ltd, Tokyo, Japan) and a rectal probe to evaluate the impact on semen traits, while ambient temperature was recorded and available for use in future statistical analyses (Table 4). Rectal temperature was recorded at each BBSE to investigate effects of body temperature on semen quality traits (Turner 1982).

Conformation traits

A comprehensive review of the importance of the physical examination of bulls was conducted by Holroyd *et al*. (2002*b*) who discussed a range of bull conformation traits and specifically the impact of leg and foot structure; sheath score; prepuce eversion; and penis erection and structure on bulls' reproductive performance. The measurement and recording of sheath score is a standardised measure in the ACV BBSE

Table 5. Summary of attrition due to culling and death of young bulls from weaning to 2 years of age

Cryptorchid, absence of one or both testes; hypoplasia, gross underdevelopment of one testicle; Other, culled due to injury, illthrift or poor temperament; Unknown, cause of death not obvious

Genotype	Exit age (months)	Culls: Cryptorchid	Culls: Hypoplasia	Culls: Other	Deaths: Injury	Deaths: Sickness	Deaths: Unknown	Total	Percent of genotype
Brahman	6–12	11	4	3	0	6	13	37	–
	13–18	4	5	0	0	3	5	17	–
	19–24	5	20	3	0	1	3	32	–
	Total	20	29	6	0	10	21	86	5.7
Tropical Composite	6–12	11	5	4	3	5	7	35	–
	13–18	1	3	0	0	3	6	13	–
	19–24	9	11	4	2	2	8	36	–
	Total	21	19	8	5	10	21	84	3.7
Crossbred	6–12	0	0	0	0	0	1	1	–
	13–18	0	2	0	0	3	1	6	–
	19–24	0	0	0	0	0	2	2	–
	Total	0	2	0	0	3	4	9	3.6
Grand total		41	50	14	5	23	46	179	–
Percent overall		1.0	1.2	0.3	0.1	0.6	1.1	4.4	–

Table 6. Numbers of young bulls by genotype, age and status at each Bull Breeding Soundness Evaluation (BBSE)

Genotype/status	Brahman: 12 months	Brahman: 18 months	Brahman: 24 months	Tropical Composite: 12 months	Tropical Composite: 18 months	Tropical Composite: 24 months
BBSE (*n*)	1340	1409	1403	1924	2081	2069
Stimulated[A] – SC $\geq$20 cm (*n*)	850	1374	1401	1863	2080	2068
Produced an ejaculate (*n*)	807	1308	1390	1843	2064	2060
With assessable sperm[B] (*n*)	103	826	1234	970	1794	1912

[A]Bulls with scrotal circumference (SC) of 20 cm or greater were electro-stimulated for ejaculate collection.

[B]Bulls assessed for percent normal sperm (PNS); a PNS value could only be recorded if $\geq$100 spermatozoa were present in the fixed ejaculate subsample.

program (Entwistle and Fordyce 2003; Fordyce *et al*. 2006) (Table 4).

Scrotal traits

Age-corrected SC is consistently reported to be a useful method of assessing reproductive function in bulls because of the favourable relationship with several sperm traits (Brinks *et al*. 1978; Silva *et al*. 2011) and fertility (Mackinnon *et al*. 1990; Eler *et al*. 2006; Schatz *et al*. 2010). As the measurement of SC is still the best method of assessing testicular development (Barth 2000) using a standard metal tape (Holroyd *et al*. 2002*b*; Entwistle and Fordyce 2003), Burns *et al*. (2011) recommended that SC should be measured regularly between weaning and 24 months of age to assess when SC may first be associated with female reproductive performance traits (Table 4).

Semen and sperm traits and morphology

In a study conducted in tropical genotype bulls managed under extensive grazing conditions and in multiple-sire mated herds in northern Australia, percent normal sperm (PNS) and the spermiogram were shown to be the best practical measures that are consistent predictors of calf output (Fitzpatrick *et al*. 2002; Holroyd *et al*. 2002*a*). PNS accounted for 35–57% of the variation in calf output between bulls (Holroyd *et al*. 2002*a*). As a consequence, Burns *et al*. (2011) recommended further investigation of PNS to determine its genetic relationship with female reproductive performance. Further, the measurements on the bulls in this study were finalised at 24 months of age and it was not logistically possible to naturally mate and evaluate the calf output of all these bulls. As a result, the researchers in this study identified PNS at 24 months of age (PNS24) as the benchmark for male fertility.

Table 7. Summary statistics for growth, carcass and testicular measures within genotype

n, number of animals recorded for each trait. Min. and Max., minimum and maximum of the trait range. s.d., standard deviation. CV, coefficient of variation is the s.d. expressed as a percentage of the mean. See Table 4 for trait description

		Brahman						Tropical Composite					
Trait	Unit	*n*	Min.	Max.	Mean	s.d.	CV	*n*	Min.	Max.	Mean	s.d.	CV
Liveweight													
Birth	kg	1473	20	59	35.3	5.77	16	2418	18	62	36.2	5.93	16
6 months (kg)	kg	1639	104	323	203.7	33.51	16	2424	96	344	220.1	39.61	18
9 months (kg)	kg	1490	110	323	217.2	34.95	16	2133	116	347	237.4	38.96	16
12 months (kg)	kg	1469	125	360	246.9	35.27	14	2106	133	420	275.2	40.80	15
15 months (kg)	kg	1462	144	430	297.4	38.43	13	2099	186	456	319.3	44.06	14
18 months (kg)	kg	1436	214	488	353.2	38.36	11	2097	228	510	368.8	45.12	12
21 months (kg)	kg	1432	225	540	365.1	42.70	12	2095	228	519	371.9	47.44	13
24 months (kg)	kg	1430	222	570	383.9	44.35	12	2087	236	580	392.1	50.70	13
Body condition score													
9 months	1–5	1421	1.3	3.3	2.4	0.33	14	1962	1.3	3.3	2.4	0.33	14
12 months	1–5	1463	1.0	3.3	2.4	0.33	14	2102	1.3	3.3	2.4	0.33	14
15 months	1–5	1415	1.0	3.3	2.5	0.28	11	2099	1.7	3.3	2.4	0.28	12
18 months	1–5	1424	1.7	3.3	2.8	0.20	7	2095	1.7	3.3	2.7	0.28	10
21 months	1–5	1424	1.0	3.3	2.7	0.27	10	2088	1.0	3.3	2.5	0.33	13
24 months	1–5	1410	1.7	3.3	2.7	0.21	8	2078	1.0	3.3	2.5	0.31	12
Carcass													
Rib fat 15 months (mm)	mm	1458	0.5	3.0	1.1	0.24	22	2099	0.5	3.0	1.0	0.14	14
Rump fat 15 months (mm)	mm	1458	0.5	5.0	1.4	0.56	40	2099	0.5	4.0	1.1	0.30	27
EMA 15 months	cm^2	1458	21	71	46.8	7.85	17	2097	21	77	50.7	8.11	16
Height of animal													
Hip height 15 months	cm	1457	110	144	128.0	4.89	4	2099	105	139	124.9	4.87	4
Scrotal circumference													
6 months	cm	1609	12	25	17.2	1.71	10	2399	11	31	19.3	2.56	13
9 months	cm	1361	13	33	19.1	2.67	14	1937	15	34	23.8	3.87	16
12 months	cm	1448	13	35	21.2	3.13	15	2093	15	37	26.5	3.37	13
15 months	cm	1108	16	40	24.7	3.73	15	1570	18	39	29.3	3.10	11
18 months	cm	1409	16	42	26.4	3.49	13	2081	19	40	29.9	3.00	10
21 months	cm	1411	19	41	28.5	3.26	11	2077	18	41	30.8	2.98	10
24 months	cm	1403	19	42	30.2	3.21	11	2069	17	42	31.6	2.87	9
Testes tone (1–5)													
12 months	1–5	1340	2	4	3.7	0.46	12	1924	2	5	3.86	0.37	10
18 months	1–5	1410	2	4	3.9	0.35	9	2083	2	4	3.83	0.39	10
24 months	1–5	1402	3	5	3.9	0.31	8	2069	2	5	3.85	0.37	10

Other traits recorded on the ejaculate in this study included crush side assessment of semen mass activity and motility. These traits were evaluated by experienced operators, trained and supervised by an accredited ACV BBSE examiner, at 12, 18 and 24 months of age. A detailed description of the traits and their measurement are presented in Table 4.

The sperm morphology traits recorded on the ejaculate in this study included PNS at 12, 18 and 24 months of age (PNS12, 18 and 24; 0–100%; Burns *et al*. 2011) and a range of sperm abnormalities (Entwistle and Fordyce 2003). An ACV-accredited sperm morphologist (research) assessed the morphology of 100 sperm in each sample judged to contain sufficient sperm for examination. Sperm abnormalities recorded included knobbed acrosomes; pyriform heads; abnormal mid piece; abnormal proximal droplet; swollen acrosomes; abnormal tails and loose heads; and sperm with vacuoles and teratoids at 12, 18 and 24 months of age. These abnormalities were based on the classification of the ACV BBSE program and the potential relationship of each abnormality category with bull fertility is described in Table 4 (Entwistle and Fordyce 2003).

Seminal plasma was collected for the intended future evaluation of seminal plasma proteins (Killian *et al*. 1993; Cancel *et al*. 1997; Brandon *et al*. 1999), sperm fertility-associated proteins (Killian *et al*. 1993; Roudebush and Diehl 2001; Brackett *et al*. 2004) and 11β-hyroxysteroid dehydrogenase (Michael *et al*. 2003) in other reproductive trait studies.

Data, statistical analyses and descriptive statistics

Data

As reported in previous papers (Upton *et al*. 2001; McKiernan *et al*. 2005), data from all experimental sites were loaded and stored on a central database developed and customised for the Beef CRC. To ensure the integrity and biological consistency of the data, each record was initially checked by site managers and their respective research team members and finally by the central database manager. The system allows all CRC collaborating partners to access and use the data.

Initial data editing excluded animals affected by illness or injury. Additionally, bulls with abnormal testicular development particularly in the form of gross hypoplasia or cryptorchidism were culled from the project and their records excluded from the data analyses. Deaths due to disease, accidental injury or unknown reasons also occurred during the course of the experimentation. Table 5 summarises the numbers of bulls exiting the project due to death or culling within genotype and age at exit. The total attrition of young bulls due to death and culling from weaning to 2 years old amounted to ~4% of animals weaned.

Table 8. Summary statistics for adaptation, hormonal and conformation traits within genotype

n, number of animals recorded for each trait. Min. and Max., minimum and maximum of the trait range. s.d., standard deviation. CV, coefficient of variation is the s.d. expressed as a percentage of the mean. See Table 4 for trait definition

Trait	Age (months)	Unit	Brahman *n*	Min.	Max.	Mean	s.d.	CV	Tropical Composite *n*	Min.	Max.	Mean	s.d.	CV
Adaptation traits														
Flight time	6a[A]	Second	1619	0.24	5.40	1.20	0.63	53	2384	0.19	5.40	1.23	0.50	41
Flight time	6b[A]	Second	1607	0.27	5.40	1.20	0.63	53	2274	0.39	5.40	1.23	0.55	45
Flight time	12	Second	1465	0.45	6.67	1.80	0.85	47	2101	0.44	7.66	1.70	0.68	40
Flight time	18	Second	1326	0.50	9.90	2.10	1.01	48	1924	0.57	9.90	2.10	0.84	40
Flight time	24	Second	1429	0.51	7.02	2.10	0.83	40	2082	0.63	7.02	1.90	0.61	32
Rectal temperature	12	°C	540	37.0	40.7	39.2	0.49	1	792	37.3	41.0	39.2	0.50	1
Rectal temperature	24	°C	509	37.2	41.5	39.3	0.66	2	785	37.1	40.8	39.3	0.55	1
Hormonal traits														
GnRH-stimulated LH	4	ng/mL	1025	0.19	29.34	5.21	4.46	86	1520	0.17	31.76	7.06	5.16	73
Inhibin	4	ng/mL	1288	3.21	16.22	7.36	1.82	25	1895	2.66	15.05	7.82	1.92	25
IGF-I	6	ng/mL	1626	56	1765	517	302	58	2415	47	1838	532	299	56
Conformation traits														
Sheath score	12	1–9	1424	2	9	4.4	1.10	25	2071	1	9	6.9	1.77	26
Sheath score	18	1–9	1437	1	8	4.3	1.19	28	2104	1	9	7.0	1.73	25
Sheath score	24	1–9	1430	1	8	4.0	1.04	26	2091	1	9	6.8	1.74	26
Prepuce eversion	12	mm	1362	0	100	11	16.6	151	1943	0	150	11	22.1	201
Prepuce eversion	18	mm	1438	0	100	18	21.0	117	2104	0	120	10	20.9	209
Prepuce eversion	24	mm	1430	0	150	26	25.6	98	2091	0	180	12	25.1	209
Leg structure	12	1–9	1362	7	9	8.9	0.33	4	1946	7	9	8.9	0.30	3
Leg structure	18	1–9	1329	6	9	8.9	0.34	4	1932	7	9	8.9	0.33	4
Leg structure	24	1–9	1431	6	9	8.9	0.31	3	2091	6	9	8.9	0.30	3
Feet structure	12	1–9	1350	5	9	8.5	0.63	7	1927	4	9	7.8	0.87	11
Feet structure	18	1–9	1315	5	9	8.4	0.69	8	1921	4	9	8.0	0.80	10
Feet structure	24	1–9	1401	4	9	8.4	0.66	8	2068	4	9	7.8	0.86	11

[A]Flight time was recorded twice at weaning (see Table 4) to derive a more reliable measure of genetic merit for flight time.

In accordance with available project funds and evolving development of trait measurement protocols not all young bulls were measured for all traits. LH was measured on birth-year cohorts 2007–10 inclusive while inhibin was measured on cohorts 2006–10 inclusive. Rectal temperatures were only recorded on 2008 and 2009 birth-year cohorts. The 12-month BBSE was not conducted on the 2004 cohort and the 2010 cohort had no BBSE or any of the post-weaning traits recorded. At BBSE, only those bulls with SC of 20 cm or greater were electro-stimulated to collect an ejaculate sample. Previous experience deemed that young bulls with SC of less than 20 cm were sexually immature and not able to provide an ejaculate with spermatozoa present. Table 6 summarises the number of young bulls presenting for BBSE, those greater than 20 cm SC and those producing ejaculates with assessable sperm at each time point within each genotype.

Statistical analyses

Companion and forthcoming papers will document in detail the statistical analyses conducted, but briefly, analytical models will include the fixed effects of year, birth location, birth month, post-weaning location, dam age and previous lactation status, dam management group, their interactions and sire as a random effect.

Table 9. Summary statistics for semen and sperm morphology traits within genotype

n, number of animals recorded for each trait. Min. and Max., minimum and maximum of the trait range. s.d., standard deviation. CV, coefficient of variation is the s.d. expressed as a percentage of the mean. See Table 4 for trait definition

Trait	Age (months)	Unit	Brahman *n*	Brahman Min.	Brahman Max.	Brahman Mean	Brahman s.d.	Brahman CV	Tropical Composite *n*	Tropical Composite Min.	Tropical Composite Max.	Tropical Composite Mean	Tropical Composite s.d.	Tropical Composite CV
Semen traits														
Ambient temperature[A]	12	°C	1361	17.0	41.0	30.5	4.49	15	1943	17.0	41.0	30.1	4.80	16
Ambient temperature	18	°C	1437	6.0	34.0	26.7	4.45	17	2103	4.0	34.0	26.0	4.96	19
Ambient temperature	24	°C	1429	16.0	40.0	29.1	4.23	15	2090	15.0	40.0	28.0	4.26	15
Volume	12	mL	807	0.0	12.0	3.6	1.97	55	1843	0.0	14.0	5.1	2.36	46
Volume	18	mL	1308	0.0	13.0	4.7	2.32	49	2058	0.5	14.0	5.7	2.35	41
Volume	24	mL	1387	0.0	15.0	6.3	2.68	43	2058	0.0	18.0	6.1	2.74	45
Density	12	1–5	753	0.5	4.0	1.7	0.75	44	1821	0.5	5.0	2.4	0.97	40
Density	18	1–5	1264	0.5	5.0	2.2	0.95	43	2041	0.0	5.0	2.8	1.00	36
Density	24	1–5	1389	0.0	5.0	3.1	0.87	28	2057	0.0	5.0	3.2	0.86	27
Mass activity	12	1–5	754	0.0	4.0	0.4	0.75	188	1822	0.0	4.5	1.5	1.35	90
Mass activity	18	1–5	1306	0.0	4.5	1.4	1.19	85	2062	0.0	5.0	2.2	1.24	56
Mass activity	24	1–5	1390	0.0	5.0	2.5	1.14	46	2060	0.0	5.0	2.8	1.06	38
Motility	12	%	754	0	90	16	26.1	163	1821	0	95	46	33.9	73
Motility	18	%	1306	0	98	41	30.8	75	2064	0	100	57	28.1	49
Motility	24	%	1390	0	98	67	25.4	38	2060	0	98	70	24.3	35
Sperm morphology														
Normal sperm	12	%	103	2	87	23	20.1	87	968	1	96	55	27.9	51
Normal sperm	18	%	826	0	98	49	29.1	59	1794	0	97	67	22.6	34
Normal sperm	24	%	1235	1	98	72	23.1	32	1912	0	99	75	19.1	25
Knobbed acrosomes	12	%	103	0	13	1	2.3	153	968	0	64	2	4.3	268
Knobbed acrosomes	18	%	826	0	52	1	3.1	281	1794	0	70	1	4.3	358
Knobbed acrosomes	24	%	1235	0	32	1	2.3	288	1912	0	82	1	4.1	410
Abnormal mid-pieces	12	%	103	1	60	19	12.3	64	968	0	83	14	12.7	91
Abnormal mid-pieces	18	%	826	0	74	15	12.3	82	1794	0	77	13	11.7	90
Abnormal mid-pieces	24	%	1235	0	87	11	12.3	109	1912	0	89	10	10.3	103
Proximal droplets	12	%	103	1	88	44	23.2	53	968	0	96	19	22.6	118
Proximal droplets	18	%	826	0	91	25	26.7	107	1794	0	82	7	11.5	169
Proximal droplets	24	%	1235	0	90	8	15.6	195	1912	0	81	4	7.5	178
Pyriform heads	12	%	103	0	10	1	1.9	173	968	0	44	1	2.0	286
Pyriform heads	18	%	826	0	16	0	1.2	240	1794	0	19	0	1.2	240
Pyriform heads	24	%	1235	0	16	0	0.8	400	1912	0	28	0	1.2	300
Swollen acrosomes	12	%	103	0	18	1	2.4	218	968	0	21	1	2.0	222
Swollen acrosomes	18	%	826	0	27	1	2.0	200	1794	0	25	1	2.4	218
Swollen acrosomes	24	%	1235	0	24	1	1.8	225	1912	0	79	1	2.6	325
Abnormal tails, heads	12	%	103	0	32	5	6.4	128	968	0	75	6	8.5	142
Abnormal tails, heads	18	%	826	0	75	6	9.2	151	1794	0	98	8	11.4	143
Abnormal tails, heads	24	%	1235	0	72	6	9.0	161	1912	0	92	6	10.2	165
Vacuoles and teratoids	12	%	103	0	56	8	10.4	125	968	0	64	4	7.0	171
Vacuoles and teratoids	18	%	826	0	84	5	9.6	178	1794	0	100	4	7.0	194
Vacuoles and teratoids	24	%	1235	0	86	3	7.3	243	1912	0	100	3	6.1	226

[A]Ambient temperature is not a trait of the animal but was recorded at time of BBSE to investigate effects on semen traits and rectal temperature.

The effect of assay or sample group will be included for blood hormone traits and age nested within birth month included as a covariate for all traits. Ambient temperature will be included as a covariate for semen collection and rectal temperature records. Terms for sire group and dam group and their interaction will be included to account for additive and possible non-additive breed and composite genotype effects.

Animal models will be used to estimate variance components and will include the fixed effects identified above for each trait with an additional random common environmental effect of the dam when significant using log-likelihood ratio tests. To be consistent across the same trait over 3–4 measurement times (e.g. LWT), the random common environment effect of the dam will be included in all models for the trait if significant at any one time point. Genetic and phenotypic correlations between traits will be estimated in a series of bivariate analyses.

Descriptive statistics

Trait means, range and coefficient of variation are presented in Tables 7–9. These summary statistics are not adjusted for fixed effects but show the mean level and variation in the traits recorded. The data shows that a large amount of variation exists for most traits in both genotypes particularly for hormones and semen quality measurements. The increase in PNS over time from 12 to 24 months of age was quite marked, especially in young BRAH bulls, and appeared to be due mainly to the decrease in the proximal droplets abnormality category. Comparison of the two genotypes is only valid from subsets of the data where BRAH and TCOMP bulls were run together as contemporaries from birth and have been correctly adjusted for other fixed effects, e.g. year, dam effects, month of birth and age. The design of the study allowed statistical models to be fitted to account for the many fixed effects and the partitioning of genetic and non-genetic sources of variation.

Conclusion

The design of this study has enabled the measurement of a comprehensive range of pre- and post-pubertal traits on BRAH and TCOMP bulls, which included growth and carcass traits, hormonal traits, adaptation traits and a BBSE strategy that included locomotory and reproductive organ conformation traits and semen and sperm morphology traits. The descriptive statistics of the range of traits presented highlights the large variation that exists in most traits, with complete overlap between genotypes. The variation indicates that there is likely to be significant opportunity to improve the phenotypes and genetics of reproduction in tropical beef cattle genotypes in northern Australia through better management and bull selection decisions. Finally, this project design has enabled the estimation of phenotypic and genetic parameters to evaluate the usefulness of bull traits as predictors of herd reproductive performance. These parameter estimates are reported in the following papers of this series.

Acknowledgements

The authors wish to acknowledge the support of the Cooperative Research Centre for Beef Genetic Technologies and its core partners and the financial support of Meat and Livestock Australia. We would also like to acknowledge the significant 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. Further, 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 this research activity. In particular, we would like to acknowledge Tim Grant, Karl Enchelmaier, Jo Campbell, Brett Ward, Jim Cook, Warren Sim, Paul Williams and Rob Young for their contributions to cattle management, data collection and handling and laboratory analyses throughout this project.

References

Anon. (1976) Notes on the Research Programme. CSIRO Australia, Division of Animal Production, Rockhampton.

Anon. (1994) Final Report UNE 30, Industry Validation of Current and New Traits for BREEDPLAN, Meat and Livestock Australia, North Sydney.

Aravindakshan JP, Honaramooz A, Bartlewski PM, Beard AP, Pierson RA, Rawlings NC (2000) Pattern of gonadotrophin secretion and ultrasonographic evaluation of developmental changes in the testes of early and late maturing bull calves. *Theriogenology* **54**, 339–354. doi:10.1016/S0093-691X(00)00353-8

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

Barr NCE, Burns MA (1972) Supplementation to increase fertility of beef cows in a drought. *Proceedings of the Australian Society of Animal Production* **9**, 159–164.

Barth AD (2000) 'Bull breeding soundness evaluation manual.' 2nd edn. (The Western Canadian Association of Bovine Practitioners, Department of Large Animal Clinical Sciences, Western College of Veterinary Medicine: Saskatoon, Canada)

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

Bourdon RM, Brinks JS (1986) Scrotal circumference in yearling Hereford bulls: adjustment factors, heritabilities and genetic, environmental and phenotypic relationships with growth traits. *Journal of Animal Science* **62**, 958–967.

Brackett BG, Bosch P, McGraw RA, DeJarnette JM, Marshall CE, Massey JB, Roudebush WE (2004) Presence of platelet-activating factor (PAF) receptor in bull sperm and positive correlation of sperm PAF content with fertility. *Reproduction, Fertility and Development* **16**, 265. doi:10.1071/RDv16n1Ab291

Brandon C, Heusner G, Caudle A, Fayrer-Hosken R (1999) Two-dimensional polyacrylamide gel electrophoresis of equine seminal plasma proteins and their correlation with fertility. *Theriogenology* **52**, 863–873. doi:10.1016/S0093-691X(99)00178-8

Brinks J, McInerney MJ, Chenoweth PJ (1978) Relationship of age at puberty in heifers to reproductive traits in young bulls. *Proceedings of the Western Section of the American Society of Animal Science* **29**, 28–30.

Burns BM, Howitt CJ, Esdale CR (1986) Relationships between adaptive traits and weight in different cattle breeds. *Proceedings of the Australian Society of Animal Production* **16**, 163–166.

Burns BM, Howitt CJ, Esdale CR (1988) Bovine Infectious Keratoconjunctivitis in different cattle breeds. *Proceedings of the Australian Society of Animal Production* **17**, 150–153.

Burns BM, Reid DJ, Taylor JF (1997) An evaluation of growth and adaptive traits of different cattle genotypes in a sub-tropical environment. *Australian Journal of Experimental Agriculture* **37**, 399–405. doi:10.1071/EA96092

Burns BM, Fordyce G, Holroyd RG (2010) Factors that impact on the capacity of beef cattle females to conceive, maintain a pregnancy and wean a calf – implications for northern Australia: a review. *Animal Reproduction Science* **122**(1–2), 1–22. doi:10.1016/j.anireprosci.2010.04.010

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

Burrow HM (1997) Measurements of temperament and their relationships with performance traits of beef cattle. *Animal Breeding Abstracts* **65**, 477–495.

Burrow HM, Corbet NJ (2000) Genetic and environmental factors affecting temperament of zebu and zebu-derived beef cattle grazed at pasture in the tropics. *Australian Journal of Agricultural Research* **51**, 155–162. doi:10.1071/AR99053

Burrow HM, Seifert GW, Corbet NJ (1988) A new technique for measuring temperament in cattle. *Australian Society of Animal Production* **17**, 154–157.

Cancel A, Chapman D, Killian G (1997) Osteopontin is the 55-kilodalton fertility associated protein in Holstein bull seminal plasma. *Biology of Reproduction* **57**, 1293–1301. doi:10.1095/biolreprod57.6.1293

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.

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.

Entwistle K, Fordyce G (2003) ‘Evaluating and reporting bull fertility.’ (Australian Association of Cattle Veterinarians: Indooroopilly, Qld)

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

Fitzpatrick LA, Fordyce G, McGowan MR, Bertram JD, Doogan VJ, De Faveri J, Miller RG, Holroyd RG (2002) Bull selection and use in northern Australia: 2. Semen traits. *Animal Reproduction Science* **71**, 39–49. doi:10.1016/S0378-4320(02)00024-6

Fordyce G, Goddard ME, Tyler R, Williams G, Toleman MA (1985) Temperament and bruising of *Bos indicus* cross cattle. *Australian Journal of Experimental Agriculture* **25**, 283–288. doi:10.1071/EA9850283

Fordyce G, Dodt RM, Wythes JR (1988*a*) Cattle temperaments in extensive beef herds in northern Queensland. 1. Factors affecting temperament. *Australian Journal of Experimental Agriculture* **28**, 683–687. doi:10.1071/EA9880683

Fordyce G, Wythes JR, Shorthose WR, Underwood DW, Shepherd RK (1988*b*) Cattle temperaments in extensive beef herds in northern Queensland. 2. Effect of temperament on carcass and meat quality. *Australian Journal of Experimental Agriculture* **28**, 689–693. doi:10.1071/EA9880689

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

Hawken P, Jorre de St Jorre T, Rodger J, Esmaili T, Blache D, Martin GB (2009) Rapid induction of cell proliferation in the adult female ungulate brain (*Ovis aries*) associated with activation of the reproductive axis by exposure to unfamiliar males. *Biology of Reproduction* **80**, 1146–1151. doi:10.1095/biolreprod.108.075341

Holroyd RG, Doogan VJ, De Faveri J, Fordyce G, McGowan MR, Bertram JD, Vankan DM, Fitzpatrick LA, Jayawardhana GA, Miller RG (2002*a*) 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

Holroyd RG, Taylor EG, Galloway D (2002*b*) Physical examination of bulls. In ‘Bull fertility: selection and management in Australia. Australian Association of Cattle Veterinarians Conference Proceedings’. (Ed. G Fordyce) pp. 3.1–3.19. (Australian Association of Cattle Veterinarians: Indooroopilly, Qld)

Hotzel MJ, Markey CM, Walkden-Brown SW, Blackberry MA, Martin GB (1998) Morphometric and endocrine analyses of the effects of nutrition on the testis of mature Merino rams. *Journal of Reproduction and Fertility* **113**, 217–230. doi:10.1530/jrf.0.1130217

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

Kaneko H, Noguchi J, Kikuchi K, Akagi S, Shimada A, Taya K, Watanabe G, Hasegawa Y (2001) Production and endocrine role of inhibin during the early development of bull calves. *Biology of Reproduction* **65**, 209–215. doi:10.1095/biolreprod65.1.209

Killian GJ, Chapman DA, Rogowski LA (1993) Fertility-associated proteins in Holstein bull seminal plasma. *Biology of Reproduction* **49**, 1202–1207. doi:10.1095/biolreprod49.6.1202

Lowman BG, Scott NA, Somerville SH (1976) Condition scoring of cattle. Bulletin No. 6, The East Scotland College of Agriculture, Animal Production, Advisory and Development Department, Edinburgh.

Mackinnon MJ, Hetzel DJS, Corbet NJ, Bryan RP, Dixon R (1990) Correlated responses to selection for cow fertility in a tropical beef herd. *Animal Production* **50**, 417–424. doi:10.1017/S0003356100004906

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

Martin GB, Oldham CM, Lindsay DR (1980) Increased plasma LH levels in seasonally anovular Merino ewes following the introduction of rams. *Animal Reproduction Science* **3**, 125–132. doi:10.1016/0378-4320(80)90039-1

Matsuzaki S, Uenoyama Y, Okuda K, Wanatabe G, Kitamura N, Taya K, Yamada J (2000) Age-related changes in the serum levels of inhibin, FSH, LH and testosterone in Holstein bulls. *The Journal of Reproduction and Development* **46**, 245–248. doi:10.1262/jrd.46.245

McCosker TH, McLean D, Holmes P (2009) Northern beef situation analysis 2009. B.NBP.0518, Final Report, Meat and Livestock Australia, North Sydney.

McCosker KD, McGowan MR, O'Rourke PK, Smith DR, Fordyce G, Burns BM, Joyner D, Phillips N, Menzies D, Newsome T, Perkins N, Morton JM, Jephcott S (2011) Cash cow – exposing northern breeder herd productivity. In 'Proceedings of the Northern beef research update conference, Darwin, 3–4 August 2011'. (Ed. RG Holroyd) pp. 19–23. (Northern Beef Research Update Committee)

McKiernan WA, Wilkins JF, Barwick SA, Tudor GD, McIntyre BL, Grahman JF, Deland MPB, Davies I (2005) CRC 'Regional Combinations Project' – effects on genetics and growth paths on beef production and meat quality: experimental design, methods and measurements. *Australian Journal of Experimental Agriculture* **45**, 959–969. doi:10.1071/EA05061

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.

Michael AE, Thurston LM, Rae MT (2003) Glucocorticoid metabolism and reproduction: a tale of two enzymes. *Reproduction (Cambridge, England)* **126**, 425–441. doi:10.1530/rep.0.1260425

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

Moura AA, Erickson BH (1997) Age-related changes in peripheral hormone concentrations and their relationships with testes size and number of Sertoli and germ cells in yearling beef bulls. *Journal of Reproduction and Fertility* **111**, 183–190. doi:10.1530/jrf.0.1110183

Perry VEA, Chenoweth PJ, Post TB, Munro RK (1990*a*) Fertility indices for beef bulls. *Australian Veterinary Journal* **67**, 13–16. doi:10.1111/j.1751-0813.1990.tb07383.x

Perry VEA, Munro RK, Chenoweth PJ, Bodero DAV, Post TB (1990*b*) Relationships among bovine male and female reproductive traits. *Australian Veterinary Journal* **67**, 4–5. doi:10.1111/j.1751-0813.1990.tb07380.x

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

Post TB, Christensen HR, Seifert GW (1987) Reproductive performance and productive traits of beef bulls selected for different levels of testosterone response to GnRH. *Theriogenology* **27**, 317–328. doi:10.1016/0093-691X(87)90220-2

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

Roudebush W, Diehl J (2001) Platelet-activating factor content in boar sperm correlates with fertility. *Theriogenology* **55**, 1633–1638. doi:10.1016/S0093-691X(01)00508-8

Schatz TJ, Jayawardhana GA, Golding R, Hearnden MN (2010) Selection for fertility traits in Brahmans increases heifer pregnancy rates from yearling mating. *Animal Production Science* **50**, 345–348. doi:10.1071/AN09165

Sharpe R, McKinnell C, Kivlin C, Fisher J (2003) Proliferation and functional maturation of Sertoli cells, and their relevance to disorders of testis function in adulthood. *Reproduction (Cambridge, England)* **125**, 769–784. doi:10.1530/rep.0.1250769

Silva MR, Pedrosa VB, Silva JCB, Eler JP, Guimaraes 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, Guimaraes SEF, Guimaraes JD (2012) Heritability estimate 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

Speck NH, Wright RL, Sweeney FC, Nix HA, Perry RA (1968) Part III. Land Systems of the Dawson–Fitzroy Area. In 'Lands of the Dawson–Fitzroy Area, Queensland. Land Research Series No. 21'. pp. 17–25. (CSIRO Publishing: Melbourne)

Turner HG (1982) Genetic variation of rectal temperature in cows and its relationship to fertility. *Animal Production* **35**, 401–412. doi:10.1017/S0003356100001094

Upton WH, Donoghue KA, Graser H-U, Johnston DJ (1999) Ultrasound proficiency testing. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **13**, 341–411.

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

Vankan DM (2005) Parentage testing of cattle. The University of Queensland Animal Genetics Laboratory Factsheet. Available at http://www.uq.edu.au/ animalgeneticslab/docs/DNA-ParentageTestingFactsheet.pdf [Verified 19 March 2009].

Wheaton J, Godfrey R (2003) Plasma LH, FSH, testosterone, and age of puberty in ram lambs actively immunized against an inhibin alpha-subunit peptide. *Theriogenology* **60**, 933–941. doi:10.1016/S0093-691X(03)00104-3

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.