Measuring reproductive traits in tropical beef cattle breeds: implications for genetic evaluation

by

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Abstract

Reproduction in beef cattle herds is a key driver of productivity and profitability of beef enterprises. Improving the efficiency of reproduction is necessary to keep pace with an increasing global demand for animal protein. Grazing lands across northern Australia, however, comprise large areas of relatively lowly productive land-types with hot, dry climates and unpredictable seasonal rainfall. The challenge for many north Australian beef enterprises is to improve reproduction in the tropically adapted beef breeds grazed extensively in these regions.

Environmental factors influenced by climate and herd management practices account for a proportion of the variation in reproduction rate, but underlying genetic factors also explain individual animal differences. Industry-wide genetic improvement of herd reproductive performance has generally been slow, mainly due to low heritability and late expression of the trait, and difficulty in capturing the necessary joining and calving data. However, selection line experiments in research herds have demonstrated genetic improvement in pregnancy rates of 3% to 5% per annum in tropically adapted breeds. Likely contributors to the genetic differences seen in selected animals are the higher heritability of component traits of reproduction and genetic correlation of these component traits with reproductive performance.

This study incorporates a series of experiments conducted across 9 years and reports moderate to high heritability of reproductive component traits. The traits studied included age at puberty, days to calving and post-partum anoestrus in females, and scrotal circumference and percent morphologically normal sperm in males. In addition, the study reports moderate genetic correlation between these key component traits and lifetime reproduction. The estimated genetic parameters indicate that selection for genetic improvement of these attributes of reproduction, in conjunction with sound breeder-herd management, offers a sustainable solution to the challenge of improving reproductive efficiency in north Australian herds.

The perceived challenge of data collection required for genetic evaluation, however, remains a barrier to the adoption of genetic improvement strategies by north Australian beef producers. With the aim of refining and automating data collection, the final two experiments report on the use of ultrasound scanning, on-animal devices and radio-frequency identification sequence through walk-over-weigh systems to autonomously

record behavioural oestrus and predict time of conception in post-partum cows. Further detailed studies are required, but on-animal devices could potentially provide a suite of technologies to help reduce the challenge of recording and formatting data. Coupled with data handling software platforms, these technologies could provide beef producers with the necessary information on individual animals to more readily develop strategies for genetic improvement of reproductive efficiency.

Declaration

By submitting this thesis for formal examination at CQUniversity Australia, I declare that it meets all requirements as outlined in the Research Higher Degree Theses Policy and Procedure.

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Authorship and Originality

All the experimental chapters in this portfolio thesis are peer-reviewed journal articles published in Animal Production Science, an international journal for animal science. I declare substantive contribution to the research and discussion presented in the chapters as outlined in the following declaration of co-authorship section. I declare that the literature review in Chapter 2 and the discussion presented in the final chapter of the thesis is original work performed by me. No content of this thesis has been submitted or considered either in whole or in part, at any tertiary institute or university for a degree or any other category of award. I also declare that any material presented in this thesis performed by another person or institute has been referenced and listed in the reference sections.

Co-authorship and Co-contribution

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Nicholas J. Corbet

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Thesis Outline

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Chapter 1. Introduction

1.1 Introduction

Herd reproduction rate is a key driver of beef enterprise profitability, the latter measured as dollar returns on kilograms of beef produced per hectare. Reproduction in beef cattle, however, is a complex trait made up of many component parts. Successful reproduction in cattle relies on a chain of hormonally controlled events that govern the fertility of both cow and bull, ultimately leading to the production of a calf per cow each year. To reach that objective the cow must first attain puberty, ovulate to produce viable ova, conceive, maintain a pregnancy, give birth to a live calf and provide a healthy maternal environment through to weaning of the calf. For his part, the bull must also reach puberty and exhibit sufficient libido, dominance and athleticism to provide viable sperm capable of successful fertilisation. The measure of efficient reproduction in cattle then, reflects the ability of each cow to conceive as a maiden heifer early in the breeding season and re-conceive post-partum to wean a calf annually. Hence, reproductive efficiency can be described by weaning rate, which is generally measured as the number of calves weaned per cows mated each year.

1.2 Preface

The Australian cattle herd at June 2018 numbered 26.4 million head with just over 12.1 million in Queensland. There were nearly 42,000 agricultural businesses with cattle and the Australian red meat and livestock industry directly employed approximately 172,000 people. The gross value of Australian cattle and calf production (including live cattle exports) in 2018-2019 was $10.9 billion and the value of total beef and veal exports were valued at AU$8 billion (ABS data cited by Meat & Livestock Australia 2019). The world demand for animal-based food products is expected to increase by up to 70% over the next 30 years. To meet the increasing demand, improved efficiency in the production of beef (kg per hectare) will need to be made.

A major challenge for north Australian beef enterprises is to improve reproduction rate in the tropically adapted beef herds. McGowan *et al*. (2014) reported that achievable pregnancy rates for 4 month mating periods in north Australian beef herds varied from 47% to 89% across different land-types. While environmental factors, influenced by climate and herd management practices, account for a proportion of the variation in reproduction rate, genetic factors also explain individual animal differences. Industry-wide improvement of reproductive performance (typically defined as weaning rate) has generally been slow,

mainly because of low trait heritability, late expression of the trait and difficulty in capturing the necessary joining and calving data (Lee and Pitchford 2015). Breed and sire differences in reproductive performance have been reported, however, and the likely contributors to these genetic differences are the reproductive component traits, such as age at sexual maturity and post-partum anoestrus period (Hetzel *et al*. 1989). Genetic improvement of these components of reproduction in conjunction with sound breeder-herd management offers a sustainable solution to the challenge of improving reproductive performance, provided the component traits are heritable and genetically correlated with the underlying profit trait: lifetime reproductive performance.

To evaluate and improve the component traits of reproduction genetically, they need to be measured on all individuals within their contemporary groups. Genetic improvement can only be made if performance and pedigree are recorded. Prediction of genetic merit of an individual is based on these observations of performance and pedigree. Animals with the highest predicted merit can then be selected as parents of the next generation to cumulatively increase genetic gain. A major barrier to the adoption of genetic selection technologies by north Australian beef enterprises is the perceived challenge of recording and collating the performance and pedigree information required to submit data for evaluation (ABRI 2015). Poor adoption rates of genetic improvement technologies could lead to the selection of breeding replacements without knowledge of their individual genetic merit for growth or reproductive capability. Uninformed selection will inevitably be directed towards the biggest and best-conditioned animals at weaning, which are likely to be so because they were born earlier in the calving season possibly to cows that failed to raise a calf the year before. As a consequence, the uninformed selection strategy may inadvertently exacerbate problems of low reproduction rate in the herd via dissemination of the dam's poor breeding value for reproductive efficiency.

Genetic improvement of reproduction traits will be dependent on accurate measurement of the traits. The extensive beef herds of northern Australia need robust but simple systems of trait recording and evaluation to identify individuals with superior genetic potential for reproductive capability to accelerate genetic improvement.

1.3 Study Aim and Overview

The aim of the research reported in this thesis is to identify strategies that enable more precise phenotypic measurements and genetic evaluation of the heritable component traits

of reproduction in beef cattle. To achieve this aim, this thesis provides a portfolio of previously published research with each chapter represented by a peer-reviewed journal article published in Animal Production Science from 2009 to 2018. The portfolio, preceded by this introductory chapter and some background information, provides a cogent story leading to a discussion and conclusion sections.

Chapters 1 and 2 introduce the topic and add some background information to expose gaps in the current knowledge of reproductive trait measurement and evaluation to help formulate the research questions. The first of the experimental chapters, Chapter 3, describes the measurement of heifer puberty traits and estimation of their genetic parameters in two tropical beef breeds raised in north Australian production environments. Here it is established that age at puberty in heifers, measured by ovarian ultrasound scanning, represents a heritable early-measured component trait of reproduction. Chapters 4 and 5 then describe measurement of traits in young bulls (progeny of the females studied in Chapter 3) and estimation of their genetic parameters, respectively. Chapter 5 highlights scrotal circumference and percent normal sperm as heritable component traits of fertility, measurable in young male cattle, with potential for use in genetic improvement programs.

Chapter 6 reports on a study of genetic correlations which identifies early-in-life male and female measures that may be useful as indirect selection criteria for improving reproduction in tropical breeds of northern Australia. Chapter 7 then considers refining the schedule of ovarian ultrasound scanning with the aim of developing a simple and robust method of measuring reproductive traits in female cattle. Continuing with the objective of simplified measurement of key aspects of reproductive performance, Chapter 8 evaluates the use of on-animal devices to autonomously record behavioural oestrus and predict time of conception in post-partum cows. The genetic parameters of the traits measured and the use of new and developing technologies to aid genetic improvement of reproduction in north Australian beef herds is discussed in Chapter 9. In Chapter 10 conclusions are drawn in response to the aim of identifying strategies for measurement and genetic evaluation of heritable component traits of reproduction in beef cattle.

Chapter 2. Background

2.1 Background

Improvement of reproduction efficiency is not only important for beef enterprise profitability but also to supply protein to an increasing global demand. Successful reproduction in cattle involves the combination of aspects of fertility in both cows and bulls. Reproductive output is typically described in terms of weaning rate, a binomial trait (Guerra 2004) not measurable until the cow has weaned or failed to wean her first calf, which typically occurs at 3.5 years of age in north Australian beef herds. Component traits of reproduction, however, have the potential to be measured earlier in life and so provide a more efficient means of identifying genetically superior individuals to be selected as breeding replacements. The requirements for a component trait to be useful as an alternative selection criterion are that it is heritable, easy to measure and genetically correlated with the target trait. The aim of this background section is to provide some definition of terms and to examine relevant literature on the genetic evaluation of reproductive component traits prior to the publication of the first experiment in this dissertation. The intent is to make a logical argument for the purpose of the research undertaken. Further specific background information is given in the introductory sections of each chapter.

2.2 Genetic evaluation

Since 1985, traits measured in Australian cattle herds have been evaluated by BREEDPLAN (Nicol *et al*. 1985). Genetic evaluation employs the mathematical techniques of restricted maximum likelihood (REML) to provide a best linear unbiased prediction (BLUP) of an animal's genetic worth for all traits recorded. The procedure uses performance data recorded on the individual and all relatives to estimate the breeding value of that animal should it be considered a potential parent. The accuracy of estimated breeding values (EBVs) increases with the number of records measured on relatives in cohort groups within the herd and the strength of genetic linkage between herds within the breed. Comparing EBVs of individuals in a herd helps to identify those with higher genetic value to be selected as the parents of the next generation and increase the frequency of favourable genes in the herd.

2.2.1 Selection

Within-breed selection generally focuses on identifying genetically superior sires for traits of interest and using these as breeding replacements to disseminate the elite genetic material

to improve the frequency of desirable genes in the population. Genetic change can be made in one generation by breed-substitution or crossbreeding, however, the gain from these mating systems tends be one-off compared to the sustained and cumulative genetic progress made by within-breed selection (Van Vleck *et al*. 1987). The rate of genetic improvement of a trait is dependent on heritability, genetic association with other important traits, generation interval and accuracy and intensity of selection. For improved enterprise profitability, the focus of genetic evaluation and selection in breeding programs is typically on economically important production traits (e.g. weight, fertility and carcass) but the breeding objective of an enterprise can change to align with market specifications and the production environment.

Genetic improvement of reproductive traits by within-herd selection in Australian beef herds has previously been demonstrated. Hetzel *et al*. (1989) reported a 12% increase in pregnancy rate over 3 years in divergent lines of Droughtmaster cattle selected for high and low pregnancy rate EBV in north Queensland. That study also reported a correlated response of increased scrotal circumference in young bulls at 600d (Mackinnon *et al*. 1990). It was suggested that shorter periods of post-partum anoestrus contributed to the improved fertility of the 'high' line and that accelerated sexual maturity in both heifers and bulls occurred as a result of the selection for cow fertility.

Schatz *et al*. (2010) demonstrated increased pregnancy rates in yearling-mated Brahman heifers at Katherine in the Northern Territory. Sires from dams with high reproductive score were selected for a balanced combination of growth, scrotal circumference and semen quality traits. After 10 years of selection, yearling mated heifers from the selected herd had an average 35% higher pregnancy rate than contemporaries sourced from commercial properties. A consequence of that selection was lower EBVs for days to calving (-5d) and larger yearling scrotal size (+2cm) for that herd when compared with the Brahman breed average for those recorded traits.

In recent years genetic evaluation in beef breeds has adopted the technology of genomics to help improve the accuracy of selection. More accurate EBVs, particularly for the more difficult to measure traits, will allow greater intensity of selection and thus increase the rate of genetic improvement. The following section provides further details on the use of genomics to enhance genetic evaluation.

2.2.2 Genomics

Genomic selection was proposed for cattle breeding by Meuwissen *et al*. (2001). Genotyping of an individual provides information on single-nucleotide polymorphisms (SNPs) from up to 800K genomic regions across the whole genome to compare the DNA sequence with other individuals. SNPs allow mapping of quantitative trait loci (QTL), the sections of DNA that correlate with the variation in the quantitative traits (phenotypes). Typically the QTL is linked to the genes that control that phenotype. Genotyping allows accurate parentage and improvement of trait EBV accuracy (Swan *et al*. 2012) and simply requires a hair sample.

Genomic prediction has the potential to improve the accuracy of selection, particularly for the more difficult to measure fertility traits (Hawken *et al*. 2012). For genomic selection to contribute effectively to genetic improvement, however, genotype information has to combine appropriately with traditional pedigree and performance data (Johnston *et al.* 2012). Accuracy of genomic predictions alone for female reproduction traits are generally low (<0.35) so the potential for genomic selection is limited by the number of animals with recorded phenotypes (Zhang *et al*. 2014). Performance records (phenotypes) are still required, at least from reference herds, to continually refine the genomic prediction equations developed from the training population. The reference populations, particularly research herds, can also provide an important resource to record key reproductive component traits (described in section 2.4) with demanding measurement protocols.

Genomic selection has been widely adopted by the dairy industry (Wiggans *et al*. 2017) and continues to be included in the genetic evaluation of beef breeds worldwide (Van Eenennaam *et al*. 2014; Boerner *et al*. 2015). The review of Georges *et al*. (2018) details how genomic selection has contributed to improved genetic progress in several livestock species over the past decade and how improvements in cost-effective collection of genomic information will increase future contributions of genomic selection to genetic improvement of production traits measured in livestock.

2.3 Genetic parameters

The genetic parameters for a trait usually refer to heritability and genetic correlation. Heritability is an estimate of the proportion of total variation in a phenotypic trait in a population due to additive gene action (inheritance). Genetic correlation is an estimate of the additive genetic variance shared by two traits. The statistic of heritability is expressed

on a scale from 0 to 1 with most traits somewhere between 0.1 and 0.8. Low heritability generally refers to estimates between 0 and 0.2; moderate estimates in the range of 0.2 to 0.5 and estimates above 0.5 are generally considered high. Response to selection will be greater for traits with higher heritability. Genetic correlation between traits is expressed on a scale of -1 to +1 and traits with high estimates of genetic correlation (e.g. absolute values greater than 0.7) are likely to be controlled by the same genes and hence selection for one will have a correlated response in the other. Estimates of genetic correlation with a negative value indicate that genetic change for the two traits will be in opposite directions which in some cases is favourable (e.g. fewer days to calving and higher pregnancy rate).

2.4 Reproductive component traits

The focus of the following sections will be to review information on genetic parameters published for traits measurable early in life and those with potential to be alternative selection criteria for improving reproductive performance. The objective is to identify gaps in the knowledge of reproductive trait measurement and genetic evaluation in tropical beef breeds.

2.4.1 Age at puberty

The age at which an animal becomes sexually mature and capable of fertilisation is measurable in both females and males. Puberty in female cattle is generally defined as the age at which a heifer first displays oestrus, develops a dominant follicle and ovulates a viable ovum. In male cattle, puberty can be defined as the age at which spermatogenesis occurs and the individual can provide an ejaculate with sufficient quantity and quality of sperm cells (e.g. 50 x 10^6 sperm with a minimum of 10% motility) to enable fertilisation. A complex network of biochemical processes influenced by both nutrition and genetics regulates the onset of puberty in both sexes (see Kenny *et al*. 2018).

2.4.1.1 Females

Age at puberty in females is associated with oestrus, ovulation and the development of an ovarian *corpus luteum* (CL) with a typical lifespan. To accurately record age at puberty, the time of first oestrus and development of the first ovarian CL must be established. Development of an ovarian CL is associated with an increase in levels of circulating progesterone and measures of age at puberty have relied on repeated blood sampling and assaying techniques to indicate elevated plasma progesterone titres (Post and Reich 1980;

Mialon *et al*. 2001). Repeat blood sampling of pre-pubertal females in extensively managed beef herds to determine progesterone levels, however, would be costly and difficult to implement.

Studies have reported heritability for age at puberty, determined by visual observation of standing heat, in *Bos taurus* breeds of beef cattle (MacNeil *et al*. 1984; Gregory *et al*. 1995) to range from 0.31 to 0.61 and one study reported a heritability of 0.42 for age at puberty for Brahmans (Vargas *et al*. 1998). There is a paucity of information on the genetic correlation between age at puberty and measures of lifetime reproductive performance. The studies reporting heritability of heifer age at puberty were conducted in herds located in the USA and Europe (Vargas *et al*. 1998; Mialon *et al*. 2001). There is a need to provide estimates of genetic parameters of age at puberty in Australian tropically adapted beef breeds to be able to effectively contribute to genetic evaluation.

2.4.1.2 Males

Establishment of the age at which young bulls in the population can first produce an ejaculate with 50 x 10^6 sperm with a minimum of 10% motility would indeed be an arduous task and grossly impractical. Age at puberty in males, however, is associated with testis size and the measure of scrotal circumference is regarded as an indicator of puberty in male cattle (Lunstra *et al.* 1978). Spermatogenesis requires a critical mass of testicular tissue with mature Sertoli cells in the seminiferous tubules (Sharpe *et al*. 2003; Rawlings et al. 2008) hence testis size in peri-pubertal bulls is considered a more accurate indicator of puberty in male cattle than either age or weight of the individual (Brito 2014). Scrotal circumference at puberty has been reported to average between 24 cm and 26 cm in *Bos indicus* breeds (Trocóniz *et al*. 1991). Scrotal circumference is moderately to highly heritable and genetically correlated with age at puberty in female relatives (Brinks *et al*. 1978; Martinez-Velázquez *et al*. 2003) and with other measures of female reproductive efficiency (Toelle and Robinson 1985; Martinez-Velázquez *et al*. 2003).

Scrotal circumference is relatively easy to measure and is the male fertility trait evaluated in Australia through BREEDPLAN. Despite this, there is a paucity of information on breed and age of measurement differences in the genetic parameters of scrotal circumference measured in Australian tropical breeds. Knowledge of likely differences in age of measurement, for example, will help improve the accuracy of genetic evaluation.

2.4.2 Semen quality

Fertilisation in cattle depends on thousands of motile, morphologically normal sperm cells arriving at the fallopian tube shortly after ovulation to break down the corona of the egg and penetrate the zona pellucida to allow fertilisation (Sutovsky 2018). Hence, it is logical that selection of sires with high quality semen will favour increased fertilisation rates in cattle herds. Earlier research has shown that using bulls with higher per cent normal sperm improves early breeding-season pregnancy rates (Holroyd *et al*. 2002*a*).

Heritability estimates for semen quality traits have been published for temperate beef breeds (e.g. Kealy *et al*. 2006; Garmyn *et al*. 2011) and for the tropical Nellore breed (e.g. Dias *et al*. 2008; Silva *et al*. 2011). Schatz *et al*. (2010) demonstrated that using percent normal sperm in an index to select young bulls improved heifer pregnancy rates in a Brahman herd. There is, however, no published information on the genetic relationships between aspects of semen quality and female reproductive traits. There is a need for genetic parameter estimates for semen quality traits in young post-pubertal Australian beef bulls to determine the value of these traits as genetic indicators of herd reproductive performance.

2.4.3 Circulating blood hormones in males

Other traits linked to aspects of male fertility and measurable in pre-pubertal bulls include circulating blood hormones such as testosterone, inhibin, luteinising hormone (LH) and insulin-like growth factor-1 (IGF-I). Aside from their links to spermatogenesis (Phillips 2005) and onset of puberty (Bagu *et al*. 2006), respectively, little is known of the genetic parameters of inhibin and LH. Heritability of testosterone levels in tropical Composite bulls at 9 and 18mths of age was reported to be 0.42 and 0.55 by Mackinnon *et al*. (1991). IGF-I has been linked to scrotal and semen traits (Yilmaz *et al*. 2004) and reported to be moderately heritable in Angus cattle (Moore *et al*. 2005). Since they could be measured early in life at a time convenient to herd management (e.g. branding/weaning), these blood hormones have potential to be useful alternative selection criteria if found to be genetically related to female reproductive performance. Research to estimate genetic parameters for blood hormones in Australian tropical breeds is warranted.

2.4.4 Pregnancy and calving traits

Heifer pregnancy rate is a record of the young female's first mating outcome and may be a predictor of lifetime performance. Estimates of heritability for yearling heifer pregnancy

rate in herds with managed breeding periods have ranged from low (0.13) in American Angus (Bormann *et al*. 2006) to high (0.66) in Brazilian Nellore (Eler *et al*. 2006) herds. Breed differences in heritability of pregnancy rate likely reflect different incidence of recorded pregnancy. In the studies cited, pregnancy rate was higher in the Angus study (93%) compared to the Nellore study (15%).

Days to calving (DTC) is calculated as the number of days from exposure to the bull to calving and is currently the only female fertility trait evaluated for north Australian herds through BREEDPLAN. Previous estimates of heritability reported for Australian Angus (0.11; Johnston and Bunter 1996) and Brahman (0.09; Meyer *et al*. 1990) herds in Australia have generally been low.

A return to normal oestrus cycles after calving signifies the end of the post-partum anoestrus interval (PPAI) which can be measured using the same strategies as for measuring age at puberty. The ability to return quickly to normal oestrus provides the cow with a better chance of reconception (Burns *et al*. 2010). In a study of French Charolias cows, Mialon *et al*. (2000) reported moderate (0.35) heritability for PPAI. There is little published information on genetic correlation of the pregnancy and calving traits with lifetime reproductive performance measured in Australian tropically adapted breeds.

2.5 Technologies to improve trait measurement

Advances in sensing devices using sound waves, such as ultrasound and ultra-high frequency radio waves, have the potential to accurately and, in some cases, autonomously record reproductive events in cattle. Biotelemetry has the added benefit of reducing labour input and associated health and safety risks involved with trait recording.

2.5.1 Ultrasound

Ultrasonic imagery can be used in livestock to evaluate the reproductive tract and determine stage of pregnancy (Ginther 2014). In studies reporting heritability of heifer age at puberty and PPAI, the traits were determined by daily observations of oestrus or repeat blood sampling and progesterone assaying techniques (Mialon *et al*. 2001). These methods of oestrus determination are time consuming, prone to inaccuracy and not practical for commercial beef enterprise management. Measurement of both age at puberty and PPAI in cattle, however, could be made if accurate detection of an ovarian CL was possible. Ultrasonography has been used to identify ovarian structures (Pierson and Ginther 1988)

and so should be investigated as a method of determining the age at which a heifer first develops a CL and the return to cyclic ovarian activity in post-partum cows.

2.5.2 Radio-frequency identification (RFID)

RFID in cattle has been mandatory in Australia since 2005 and the technology has increased the potential of improving productive efficiency in the beef industry. Walk-over-weighing (WoW) systems have been developed where animals are encouraged to access watering points via a race over a weighing platform (Charmley *et al*. 2006). The WoW systems typically include RFID readers so individual weights can be recorded. The RFID readers can be coupled with a computer and modem to live-stream the data via communication networks to a server. Data handling platforms provide a means of data storage, analysis and reporting. The sequence of individuals passing over the weigh platform to access water could also provide insight into relationships among individuals. The associations detectable by RFID sequence could include familial relationships (e.g. dam and calf) and sexual behaviour (e.g. oestrus female and bull). Studies in sheep flocks using RFID sequence (Richards and Atkins 2007) have demonstrated the utility of temporal proximity of ewes to their lambs to autonomously determine maternal parentage. Examination of algorithms to test the utility of RFID sequence in cattle to detect maternal parentage and possibly cows in oestrus when followed closely by a bull through a WoW system should be considered.

2.5.3 Proximity loggers

Collars with UHF transceivers (proximity loggers) have been developed to log pair-wise contacts between conspecifics or between individuals and watering points or nesting sites. In wildlife studies, this data provides information to help manage endangered populations (Drewe *et al*. 2012; Sanchez *et al*. 2015). In cattle herds, contacts with conspecifics, particularly cows and calves, can identify maternal parentage (Swain and Bishop-Hurley 2007). Logged contact data can also provide information on changed behaviour such as the increased interaction of individuals forming sexually active groups during oestrus. O'Neill *et al*. (2014) showed that the number and duration of bull-cow contacts recorded by proximity loggers was significantly greater in oestrus cows compared to anoestrus cows. Increased activity during oestrus recorded by the proximity loggers has the potential to determine age at puberty in heifers and post-partum anoestrus intervals in cows. Automated oestrus detection has implications for measurement and genetic evaluation of reproductive efficiency.

Conceptually, biotelemetry has the capacity to accurately record growth, adaptation and reproductive performance of livestock. In reality, logistical constraints to installation, spatial constraints to data transfer and temporal constraints to power supply have meant that the technologies have not yet reached full commercial application.

2.6 Research questions

In summary, improving reproductive efficiency in tropical beef breeds is important for the productivity and profitability of Australian beef enterprise. There are gaps, however, in the knowledge of genetic parameters for indicator traits that could potentially provide a more efficient means of identifying elite genetic material. Additionally, and possibly as a consequence, uptake of genetic evaluation technology to provide more accurate estimates of individual genetic merit by the beef industry is slow. In response to these knowledge gaps the following research questions have been formulated:

1. What are the genetic parameters of key component traits of reproduction in Australian tropical breeds; are they heritable, and are they genetically related to lifetime reproduction?
2. Can new and developing technologies be used to more simply and accurately provide measures of reproductive traits for genetic evaluation?

Chapter 3. Genetics of Heifer Puberty

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Genetics of heifer puberty in two tropical beef genotypes in northern Australia and associations with heifer-and steer-production traits

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Abstract. A total of 2115 heifers from two tropical genotypes (1007 Brahman and 1108 Tropical Composite) raised in four locations in northern Australia were ovarian-scanned every 4–6 weeks to determine the age at the first-observed corpus luteum (CL) and this was used to define the age at puberty for each heifer. Other traits recorded at each time of ovarian scanning were liveweight, fat depths and body condition score. Reproductive tract size was measured close to the start of the first joining period. Results showed significant effects of location and birth month on the age at first CL and associated puberty traits. Genotypes did not differ significantly for the age or weight at first CL; however, Brahman were fatter at first CL and had a small reproductive tract size compared with that of Tropical Composite. Genetic analyses estimated the age at first CL to be moderately to highly heritable for Brahman (0.57) and Tropical Composite (0.52). The associated traits were also moderately heritable, except for reproductive tract size in Brahmans (0.03) and for Tropical Composite, the presence of an observed CL on the scanning day closest to the start of joining (0.07). Genetic correlations among puberty traits were mostly moderate to high and generally larger in magnitude for Brahman than for Tropical Composite. Genetic correlations between the age at CL and heifer- and steer-production traits showed important genotype differences. For Tropical Composite, the age at CL was negatively correlated with the heifer growth rate in their first postweaning wet season (–0.40) and carcass marbling score (–0.49) but was positively correlated with carcass P8 fat depth (0.43). For Brahman, the age at CL was moderately negatively genetically correlated with heifer measures of

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bodyweight, fatness, body condition score and IGF-I, in both their first postweaning wet and second dry seasons, but was positively correlated with the dry-season growth rate. For Brahman, genetic correlations between the age at CL and steer traits showed possible antagonisms with feedlot residual feed intake (–0.60) and meat colour (0.73). Selection can be used to change the heifer age at puberty in both genotypes, with few major antagonisms with steer- and heifer-production traits.

Additional keywords: beef, fertility, puberty, ultrasound, heritability, genetic correlations.

Introduction

Improved female reproductive performance of beef breeds in northern Australia is an important means of increasing profitability (Taylor and Rudder 1986). Several studies have shown that breed differences exist for female fertility traits of tropical genotypes in northern Australia (e.g. Mackinnon *et al*. 1989; Prayaga 2004). The review of Davis (1993) identified significant within-breed genetic differences for female reproduction traits related to calf output, and results from a large divergent selection study for pregnancy rate in a tropical beef herd generated significant differences in pregnancy rate between the high and low lines (Hetzel *et al*. 1989; Mackinnon *et al*. 1990; Davis *et al*. 1993). However, industry-wide improvement of female reproductive performance by genetic selection has generally proved difficult, mainly because of low heritabilities and the late expression of traits, and difficulties in capturing the necessary joining and reproductive data. Currently, female fertility traits are generally not included in beef genetic-evaluation schemes worldwide, except for days to calving in Australia (Graser *et al*. 2005) and heifer pregnancy percentage in the USA (Evans *et al*. 1999). Therefore, inclusion of female fertility traits into beef genetic-evaluation systems may require identification of new traits that can be recorded early in life, are heritable and genetically correlated with the underlying profit trait.

One possible contributor to the observed genetic differences in female reproductive performance is the age at puberty. Breed differences have been reported for the age and weight at puberty (Gregory *et al*. 1991; Burns *et al*. 1992; Martin *et al*. 1992; Thallman *et al*. 1999) and specifically, *Bos indicus* breeds (e.g. Brahmans) have been reported to be older at puberty than other breeds (Gregory *et al*.

1979; Morgan 1981; Bolton *et al*. 1987; Hearnshaw *et al*. 1994; Thallman *et al*. 1999). Several studies have shown that the age at puberty was heritable in *Bos taurus* breeds of beef cattle (MacNeil *et al*. 1984; Gregory *et al*. 1995). Limited estimates exist for *Bos indicus* genotypes, although in a small study, Vargas *et al*. (1998) reported a heritability of 0.42 for the age at puberty for Brahmans. For the age at puberty to be useful in a genetic-evaluation scheme it needs to be genetically correlated with female reproductive traits measured in industry herds. However, results are inconclusive. Several studies have shown improved pregnancy or calving rates to be associated with the age at puberty (Laster *et al*. 1979; Morris *et al*. 2000; Phocas and Sapa 2004) and Mackinnon *et al*. (1990) postulated the selection response in female fertility in a divergently selected tropical beef herd was likely due to earlier sexual maturity. Mialon *et al*. (2001) showed a positive genetic correlation between the age at first oestrus and the postpartum return to oestrus interval. However, others (e.g. Dow *et al*. 1982; Martin *et al*. 1992; Patterson *et al*. 1992) have reported no relationship, or unfavourable relationships.

Measuring heifer age at puberty in beef cattle is challenging, particularly on large numbers required for genetic analyses. The two most common methods used to determine the heifer age at puberty are oestrus observation and progesterone assays. Recently, ultrasonography has been used to measure ovarian activity, in particular follicular size and the occurrence of a *corpus luteum* (CL) in livestock, including cattle (Pierson and Ginther 1988; Griffin and Ginther 1992; Garcia *et al*. 2002), and consequently could be a practical means for determining puberty in large numbers of heifers. An alternative approach of reproductive tract scoring has also been proposed for pubertal detection in yearling heifers (Andersen *et al*. 1991, as cited by Martin *et al*. 1992). The present paper reports results from a large breeding project which aimed to estimate genetic components of whole herd profitability in northern Australia, and to improve production efficiency and product quality, without compromising female performance or adaptation. The primary aim of the present study was to estimate genetic parameters for puberty traits by ovarian ultrasound scanning in two tropical beef genotypes raised in production environments of northern Australia. The study also aimed to estimate genetic relationships between heifer puberty traits and production traits of both heifers and steers, including liveweight and body composition, steer

feed intake, net feed intake, and carcass- and meat-quality traits.

Materials and methods

Animals

Females used in the present study were part of a northern Australia breeding project of the Cooperative Research Centre for Cattle and Beef Quality (CRC; Burrow *et al*. 2003). Ethics approval was provided by Rendel Laboratory AEC under RH198/04. Brahman (BRAH) and Tropical Composite (TCOMP) breeds were used, these each being widely used in the subtropical and tropical regions of northern Australia. The TCOMP genotype animals comprised ~50% tropically adapted breeds and 50% non-tropically adapted *Bos taurus* breeds. On average, the 50% tropically adapted component was approximately one-half derived from the *Bos indicus* (viz. Brahman) and one-half from tropically adapted Taurine breeds (viz. 24% Africander and 2% N'Dama, through the Senepol). A complete description of the TCOMP genotype by property of origin is presented in Barwick *et al*. (2009*a*).

The cattle were bred in northern Australia on seven cooperator properties (four BRAH and three TCOMP) and at the 'Belmont' Research Station (both BRAH and TCOMP). Calves were generated by artificial insemination (AI) and natural service. At each property of origin, calf sex, date of birth, dam identification number and dam year of birth were recorded. Sire parentage was determined by DNA fingerprinting. Genetic linkage, across properties of origin and year within a genotype, was generated by AI. Full genetic-linkage statistics for the heifer data are presented in Barwick *et al*. (2009*b*).

Heifer allocation and management

Calves were generated during 4 and 3 years for BRAH and TCOMP, respectively. After weaning each year (average age 6.4 months), the complete calf crop for the project from each property of origin was delivered to the control of the project. Heifers were allocated according to the genotype, property of origin and sire to one of the following four Queensland research stations: 'Brian Pastures' (BRIANP), 'Swans Lagoon' (SWANS), 'Belmont' (BELMONT) or 'Toorak' (TOORAK) research stations (see Table 3-1). Distribution of BRAH heifers was proportionally greater to the harsher environments (SWANS and BELMONT), whereas TCOMP were allocated in greater numbers to the more benign locations (i.e. TOORAK and BRIANP). No BRAH heifers were allocated to BRIANP and no TCOMP heifers were allocated to SWANS. At BELMONT, the BRAH and TCOMP

heifers that were born and located there were managed as contemporaries throughout the experiment. Further details of heifer management and of the postweaning heifer locations are given by Barwick *et al*. (2009*b*).

At each location, all heifers of the same year of birth were managed as a single group (defined as a cohort). Each cohort was grown out at pasture and joined at ~27 months (i.e. to have the first calve as 3-year olds). Slight differences (i.e. less than 2 months) existed in the commencement date of joining across locations within a year, reflecting regional management preferences.

Ovarian measures and measurement procedures

Ovarian scanning

Ovarian activity was assessed in heifers by real-time ultrasound scanning performed by one of four trained operators. At scanning, each ovary was viewed by ultrasound imaging (Aloka SSD-500; Corometrics Medical Systems, Wallington, CT, USA, with linear array 7.5 MHz rectal transducer; or Honda HS-2000V; Honda Electronics, Toyohashi City, Japan, with variable-frequency transducer set at 10 MHz) and the presence of a CL or *corpus albicans* (CA) was recorded. An experienced ultrasonographer provided training in ovarian scanning.

Assessment of ovarian activity commenced for a cohort when heifers reached ~200-kg liveweight at 10–12 months of age. Assessments were conducted at intervals of between 3 and 12 weeks, with most being 4–6 weeks. Intervals closer to the start of the assessment (i.e. the first 4 months) for a cohort tended to be longer (approximately every 8 weeks), coinciding with the first 'dry' season that heifers experienced after weaning. Following this early period, and coinciding with the 'wet' season, the measurements became much more frequent (average interval of 4.6 weeks) and continued for a further 15 months. Some exceptions occurred because of seasonal conditions and availability of technicians. In the 2001 cohorts, assessments were temporarily discontinued following the detection of the first CL or CA.

Reproductive tract size

Reproductive tract size was recorded on heifers when the average cohort age was ~1.5 years, and again 6 months later prior to their first joining. Diameter of the uterine horn proximal to the bifurcation was estimated by manual palpation. The system used was similar, but not identical, to the system described by Andersen *et al*. (1991), as cited by Martin *et al*. (1992).

Table 3-1 Numbers of heifers allocated after weaning to each location by genotype and birth year

Year	Location				
	SWANS	BELMONT	TOORAK	BRIANP	Total
		Brahman genotype			
2000		73			73
2001	188	111	65		364
2002	209	119	101		429
2003	42	124			166
Total	439	427	166	0	1032
		Tropical Composite genotype			
2001		113	160	146	419
2002		140	184	272	596
2003		48		79	127
Total	0	301	344	497	1142

Liveweight and fatness measures

All heifers were weighed, ultrasound-scanned for fat depth at the P8 site (Perry *et al*. 2001) and body condition scored (Barwick *et al*. 2009a) at the time of ovarian scanning. Assessors across all locations were trained before the commencement of the study to ensure consistency of all measures and scores. Periodic checks also occurred throughout the experiment to maintain standards.

Trait definitions

For each individual heifer, the age at CL (AGECL) was defined as the age (in days) of the heifer at the first-observed CL (or CA) and was used as an estimate of puberty (i.e. the first confirmed evidence). The date of the first CL for each heifer was then used to identify other measures recorded on the heifer at this time (or within 7 days) and included heifer liveweight at first CL (WTCL), ultrasound scan P8 fat depth at first CL (FATCL) and body condition score at first CL (CSCL) (see Table 3-2). Three additional traits were defined by first identifying the date of the commencement of the first joining period for each heifer cohort. Reproductive tract size (TSIZE) assessed on average 20 days before the commencement of joining was used with the exception of one BRAH cohort ($n = 41$) where the scoring occurred 7 months before joining. The other two traits were binary scores that simply classified each heifer (yes = 1, no = 0), regarding the observation of a CL. The first trait was defined as the observation of a CL or CA at any time before, or on, the day of scanning closest to the commencement of joining (CLPRIOR) The second trait was a subset of the first and was defined as the observation of CL or CA on the day of scanning closest to the start of the joining period (CLJOIN)..

Table 3-2 Description of heifer puberty measures

CA, corpus albicans; CL, corpus luteum

Code	Trait	Description
AGECL	Age at first CL (days)	Number of days from birth to the first CL or CA on either the left or right ovary, observed by real-time ultrasound scan
WTCL	Weight at first CL (kg)	Heifer liveweight on the day (or within 7 days) of the first-observed CL or CA
FATCL	Fat depth at first CL (mm)	Heifer ultrasound P8 fat depth on the day (or within 7 days) of the first-observed CL or CA
CSCL	Condition score at first CL	Subjective score of body condition on a 15-point scale: 1, Poor; 2, Backward; 3, Forward; 4, Prime, 5, Fat with + and – for each level, scored on the day (or within 7 days) of the first-observed CL or CA; for analysis, the scores were recoded 1–15
TSIZE	Reproductive tract size (mm)	Subjective diameter of the uterine horn, proximal to the bifurcation, by manual palpation; measurements were recorded before the first day of joining
CLPRIOR	Presence of a CL or CA into first mating	The presence (=1) or absence (=0) of a CL or CA at any time before, or on, the scanning day closest to the first day of joining (i.e. the first bull-in date)
CLJOIN	Presence of a CL or CA on the scanning day into mating	The presence (=1) or absence (=0) of a CL or CA on the scanning day closest to the first day of joining

Scan CL-data editing

Checks were performed on all records before analyses. Records from heifers that were sick or unable to be ovarian-scanned (n = 4) and those from heifers who were pregnant without being identified as having a prior CL (n = 6) were removed. Within each cohort, AGECL records more than three standard deviations from the mean were removed (n = 14). A small number (n = 10) of BRAH heifers did not have their first CL observed by the time of analysis, despite being >26 months of age. These received a penalty AGECL record based on the last scanning date at their location plus 30 days.

Heifer growth and composition measures

Heifer growth and body composition traits studied included measures recorded on each heifer at the end of their first postweaning 'wet' season (ENDWET) and at the end of their second postweaning 'dry' season (ENDDRY), and corresponding to heifer ages of ~18 and 24 months, respectively. These measures were described by Barwick *et al*. (2009*b*) and included liveweight (LWT), ultrasound-scanned fat depth at the P8 site (SP8) and over the 12/13th rib (SRIB), scanned area of the *M. longissimus thoracis et lumborum* (LTL) at the 12/13th rib (SEMA), body condition score (CS), hip height (HH), concentration of the insulin-like growth factor I (IGF-I) in serum and average daily liveweight gain (ADG). ADG was computed by individual animal regressions of liveweight on days for multiple weights recorded during the 6-month period defined for both ENDWET and ENDDRY.

Steer growth, and carcass- and meat-quality measures

Records taken on the steer paternal half-sibs of the heifers were used to investigate relationships between heifer measures of puberty and steer production, and carcass- and meat-quality traits. The growth, body composition and feed-intake traits examined are described by Barwick *et al*. (2009*a*) and include measures of feed intake collected during the feedlot finishing phase and measures recorded at feedlot exit (EXIT). In brief, steers (n = 2216) were managed in 12 postweaning grow out groups and entered the feedlot at ~400 kg liveweight. They were fed for an average of 119 days on a high-energy feedlot ration and slaughtered at an average liveweight of 568 kg. Measures recorded on steers included LWT, HH, SEMA, SP8, SRIB, CS, IGF-I, scanned percent intramuscular fat (SIMF), daily feed intake (DFI), residual feed intake (RFI) and feed-test average daily gain (ADG).

Steers were slaughtered in one of two commercial abattoirs where several carcass measures were recorded and meat sample was removed from each carcass for subsequent carcass meat- quality measures. Abattoir carcass measures (CARCASS), described by Wolcott *et al*. (2009), included hot carcass weight (CWT), cold P8 fat depth (P8c), bone-out retail beef yield percentage (RBY) and Meat Standards Australia (MSA) measured rib fat depth (RIB), eye muscle area (EMA), marbling score (MS), ossification score (OSS) and hump height (HMP). Measures of meat quality were all performed on the LTL muscle sample from the Achilles hung side of the carcass (see Wolcott *et al*. (2009) for a complete description) and included intramuscular fat percentage (CIMF), shear force (SF_A), compression (CMP_A), cooking loss (LOSS_A) and Minolta L* meat colour (L*).

Statistical analyses

Fixed-effect modelling

Significant fixed effects for each heifer puberty trait were identified by the mixed-model procedure in SAS (SAS Institute, Cary, NC, USA). Analyses were first performed separately for each genotype. All initial models included the independent variables of heifer's birth month, cohort, property of origin and age of dam, and for TCOMP also terms for sire group and dam group (Barwick *et al*. 2009a). Birth month of the heifer was included to account for differences in both age and seasonal conditions across the calving period, as the average calving period was 4–5 months within an origin, and differences occurred in the starting calving month across origins. Within a cohort and origin

subclass, any adjacent birth months that had less than five animals were combined. Age of dam was recorded in years, and when unknown (~15%) was assigned to be the median for the origin. For TCOMP, sire group, dam group (nested within origin) and their interaction were modelled to account for average additive differences between the composite groups and possible differences in the level of non-additive effects in differing combinations of sire groups and dam groups. Sire was included in all models as a random effect. Initial models for each trait included main effects and all first-order interactions. Non-significant ($P > 0.05$) terms were sequentially removed to yield the final models for each trait. Final models for BRAH included the effects of cohort and birth month for all traits. Origin was significant for all traits except for WTCL and FATCL. The age of dam was significant only for AGECL and WTCL. Interactions between some of these main effects also were significant, mainly interactions with origin. For TCOMP, final models included cohort and origin for all traits. Birth month was significant for all traits except FATCL. Sire group and dam group were significant for AGECL and CLJOIN, and dam group also for TSIZE and CLPRIOR. Interaction terms were also significant, mainly those with cohort.

Significant fixed effects were also identified for each trait by using a combined dataset for BRAH and TCOMP. These models initially included all the significant effects identified above for each genotype, with the addition of terms for genotype and all first-order interactions of effects with genotype. Each model was reduced by removing non-significant ($P > 0.05$) effects to yield the final model for use in the combined-genotype analyses.

Variance component estimation

Additive genetic variances and heritabilities for the seven heifer puberty traits were estimated in univariate analyses for BRAH and TCOMP separately, by using restricted maximum likelihood procedures in ASReml (Gilmour *et al*. 1999). All traits were analysed by using an animal model that included the set of fixed effects identified with SAS and random effects of animal and residual. For each trait, analyses were performed with and without a random maternal common environmental effect, and the best fitting model was determined by a log-likelihood ratio test. A relationship matrix ($n = 8640$) was used that contained up to three generations of both paternal and maternal pedigree when known. In total, 54 BRAH and 51 TCOMP sires were represented, and across both genotypes there was a total of 51 sires

having 20 or more daughters with AGECL records.

Genetic correlations among pairwise combinations of the seven puberty traits were estimated in a series of bivariate analyses with ASReml for each genotype separately, by using models described above. Genetic correlations were also estimated in bivariate models between the seven puberty traits and the groups of heifer (i.e. ENDWET and ENDDRY) and steer (i.e. EXIT and CARCASS) production traits. Models for the steer- and heifer-production traits were described by Barwick *et al*. (2009*a*, 2009*b*) and Wolcott *et al*. (2009).

Model-predicted means

Predicted means for location genotype and birth-month effects, for each of the puberty traits, were computed in ASReml as linear functions of terms included in the model from the combined-genotype dataset by using the procedure described by Gilmour *et al*. (2004). The predicted means were averaged across all other fixed-effect levels present. Data on 15 BRAH heifers born in January were excluded from the prediction of genotype means to avoid averaging across unequally represented birth months. The predicted location X genotype means for the location BELMONT allowed the direct comparison of the two genotypes (i.e. BRAH v. TCOMP) and comprised 297 BRAH and 290 TCOMP heifers, representing 32 and 26 sires, respectively. Because there was a predominance of Belmont Red dams at BELMONT, the TCOMP-predicted means were for a sample of the genotype where the contribution of Africander to the tropically adapted component was higher (i.e. ~40% Africander, 1% N'Dama, 10% Brahman) than existed on average in the whole data. The direct genotype comparison was computed with all BRAH and TCOMP heifers that were born and located at BELMONT. At TOORAK, the comparison of genotypes was confounded with preweaning properties of origin and therefore model-predicted means for each trait at TOORAK were estimated within genotype.

Results and discussion

Summary statistics for each of the puberty traits are presented for BRAH and TCOMP in Table 3-3 and show the mean level and variation in the traits recorded. These summary statistics presented are not adjusted for fixed effects.

Genotype differences

Predicted genotype trait means are presented in Table 3-4 for each of the heifer puberty traits. BRAH heifers at BELMONT were significantly fatter at first CL (i.e. FATCL difference of 1.5 mm and

CSCL of 0.4 score) than were TCOMP at BELMONT. The genotypes were not significantly different for WTCL, AGECL, CLPRIOR and CLJOIN, whereas there was a trend for BRAH to be slightly older at AGECL, with lower percentages for CLPRIOR and CLJOIN, and significantly smaller TSIZE (–1.2 mm). Increased age at puberty in Brahman heifers has been reported in other studies (Gregory *et al*. 1979; Bolton *et al*. 1987; Hearnshaw *et al*. 1994). However, Post and Reich (1980) reported from a small study of mixed tropically adapted breed groups that Brahmans had the youngest age at puberty. Also Burns *et al*. (1992), in a genotype (i.e. Belmont Red) comparable to the TCOMP, reported a heifer average age at puberty of 583 days and weight at puberty of 319 kg, with 88.2% of heifers estimated to be pubertal into joining at 26 months. These differences in the mean performance, compared with our study, could be due to a range of factors such as seasonal differences, location effects and different methods used to determine the age at puberty. Thus, direct comparison of performance across studies is generally not possible.

Location differences

Location had a large effect on most of the puberty traits in each genotype (Table 3-4).

Table 3-3 Unadjusted trait means ± s.d. and ranges for Brahman and Tropical Composite puberty traits

See Table 3-2 for a description of traits

Trait	n	Mean ± s.d.	Min.	Max.
		Brahman		
AGECL (days)	1007	750.6 ± 142.1	394	1211
WTCL (kg)	993	334.4 ± 44.8	196	485
FATCL (mm)	951	4.47 ± 2.19	1.0	15.0
CSCL (score)	951	8.2 ± 1.4	4.0	12.0
TSIZE (mm)	947	13.5 ± 3.8	5.0	25.0
CLPRIOR	1008	0.51 ± 0.50	0	1.0
CLJOIN	978	0.43 ± 0.50	0	1.0
		Tropical Composite		
AGECL (days)	1108	650.8 ± 119.5	344	945
WTCL (kg)	1094	329.6 ± 45.9	206	474
FATCL (mm)	1083	2.90 ± 1.66	0.5	11.0
CSCL (score)	1108	7.2 ± 1.2	3.0	11.0
TSIZE (mm)	1119	16.3 ± 4.8	5.0	30.0
CLPRIOR	1108	0.79 ± 0.41	0	1.0
CLJOIN	1103	0.63 ± 0.48	0	1.0

For TCOMP, AGECL was similar at BRIANP and TOORAK and both were significantly younger than was the case for heifers at BELMONT. For BRAH, heifers at BELMONT and TOORAK were significantly younger at AGECL than at SWANS. These location trends are generally in line with expected environmental differences, on the basis of differences in heifer growth rates and bodyweights across locations. The possible exception was AGECL at TOORAK, where BRAH were older (but not significantly) than at BELMONT. Hearnshaw *et al*. (1994) found large nutrition by genotype interaction effects on the age at puberty, where Brahman growth rate did not respond to increasing nutrition

compared with other genotypes and had extremely low percentages of heifers pubertal at 22 months of age in a subtropical environment.

For TCOMP, there was a positive association between location means for WTCL and AGECL. For BRAH, however, the mean WTCL declined with increasing AGECL. This may indicate a genotype difference, although is more likely to reflect the influence of location on growth rate, particularly the very low dry-season growth rate at SWANS relative to the other two locations. Several studies have shown that differences in growth rates affect both age and weight at puberty. Yelich *et al*. (1995) observed that increased growth rate in Angus X Hereford heifers resulted in decreased age at puberty, increased weight, and also increased fatness at puberty, which supports our findings for BRAH (Table 3-4) although not in TCOMP. Ferrell (1982) reported that slower postweaning growth rate delayed the age at puberty and subsequently reduced pregnancy rates compared with heifers that gained weight rapidly after weaning, suggesting that weight was more important than age in determining puberty. Mackinnon *et al*. (1989) hypothesised that once sexual maturity was reached in Brahman-based breeds there was little effect of increasing weight at mating on subsequent fertility.

No clear trends in predicted location means were observed for FATCL or CSCL, although for TCOMP the BRIANP heifers were significantly leaner at puberty. For BRAH, heifers at SWANS had significantly higher CSCL than those at TOORAK and BELMONT, whereas heifers at BELMONT had significantly higher FATCL than those at TOORAK and SWANS. Hall *et al*. (1995) showed heifers fed to gain faster postweaning were heavier, taller and younger at puberty, and that puberty was independent of body fat.

These results across locations illustrate that puberty in beef heifers is not simply controlled by weight, growth rate or age alone, but appears to involve a combination of factors relating to physiological age, size and growth rate, and probably also involves body condition for BRAH. The large location effects on puberty traits in the present study also highlight that extrapolation of the observed genotype differences beyond the environment in which they were directly compared (i.e. BELMONT) should not be made. TCOMP were purposely not located at SWANS because it was perceived, and accepted by industry, that they would be too poorly adapted to that environment.

Table 3-4 Model-predicted means for heifer puberty traits by location and comparison of Brahman and Tropical Composite genotype at the common BELMONT location

See Table 3-2 for a description of traits. The location effect at TOORAK was considered separately for Brahman (TOORAK_B) and Tropical Composite (TOORAK_C) because of confounding of genotype with the property of origin. Within the BELMONT location (column), trait means followed by different letters indicate significant differences between the two genotypes ($P < 0.05$). Within rows, means followed by different letters indicate significant location differences within a genotype ($P < 0.05$)

Trait	Genotype	Location				
		TOORAK_C	BRIANP	BELMONT	TOORAK_B	SWANS
AGECL (days)	BRAH			724a	750a	805b
	TCOMP	643b	652b	706a		
WTCL (kg)	BRAH			357a	339b	323c
	TCOMP	314c	334b	353a		
FATCL (mm)	BRAH			4.9b	4.3a	4.5a
	TCOMP	3.5a	2.9b	3.4a		
CSCL (score)	BRAH			7.8c	7.3b	8.9a
	TCOMP	7.5a	7.2b	7.4ab		
TSIZE (mm)	BRAH			14.4b	12.5a	13.1c
	TCOMP	14.9c	18.0b	15.6a		
CLPRIOR	BRAH			0.56a	45b	43b
	TCOMP	0.91c	0.79b	0.64a		
CLJOIN	BRAH			0.49a	0.33b	0.37b
	TCOMP	0.70b	0.60a	0.54a		

Significant location effects were observed for TSIZE. However, there were no clear trends in either TCOMP or BRAH. The predicted means for CLPRIOR and CLJOIN showed significant differences across locations with each genotype. Heifers at BRIANP had a predicted CLPRIOR mean of 91% compared with 64% at BELMONT. For BRAH, heifers from SWANS and TOORAK had significantly lower CLPRIOR and CLJOIN than those at BELMONT. The trends observed for TCOMP correspond to the expected average environment differences across locations (Barwick *et al*. 2009*b*). Similarly for Brahmans, the difference in CLPRIOR means for BELMONT and SWANS was as expected. However, the lower than expected percentage with a CLPRIOR at TOORAK most likely reflects small regional differences in the commencement date of joining, where at TOORAK the heifers were on average 30 days younger than at the other two locations.

Birth-month differences

Birth month had a significant effect on all puberty traits (Table 3-5). As the heifer's birth month became later in the calving season (i.e. from August to April) there was a trend for AGECL to increase and TSIZE to decrease. Both FATCL and CSCL increased and there was no observed effect on WTCL. CLPRIOR and CLJOIN

both declined as the birth month became later. On average, early born heifers (i.e. August to September) reached puberty by ~20 months of age, coinciding with the end of their first postweaning wet season (i.e. May). For late-born heifers (i.e. February to March), the average age at puberty was delayed until the following May, at ~26 months of age. This suggests that heifers that did not achieve puberty before the start of their second postweaning dry season were significantly delayed in reaching puberty, which can have a dramatic impact on the number of heifers with a CL into mating. The dramatic reduction in the growth rate that can be experienced during the dry season (Barwick *et al*. 2009*b*) could be a major factor contributing to the delayed onset of puberty in BRAH heifers. Bolton *et al*. (1987) reported a decrease in the percentage of heifers pubertal into joining of fall-born compared with spring-born calves and the effect was more pronounced as Brahman percentage increased. Arije and Wiltbank (1971) observed that reduced pasture availability during winter delayed puberty in Hereford heifers, such that early born heifers were older at puberty when the spring flush occurred. In a study by Burns *et al*. (1992), no significant effect of birth month on the age at puberty was observed, although early born heifers were reported to be heavier at puberty.

Additive genetic variances and heritabilities of heifer puberty traits

AGECL, WTCL, FATCL and CSCL were all moderately heritable (Table 3-6). Additive variances for these traits tended to be larger for BRAH than for TCOMP.

Table 3-5 Model predicted means for heifer puberty traits by month of birth (for combined genotypes)

See Table 3-2 for a description of traits. s.e.d., overall standard error of the difference

Month of birth	AGECL (days)	WTCL (kg)	FATCL (mm)	CSCL (score)	TSIZE (mm)	CLPRIOR	CLJOIN
Aug.	598	341	3.6	8.1	15.3	0.95	0.74
Sept.	618	329	3.5	7.5	18.6	0.91	0.68
Oct.	671	335	3.7	7.6	16.3	0.86	0.67
Nov.	703	336	3.7	7.5	15.8	0.71	0.62
Dec.	719	335	3.6	7.7	14.8	0.54	0.45
Jan.	773	335	4.7	8.3	11.8	0.34	0.31
Feb.	816	332	5.0	8.4	11.1	0.16	0.14
Mar.	854	341	4.6	8.1	10.6	0.09	0.11
Apr.	797	339	4.7	8.5	9.2	0.14	0.10
s.e.d.	20	8	0.4	0.2	0.5	0.07	0.08

Heritability estimates (and approximate standard errors) for AGECL were 0.57 ± 0.12 and 0.52 ± 0.12 for BRAH and TCOMP, respectively, and were slightly higher than a pooled estimate of 0.40 for the age at puberty reported in the review of Martin *et al*. (1992). Our study differed from other reports in that puberty was determined by ultrasound scanning and no literature estimates of heritabilities were found for the age at puberty determined by this technique. The heritability estimates observed provide good evidence that the ovarian ultrasound-scanning technique used, and the frequency with which the observations were taken, were suitable for determining genetic differences in heifer puberty traits. TSIZE was heritable in TCOMP (0.20 ± 0.09) whereas it was lowly heritable in BRAH (0.03 ± 0.06), most likely reflecting the lower average weight and smaller mean reproductive tract size of BRAH (Table 3-6). Martin *et al*. (1992) reported a heritability of prejoining reproductive tract score of 0.28, by using a scoring system that subjectively scored the development of the reproductive tract. We observed the binary traits CLPRIOR and CLJOIN were heritable in BRAH (0.33 ± 0.10 and 0.20 ± 0.09, respectively) whereas they were less heritable inTCOMP (0.13 ± 0.07 and 0.07 ± 0.05), which is likely because the majority of TCOMP heifers had an observed CL before, or on, the day of joining. The genetic variation observed in BRAH for AGECL, CLPRIOR and CLJOIN compared with TCOMP suggests a greater importance of genetic differences in the age at puberty, given the expected influence of these traits on subsequent reproductive performance from their first joining. This is supported by the findings of Phocas and Sapa (2004) who reported a large positive genetic correlation between the percentage pubertal at 15 months and the subsequent calving success in two large European breeds of cattle.

Table 3-6 Additive (σ^2_a) and phenotypic (σ^2_p) variances, heritabilities (h^2) and approximate standard errors (in parentheses) for heifer puberty traits in Brahman and Tropical Composite

See Table 3-2 for a description of traits

Trait	Brahman			Tropical Composite		
	σ^2_a	σ^2_p	h^2	σ^2_a	σ^2_p	h^2
WTCL	981	1755	0.56 (±0.12)	789	1701	0.46 (±0.11)
FATCL	2.41	4.37	0.55 (±0.13)	0.88	2.29	0.39 (±0.11)
CSCL	0.34	5.6	0.22 (±0.10)	0.17	1.02	0.16 (±0.07)
TSIZE	0.12	5.05	0.03 (±0.06)[B]	1.92	9.48	0.20 (±0.09)
CLPRIOR[A]	0.052	0.156	0.33 (±0.10)	0.022	0.131	0.13 (±0.07)
CLJOIN	0.034	0.169	0.20 (±0.09)	0.016	0.222	0.07 (±0.05)[B]

[A]Maternal environmental effect significant for TCOMP.
[B]Traits with h^2 less than 10% were not considered for estimation of correlations.

Relatedness of heifer puberty measures

Genetic correlations among AGECL and the other puberty measures are presented in Tables 3-7 and 3-8 for BRAH and TCOMP, respectively. Correlations were generally in the same direction for BRAH and TCOMP although the size of the correlations tended to be larger for BRAH. Moderate to strong positive correlations were estimated between each of the puberty traits AGECL, WTCL, FATCL, and CSCL. They show that heifers that were older at AGECL were genetically heavier and fatter when they reached puberty. This is likely due to the fundamental association between the age and the weight. The estimates were of magnitude similar to the 0.52 genetic correlation reported by Laster *et al*. (1979) between the age and the weight at puberty. The genetic correlations suggest AGECL, WTCL, FATCL and CSCL are related ways of expressing the same physiological event, and that selection for reduced AGECL would lead to correlated reductions in the other measures. It is likely that AGECL is the trait of most importance to a breeding program because of the annual cycle of beef production, particularly in northern Australia. Genetic differences, or correlated changes, in WTCL may also be important for management considerations, in particular the importance of a minimum heifer weight for natural service mating and also the expected ease of calving.

The moderate heritabilities and additive genetic variances estimated for puberty traits for BRAH and TCOMP suggest it should be possible to change these traits by selection, and studies (Laster *et al*. 1979; Morris *et al*. 2000) have shown the age at puberty to be genetically correlated with measures of reproductive performance of the cow. The prerequisite for this, however, will be the availability of a suitable selection criterion that is heritable and measurable early in life. Although AGECL was heritable, the measurement protocols would most likely preclude its measurement across large numbers of animals in industry herds. However, AGECL was highly negatively correlated with CLPRIOR (–1.0 for BRAH and –0.96 for TCOMP) and CLJOIN (–1.0 for BRAH). These estimates suggest that sires whose daughters were genetically younger at AGECL would have daughters with a higher probability of showing a CL before the commencement of their first joining, and for BRAH, a higher probability of a CL observed on a single scan day close to the start of joining. Therefore, it may be possible to develop a simplified scanning protocol to identify the presence of a CL on the basis of the measures of CLPRIOR

or CLJOIN, which could be incorporated into a genetic-evaluation system.

Another possible indirect measure of the age at puberty was TSIZE in TCOMP. TSIZE measured before the first joining was genetically correlated with CLPRIOR (0.70) and AGECL (–0.58) and lowly correlated with WTCL, CSCL and FATCL. TSIZE could also provide a relatively inexpensive indirect genetic measure of puberty. The opportunity also exists to improve measurement of this trait by incorporating additional features of the uterine tract, ovaries and possibly the presence of a CL. Enhancements to the scoring of TSIZE may also improve the heritability estimate for BRAH.

Genetic predictors of heifer puberty

Other measures recorded on the heifers and steers may also be genetically correlated with AGECL. These may prove useful as indirect selection criteria and also provide estimates of any trait antagonisms that exist with heifer puberty traits. Table 3-9 (BRAH) and Table 3-10 (TCOMP) present estimated genetic correlations of AGECL and associated puberty traits with measures of heifer growth and body composition measures at ENDWET and ENDDRY. Table 3-11 (BRAH) and Table 3-12 (TCOMP) present estimated genetic correlations of AGECL and associated puberty traits with measures of steer EXIT traits.

Growth and muscling measures

Genetic correlations for measurements of LWT and SEMA, expressed at a constant age, showed they were moderately negatively correlated with AGECL in heifers and less so in steers, e.g. LWT at ENDWET –0.33 for BRAH (Table 3-9) and –0.38 for TCOMP (Table 3-10). A similar estimate of –0.32 was reported in Charolais by Mialon *et al*. (2001).

Table 3-7 Genetic and phenotypic correlations among heifer puberty traits for Brahman

See Table 3-2 for a description of traits. Genetic correlations above diagonal, phenotypic below and all estimates from bivariate analyses; approximate standard errors in parentheses; standard errors for phenotypic correlations ranged from 0.02 to 0.03

Trait	AGECL	WTCL	FATCL	CSCL	CLPRIOR	CLJOIN
AGECL		0.84 (0.07)	0.61 (0.12)	0.74 (0.16)	–1.0 (0.04)A	–1.0 (0.12)[A]
WTCL	0.66		0.53 (0.13)	0.63 (0.16)	–0.89 (0.11)	–0.90 (0.18)
FATCL	0.30	0.44		0.51 (0.18)	–0.68 (0.15)	–0.67 (0.19)
CSCL	0.19	0.37	0.57		–0.69 (0.19)	–0.59 (0.24)
CLPRIOR	–0.55	-0.45	-0.28	-0.26		1.0 (0.04)[A]
CLJOIN	–0.39	–0.32	–0.24	–0.24	0.79	

[A]Estimate exceeded bounds.

Table 3-8 Genetic and phenotypic correlations among heifer puberty traits for Tropical Composite

See Table 3-2 for a description of traits. Genetic correlations above diagonal, phenotypic below and all estimates from bivariate analyses; approximate standard errors in parentheses; standard errors for phenotypic correlations ranged from 0.02 to 0.03

Trait	AGECL	WTCL	FATCL	CSCL	TSIZE	CLPRIOR
AGECL		0.68 (0.11)	0.41 (0.18)	0.45 (0.22)	–0.58 (0.20)	–0.96 (0.09)
WTCL	0.68		0.28 (0.19)	0.51 (0.20)	–0.16 (0.24)	–0.76 (0.14)
FATCL	0.22	0.31		0.84 (0.12)	–0.11 (0.26)	–0.67 (0.21)
CSCL	0.13	0.33	0.50		–0.05 (0.32)	–0.57 (0.29)
TSIZE	–0.17	–0.06	–0.01	0.01		0.70 (0.23)
CLPRIOR	–0.53	–0.41	–0.16	–0.09	0.30	

Table 3-9 Genetic correlations between heifer puberty traits and heifer production traits for the end of the first postweaning wet (ENDWET) and the subsequent second dry (ENDDRY) season measurement times for Brahman

See Table 3-2 for a description of traits. ADG, season average daily weight gain; CS, condition score; HH, hip height; IGF-I, insulin- like growth factor-I concentration; LWT, liveweight; SEMA, scanned eye muscle area; SP8, scanned fat depth p8 site; SRIB, scanned 12/13 rib fat. Standard errors are in parentheses

Trait	AGECL	WTCL	FATCL	CSCL	CLPRIOR	CLJOIN
			ENDWET			
LWT	–0.33 (0.17)	0.21 (0.18)	–0.18 (0.20)	–0.04 (0.27)	0.24 (0.21)	0.23 (0.26)
HH	–0.03 (0.19)	0.32 (0.16)	–0.21 (0.19)	–0.01 (0.28)	0.00 (0.22)	0.09 (0.26)
ADG	–0.19 (0.21)	0.18 (0.20)	–0.06 (0.22)	–0.08 (0.29)	0.08 (0.25)	–0.04 (0.30)
SEMA	–0.36 (0.18)	0.12 (0.21)	–0.36 (0.20)	0.31 (0.29)	0.38 (0.22)	0.28 (0.28)
SP8	–0.35 (0.16)	–0.26 (0.17)	0.52 (0.15)	0.19 (0.23)	0.19 (0.20)	0.13 (0.24)
SRIB	–0.29 (0.16)	–0.27 (0.16)	0.28 (0.17)	0.32 (0.22)	0.21 (0.19)	0.21 (0.23)
CS	–0.53 (0.15)	–0.44 (0.16)	0.15 (0.20)	0.33 (0.24)	0.45 (0.19)	0.54 (0.23)
IGF-I	–0.70 (0.13)	–0.67 (0.14)	–0.43 (0.18)	–0.38 (0.25)	0.75 (0.15)	0.96 (0.18)
			ENDDRY			
LWT	–0.20 (0.19)	0.38 (0.17)	–0.23 (0.19)	–0.04 (0.17)	0.21 (0.22)	0.22 (0.26)
HH	–0.03 (0.19)	0.33 (0.17)	–0.10 (0.20)	–0.09 (0.16)	–0.07 (0.22)	–0.23 (0.28)
ADG	0.58 (0.24)	0.56 (0.22)	–0.10 (0.26)	0.03 (0.21)	–0.47 (0.29)	–0.74 (0.39)
SEMA	–0.22 (0.18)	0.19 (0.18)	–0.27 (0.19)	0.34 (0.17)	0.34 (0.20)	0.32 (0.24)
SP8	–0.33 (0.16)	–0.34 (0.17)	0.49 (0.15)	–0.07 (0.17)	0.22 (0.20)	0.21 (0.24)
SRIB	–0.38 (0.15)	–0.41 (0.15)	0.12 (0.17)	0.04 (0.17)	0.15 (0.19)	0.12 (0.23)
CS	–0.43 (0.17)	–0.32 (0.18)	–0.02 (0.20)	0.13 (0.15)	0.34 (0.21)	0.43 (0.24)
IGF-I	–0.43 (0.19)	–0.40 (0.18)	–0.04 (0.22)	–0.01 (0.28)	0.32 (0.24)	0.43 (0.27)

Gregory *et al*. (1995) reported lower correlations of –0.05 and 0.11, respectively, for 12- and 24-month weights and the age at puberty. In general, the genetic correlations between growth measures and CLPRIOR and CLJOIN were low. For TCOMP, weights at ENDWET (0.54), ENDDRY (0.52) and ENDWET ADG (0.61) were positively correlated with TSIZE, as were measures of liveweight in steers (0.49; Table 3-12). Our results indicate that selection for increased heifer weight at ENDWET or ENDDRY would genetically decrease the age at puberty and would also result in a small correlated increase in WTCL. For BRAH, correlations between AGECL and heifer measures of HH were generally low,

although the correlation was positive with steer EXIT HH (0.50; Table 3-11). A genetic correlation of 0.25 between the heifer age at puberty and hip height was also reported in Brahmans by Vargas *et al*. (1998), suggesting for BRAH, that the age at puberty may be influenced by the frame size.

Genetic correlations between growth rate and heifer puberty traits differed between the genotypes and also with the season of measurement (Tables 3-9 and 3-10). For TCOMP, correlations of ADG with AGECL and WTCL were –0.40 and 0.38 at ENDWET, whereas they were 0.08 and 0.49, respectively, at ENDDRY. For BRAH, the correlations were –0.19 and 0.18 at ENDWET, whereas they were 0.58 and 0.56, respectively, at ENDDRY. The genetic correlations between AGECL and steer feedlot ADG were –0.21 and 0.30 for TCOMP (Table 3-12) and BRAH (Table 3-11), respectively. These correlations indicate that within Brahmans, those with the genetic potential for high growth rate (i.e. also larger HH and possibly larger mature size), particularly at ENDDRY, will have genetically older AGECL. This is likely to be a function of the large negative genetic correlations reported by Barwick *et al*. (2009*b*) in these heifers at ENDDRY between ADG and the measures of fatness (e.g. –0.81 with SRIB) and may also be influenced by the negative genetic correlation observed between IGF-I and AGECL.

Martin *et al*. (1992) also concluded that faster-gaining breeds of larger mature size reach puberty at later ages. There is generally evidence, including in tropical genotypes in northern Australia (Burrow *et al*. 1991), that selection for weight gain can lead to genetically improved female reproductive rate. It appears that the season or stage at which the growth rate is measured may be important, as a greater dry-season growth rate in the present study had a detrimental genetic effect on BRAH AGECL. However, Fordyce *et al*. (1988) reported that increasing the rate of weight gain of Brahman cross heifers during the first postweaning dry season increased the probability of conception at 2 years of age.

Table 3-10 Genetic correlations between heifer puberty traits and heifer production traits for the end of the first postweaning wet (ENDWET) and subsequent second dry (ENDDRY) season measurement times for Tropical Composite

See Table 3-2 for a description of traits. ADG, season average daily weight gain; CS, condition score; HH, hip height; IGF-I, insulin- like growth factor-I concentration; LWT, liveweight; SEMA, scanned eye muscle area; SP8, scanned fat depth p8 site; SRIB, scanned 12/13 rib fat. Standard errors are in parentheses

Trait	AGECL	WTCL	FATCL	CSCL	TSIZE	CLPRIOR
			ENDWET			
LWT	–0.38 (0.16)	0.43 (0.15)	–0.09 (0.19)	–0.08 (0.25)	0.54 (0.20)	0.27 (0.25)
HH	–0.24 (0.18)	0.35 (0.16)	–0.35 (0.17)	–0.37 (0.23)	0.12 (0.24)	0.16 (0.26)
ADG	–0.40 (0.18)	0.38 (0.18)	–0.06 (0.22)	–0.19 (0.27)	0.61 (0.22)	0.28 (0.28)
SEMA	–0.33 (0.16)	0.11 (0.19)	0.17 (0.20)	0.28 (0.24)	0.08 (0.24)	0.18 (0.26)
SP8	–0.18 (0.20)	0.01 (0.21)	0.91 (0.08)	0.57 (0.22)	0.24 (0.25)	0.00 (0.29)
SRIB	0.00 (0.21)	0.16 (0.21)	0.85 (0.10)	0.54 (0.24)	0.23 (0.26)	–0.01 (0.29)
CS	–0.02 (0.21)	0.24 (0.21)	0.74 (0.14)	1.00 (0.13)	–0.02 (0.27)	–0.40 (0.31)
IGF-I	–0.36 (0.20)	–0.37 (0.21)	–0.05 (0.24)	–0.49 (0.27)	0.32 (0.27)	0.53 (0.25)
			ENDDRY			
LWT	–0.28 (0.17)	0.47 (0.14)	–0.07 (0.19)	0.07 (0.25)	0.52 (0.21)	0.21 (0.25)
HH	–0.27 (0.17)	0.42 (0.14)	–0.39 (0.16)	–0.39 (0.22)	0.18 (0.23)	0.37 (0.26)
ADG	0.08 (0.24)	0.49 (0.21)	0.07 (0.25)	0.40 (0.28)	0.29 (0.29)	0.06 (0.34)
SEMA	–0.16 (0.18)	0.24 (0.19)	0.30 (0.19)	0.24 (0.25)	0.21 (0.24)	0.16 (0.26)
SP8	–0.07 (0.18)	–0.08 (0.18)	0.86 (0.08)	0.47 (0.23)	0.38 (0.21)	–0.01 (0.27)
SRIB	–0.01 (0.19)	0.05 (0.19)	0.70 (0.13)	0.32 (0.25)	0.26 (0.24)	–0.04 (0.28)
CS	0.03 (0.20)	0.22 (0.20)	0.79 (0.12)	1.00 (0.11)	0.06 (0.25)	–0.33 (0.29)
IGF-I	–0.09 (0.28)	–0.22 (0.27)	0.15 (0.30)	–0.25 (0.36)	–0.30 (0.37)	–0.08 (0.38)

Fatness, condition score and IGF-I

Genetic correlations between heifer puberty traits and body composition measures varied between the genotypes and the various measurement stages. In general, estimates for BRAH (Table 3-9) showed that selection for increased heifer fatness or condition score at either ENDWET (–0.35 for SP8; –0.53 for CS) or ENDDRY (–0.38 for SRIB; –0.43 for CS) would reduce AGECL and also genetically decrease the weight at puberty. Mialon *et al*. (2001) reported a genetic correlation of –0.57 between the age at the first oestrus and yearling body condition score in Charolais heifers. However, these relationships were not observed for steer measures of fat for BRAH (e.g. 0.04 for SP8 at EXIT; Table 3-11), and may reflect genetic correlations in fat measures between sexes that were significantly different from one. For example, the genetic correlations of scan P8 fat depth of the heifers with that of the steers at EXIT were 0.79 and 0.60 at ENDWET and ENDDRY, respectively (Barwick *et al*. 2009*b*). Genetic correlations for TCOMP between AGECL and fatness measures (Table 3-10) were low in heifers (e.g. 0.0 and –0.01 for SRIB at ENDWET and ENDDRY, respectively) and steers (e.g. 0.21, 0.13 at EXIT for SP8 and SRIB, respectively; Table 3-12), suggesting that

selection for increased fatness in TCOMP would have little effect on AGECL or WTCL, whereas it would clearly increase FATCL and CSCL. Gregory *et al*. (1995) also reported no relationship between the age at puberty and condition score.

Values of IGF-I measured in heifers at ENDWET and ENDDRY were both negatively correlated with AGECL, again with estimates for BRAH (Table 3-9) being significantly more negative (i.e. –0.70 ± 0.13 and –0.43 ± 0.19, respectively) than those for TCOMP (–0.36 ± 0.20 and –0.09 ± 0.28, respectively). IGF-I measured in steers at EXIT was negatively genetically correlated with AGECL for TCOMP (–0.58; Table 3-12) but not for BRAH (–0.07; Table 3-11). These results suggest IGF-I may also play a role in the onset of puberty. This is consistent with the review of Wettemann and Bossis (2000) who presented evidence for a role of IGF-I in ovarian function and concluded that reduced levels of IGF-I can cause a cessation of ovulation. However, the reported effect of IGF-I on the onset of puberty in beef heifers is varied. Yilmaz *et al*. (2006) reported no difference in the heifer age at puberty in small numbers (*n* = 51) of Angus divergently selected for IGF-I.. However, Yelich *et al*. (1995) found no significant change in plasma IGF-I at the onset of heifer puberty. The genetic correlations estimated in the present study suggest IGF-I, particularly when measured in heifers at ENDWET, is a good genetic indicator of not only AGECL, but also CLPRIOR, particularly for BRAH (0.75). The utility in a genetic-evaluation system of AGECL, or any of the indirect measures, will depend on their genetic correlation with subsequent measures of female reproductive performance and the direction and magnitude of genetic correlations with other traits of economic importance.

Genetic relationships between steer feed intake, and carcass- and meat-quality traits with heifer puberty traits

In a multiple-trait selection framework it is important to know whether there are sizeable genetic correlations with production and meat-quality traits of the slaughter steer, as well as with aspects of female reproduction. This is particularly so if antagonisms exist that would need to be considered in a selection index. Estimates of genetic correlation between heifer puberty traits and steer exit-feedlot feed-intake measures, and with carcass- and meat-quality (CARCASS) measures are presented in Table 3-11 (BRAH) and Table 3-12 (TCOMP).

Table 3-11 Genetic correlations (± s.e.) between heifer puberty traits and steer feed intake, feedlot exit (EXIT), and carcass- and meat-quality traits (CARCASS) for Brahman

See Table 3-2 for a description of traits. ADG, feedlot average daily weight gain; CMP_A, LTL compression; CS, body condition score; CWT, carcass weight; DFI, average daily feed intake; EMA, MSA eye muscle area; HH, hip height; HMP, MSA hump height; IGF-I, insulin-like growth factor-I concentration; IMF, chemical intramuscular fat %; L*, Minolta L* meat colour; LTL, *M. longissimus thoracis et lumborum*; LWT, liveweight; MS, MSA marbling score; MSA, Meat Standards Australia; OSS, MSA ossification score; P8c, carcass cold P8 fat depth; RBY, bone-out retail beef yield percent; RFI, residual feed intake; RIB, MSA rib fat depth; SEMA, scanned eye muscle area; SF_A, LTL shear force from Achilles hung side; SIMF, scanned intramuscular fat percent; SP8, scanned fat depth P8 site; SRIB, scanned 12/13 rib fat

Trait	AGECL	WTCL	FATCL	CSCL	CLPRIOR	CLJOIN
			EXIT			
LWT	0.09 (0.21)	0.32 (0.19)	0.06 (0.22)	0.13 (0.28)	–0.16 (0.24)	0.08 (0.28)
HH	0.50 (0.18)	0.58 (0.16)	–0.07 (0.21)	–0.10 (0.27)	–0.19 (0.23)	0.11 (0.26)
ADG	0.30 (0.19)	0.33 (0.18)	0.21 (0.20)	0.21 (0.26)	–0.39 (0.20)	–0.27 (0.25)
SEMA	0.12 (0.35)	0.15 (0.34)	–0.53 (0.33)	0.52 (0.45)	–0.02 (0.39)	0.04 (0.45)
SP8	0.04 (0.21)	0.08 (0.20)	0.65 (0.16)	0.19 (0.27)	–0.14 (0.24)	–0.11 (0.28)
SRIB	0.02 (0.19)	–0.12 (0.19)	0.32 (0.19)	0.27 (0.25)	–0.12 (0.22)	0.03 (0.26)
CS	0.26 (0.26)	0.25 (0.25)	0.43 (0.25)	0.13 (0.38)	–0.12 (0.30)	0.09 (0.38)
SIMF	0.26 (0.28)	0.14 (0.28)	0.45 (0.29)	0.41 (0.37)	–0.52 (0.30)	–0.56 (0.34)
IGF-I	–0.07 (0.24)	–0.12 (0.23)	–0.03 (0.26)	–0.27 (0.32)	0.11 (0.27)	–0.05 (0.33)
DFI	–0.02 (0.22)	0.14 (0.21)	–0.04 (0.23)	0.07 (0.28)	0.00 (0.25)	0.10 (0.29)
RFI	–0.60 (0.23)	–0.49 (0.24)	–0.50 (0.24)	0.15 (0.35)	0.84 (0.25)	0.70 (0.32)
			CARCASS			
CWT	0.20 (0.19)	0.39 (0.17)	0.09 (0.21)	0.42 (0.23)	–0.26 (0.22)	0.11 (0.26)
P8c	0.05 (0.21)	0.00 (0.20)	0.66 (0.16)	0.21 (0.28)	–0.10 (0.24)	–0.03 (0.28)
RIB	–0.10 (0.24)	–0.14 (0.23)	0.04 (0.25)	0.12 (0.31)	–0.21 (0.26)	–0.16 (0.31)
EMA	0.04 (0.25)	0.41 (0.23)	–0.19 (0.26)	0.19 (0.33)	–0.02 (0.29)	–0.04 (0.34)
MS	0.19 (0.26)	0.32 (0.26)	0.50 (0.24)	0.58 (0.30)	–0.19 (0.30)	–0.10 (0.35)
OSS	–0.05 (0.19)	–0.37 (0.18)	0.06 (0.20)	–0.11 (0.26)	0.16 (0.22)	0.28 (0.25)
HMP	–0.02 (0.24)	0.15 (0.23)	0.28 (0.24)	0.42 (0.30)	0.01 (0.27)	–0.14 (0.32)
RBY	–0.55 (0.28)	–0.75 (0.21)	–0.09 (0.36)	–0.50 (0.33)	0.66 (0.28)	0.83 (0.28)
IMF	0.06 (0.24)	0.16 (0.23)	0.18 (0.25)	0.21 (0.31)	0.00 (0.27)	0.24 (0.29)
SF_A	–0.16 (0.23)	–0.22 (0.22)	0.19 (0.24)	0.03 (0.26)	0.10 (0.24)	0.11 (0.27)
CMP_A	–0.43 (0.30)	–0.47 (0.24)	–0.05 (0.29)	–0.12 (0.32)	0.26 (0.26)	–0.02 (0.33)
L*	0.73 (0.23)	0.90 (0.18)	0.37 (0.25)	0.74 (0.26)	–0.77 (0.21)	–0.75 (0.24)

Feed intake and residual feed intake

Barwick *et al*. (2009*a*) reported the heritability of DFI and RFI to be 0.49 and 0.24, respectively, for BRAH and 0.51 and 0.38, respectively, for TCOMP. The estimates of genetic correlation between AGECL and DFI were low in both genotypes (Tables 3-11 and 3.-12) and for RFI in TCOMP (Table 3-12). However, for BRAH, RFI was negatively genetically correlated (Table 3-11) with heifer AGECL (–0.60) and was also moderately to strongly correlated with the other puberty traits. These correlations showed that selection for reduced RFI (i.e. improved feed efficiency) in a steer feedlot-finishing test in BRAH would increase AGECL (and WTCL and FATCL) and reduce CLPRIOR. Improved RFI is genetically correlated (–0.61, Barwick *et al*. 2009*a*)

with taller steers at exit for BRAH, and HH at EXIT was positively correlated (0.50) with AGECL in the present study.

Carcass and meat quality

There was little evidence of genetic antagonisms between heifer puberty traits and carcass- and meat-quality measures (Tables 3-11 and 3-12).

Table 3-12 Genetic correlations (± s.e.) between heifer puberty traits and steer feed intake, feedlot exit (EXIT), and carcass- and meat-quality traits (CARCASS) for Tropical Composite

See Table 3-2 for a description of traits. ADG, feedlot average daily weight gain; CMP_A, LTL compression; CS, body condition score; CWT, carcass weight; DFI, average daily feed intake; EMA, MSA eye muscle area; HH, hip height; IGF-I, insulin-like growth factor-I concentration; IMF, chemical intramuscular fat %; L*, Minolta L* meat colour; LOSS_A, LTL cooking loss; LTL, *M. longissimus thoracis et lumborum*; LWT, liveweight; MS, MSA marbling score; MSA, Meat Standards Australia; OSS, MSA ossification score; P8c, carcass cold P8 fat depth; RBY, bone-out retail beef yield percent; RFI, residual feed intake; RIB, MSA rib fat depth; SEMA, scanned eye muscle area; SF_A, LTL shear force from Achilles hung side; SIMF, scanned intramuscular fat percent; SP8, scanned fat depth P8 site; SRIB, scanned 12/13 rib fat

Trait	AGECL	WTCL	FATCL	CSCL	TSIZE	CLPRIOR
			EXIT			
LWT	–0.17 (0.18)	0.61 (0.13)	–0.32 (0.18)	–0.01 (0.25)	0.49 (0.21)	0.29 (0.25)
HH	–0.31 (0.21)	0.42 (0.14)	–0.24 (0.22)	–0.45 (0.26)	0.45 (0.24)	0.39 (0.30)
ADG	–0.21 (0.18)	0.32 (0.19)	–0.31 (0.19)	0.12 (0.26)	0.26 (0.25)	0.25 (0.26)
SEMA	0.02 (0.20)	0.40 (0.19)	0.00 (0.21)	0.25 (0.25)	0.01 (0.25)	–0.12 (0.28)
SP8	0.21 (0.19)	0.36 (0.17)	0.72 (0.12)	0.62 (0.21)	0.10 (0.25)	–0.21 (0.26)
SRIB	0.13 (0.22)	0.38 (0.18)	0.74 (0.13)	0.74 (0.22)	0.40 (0.26)	–0.15 (0.29)
CS	0.30 (0.23)	0.62 (0.18)	0.30 (0.22)	0.26 (0.28)	0.29 (0.28)	–0.08 (0.31)
SIMF	0.01 (0.19)	0.04 (0.18)	0.59 (0.15)	0.33 (0.24)	0.17 (0.24)	0.03 (0.27)
IGF-I	–0.58 (0.18)	–0.55 (0.17)	–0.21 (0.24)	–0.14 (0.29)	–0.39 (0.28)	0.34 (0.29)
DFI	0.10 (0.21)	0.50 (0.17)	–0.13 (0.21)	0.26 (0.27)	0.44 (0.24)	0.21 (0.28)
RFI	0.02 (0.23)	0.11 (0.23)	0.20 (0.23)	0.52 (0.26)	0.16 (0.29)	–0.21 (0.31)
			CARCASS			
CWT	–0.22 (0.20)	0.61 (0.18)	0.05 (0.22)	0.24 (0.26)	0.42 (0.24)	0.22 (0.28)
P8c	0.43 (0.20)	0.64 (0.17)	0.78 (0.12)	0.84 (0.17)	0.04 (0.27)	–0.33 (0.28)
RIB	0.09 (0.25)	0.22 (0.24)	0.31 (0.24)	0.35 (0.30)	0.34 (0.30)	–0.23 (0.32)
EMA	–0.17 (0.23)	0.27 (0.22)	0.06 (0.24)	0.53 (0.26)	–0.06 (0.29)	0.00 (0.31)
MS	–0.49 (0.17)	–0.20 (0.20)	0.10 (0.22)	–0.01 (0.27)	0.19 (0.26)	0.62 (0.23)
OSS	–0.29 (0.19)	–0.34 (0.19)	–0.26 (0.20)	–0.34 (0.24)	0.22 (0.26)	0.33 (0.26)
RBY	–0.10 (0.32)	0.01 (0.30)	–0.07 (0.31)	0.19 (0.36)	–0.67 (0.27)	0.07 (0.41)
IMF	–0.16 (0.19)	–0.05 (0.19)	0.36 (0.18)	0.10 (0.25)	0.15 (0.24)	0.23 (0.26)
SF_A	–0.05 (0.21)	0.18 (0.20)	0.02 (0.22)	0.18 (0.27)	0.06 (0.27)	0.00 (0.30)
CMP_A	–0.17 (0.23)	–0.24 (0.22)	0.04 (0.24)	–0.20 (0.29)	0.04 (0.30)	0.13 (0.33)
LOSS_A	0.21 (0.22)	–0.20 (0.23)	0.12 (0.23)	0.09 (0.29)	–0.60 (0.22)	0.02 (0.32)
L*	–0.17 (0.20)	0.04 (0.20)	–0.18 (0.21)	–0.10 (0.26)	–0.19 (0.25)	0.13 (0.28)

The exception was meat colour (L*) for BRAH, where the genetic correlation with AGECL was 0.73. Of particular interest were the low correlations between tenderness and AGECL (e.g. SF_A = –0.16 and –0.05 for BRAH and TCOMP, respectively), indicating selection for improved meat tenderness and female puberty could occur independently. Wolcott *et al*. (2009) reported that L*

could be considered as an indirect selection criterion for meat tenderness, with a genetic correlation of –0.66 with SF_A.

However, the positive genetic correlation between meat colour and AGECL in BRAH indicated that selection for increased L* (i.e. to reduced shear force) would genetically increase AGECL in this breed. This may also be associated with observed correlations in BRAH between L* and heifer ENDWET IGF-I (–0.72) and ENDDRY ADG (0.60) reported by Wolcott *et al*. (2009), suggesting possible biological associations among measures of meat colour, weight gain and IGF-I concentration.

Some carcass traits had potentially favourably genetic correlations with AGECL. For BRAH, RBY was negatively (–0.55) correlated with AGECL (Table 3-11), suggesting selection to increase beef-yield percentage would reduce AGECL, and would also genetically increase CLPRIOR (0.66) and CLJOIN (0.83). Laster *et al*. (1979) reported a negative correlation (–0.70) between the breed-group means of heifer age at puberty and the fat trim percentage. Whereas Mialon *et al*. (2001) reported no genetic association between the heifer age at the first oestrus and the fat content of male carcasses in Charolais cattle. For TCOMP (Table 3-12), AGECL was negatively correlated with MS (–0.49) and not correlated with RBY (–0.10), suggesting that selection to increase MS in TCOMP would favour reduced AGECL. However, Bergfeld *et al*. (1995) reported no differences in the age at puberty in Angus heifers sired by high- and low- marbling EPD sires. The genetic correlation with P8c was also positive with AGECL (0.43) and WTCL (0.64) for TCOMP, suggesting that decreased carcass P8 fatness would be genetically associated with decreased AGECL and WTCL.

Conclusions

Heifer age at puberty is affected by genetic and environmental influences. Age at puberty can be significantly delayed in late- born calves and also in environments that limit growth rates, particularly during the dry season. Therefore, management can be used to reduce the age at puberty by controlling the month of start of calving and its duration, and the nutrition management of the pre-pubertal heifer. Genotype differences existed and could be exploited through the choice of breeds, and within both genotypes sufficient genetic variation exists such that selection could be used to reduce the age at puberty. However, differences between the genotypes Brahman and Tropical Composite in their genetic relationships between traits suggest differences in their biology for mechanisms controlling puberty and the

need for separate genetic-evaluation schemes. In general, more genetic variation was observed for Brahman than for Tropical Composite. The genetic differences observed for the age at first CL for Brahman appear to be more important than those for Tropical Composite because of the expected influence of age at puberty on reproductive performance from their first joining, given the lower percentage of Brahman heifers observed with a CL before joining. Although significant genetic variation existed for heifer puberty traits in the Tropical Composite, it is yet to be determined whether they are important as predictors of a lifetime calving performance.

In general, there were few strong genetic indicators of heifer age at puberty, except for IGF-I in Brahman heifers measured at the end of their first postweaning wet season. Genetic relationships indicate that selection to improve heifer age at puberty and steer traits could occur reasonably independently, except for Brahman residual feed intake and meat colour. Other correlations of lower magnitude, given the moderate to large standard errors, could also be economically important.

These results and measures form the basis for further studies examining the genetic associations of puberty traits with tropical adaptation traits, and importantly, their associations with the first and subsequent calving performances of these females. These results will ultimately determine the utility of measuring early-in-life female puberty traits and including them in a genetic-selection scheme.

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Chapter 4. Male traits 1. Experimental design

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

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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.

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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 anoestrus 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 4-1 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 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 4-2). 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 4-2.

Table 4-1 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 sires[A]	% link	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

Table 4-2 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
	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

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 (CSIRO 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 4-3. 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 4-3).

Table 4-3 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

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 (*Cenchruciliaris*) 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 4-3). 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 (CSIRO 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 4-2). 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.

Table 4-4 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 (cm2)	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 X 1′ (0.9 X·25 mm) BD Vacutainer Precision Glide needle (Becton, Dickinson and Co.). Blood samples were centrifuged crush side at 2500g for 20 min and the sera frozen at -20^{O}C until assayed for concentrations of inhibin. Sera were assayed by Monash University using established protocols (Phillips 2005).

Component traits	Code	Description
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 X 1′ (0.9 X 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 2500g for 20 min and the plasma frozen at -20^{O}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 X 1′ (0.9 X 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 (AGBU 1994).
	LCode	Accompanying a 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 (AGBU 1994).
	FCode	Accompanying a 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 (AGBU 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

Component traits	Code	Description
		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·x1000 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.
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 4-3). 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.

Component traits	Code	Description
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).

(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 4-4. 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 4-4). 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 ≥20 cm. If an animal did not produce an ejaculate following electro-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 4.4).

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 4-4).

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 4-4).

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 4-4. 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 4-4). 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 4-4).

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 4-4). 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 4-4).

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

Table 4-5 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)	Cryptorchid	Culls Hypoplasia	Other	Injury	Deaths Sickness	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	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 4-6 Numbers of young bulls by genotype, age and status at each Bull Breeding Soundness Evaluation (BBSE)

Genotype/status	Brahman			Tropical Composite		
	12 months	18 months	24 months	12 months	18 months	24 months
BBSE (n)	1340	1409	1403	1924	2081	2069
Stimulated[A] – SC ≥220 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 ≥ 100 spermatozoa were present in the fixed ejaculate subsample

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 4-4).

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.

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 4-4.

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 4-4 (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 11b-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. Deaths due to disease, accidental injury or unknown reasons also occurred during the course of the experimentation. Table 4-5 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 weanedIn 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 4-6 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. 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.

Table 4-7 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 4-4 for trait description

Trait		Brahman						Tropical Composited					
	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	1639	104	323	203.7	33.51	16	2424	96	344	220.1	39.61	18
9 months	kg	1490	110	323	217.2	34.95	16	2133	116	347	237.4	38.96	16
12 months	kg	1469	125	360	246.9	35.27	14	2106	133	420	275.2	40.80	15
15 months	kg	1462	144	430	297.4	38.43	13	2099	186	456	319.3	44.06	14
18 months	kg	1436	214	488	353.2	38.36	11	2097	228	510	368.8	45.12	12
21 months	kg	1432	225	540	365.1	42.70	12	2095	228	519	371.9	47.44	13
24 months	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	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	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

Table 4-8 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 4-4 for trait definition

Trait	Age (months)	Unit	Brahman						Tropical Composite					
			n	Min	Max	Mean	s.d.	CV	*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	ºC	540	37.0	40.7	39.2	0.49	1	792	37.3	41.0	39.2	0.50	1
Rectal temperature	24	ºC	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

Animal models will be used to estimate variance components and will include the fixed effects identified above for each with an additional random common trait. 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.

Table 4-9 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 4-4 for trait definition

Trait	Age (months)	Unit	Brahman						Tropical Composite					
			n	Min	Max	Mean	s.d.	CV	n	Min	Max	Mean	s.d.	CV
Semen units														
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

Descriptive statistics

Trait means, range and coefficient of variation are presented in Tables 4-7 to 4-9. 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.

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Chapter 5. Male traits 2. Genetic parameters

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

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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.

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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 measurable 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

Ethics approval was provided under RH219/06 by CSIRO Rendel Laboratory AEC. 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 5-1). 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).

Statistical analyses

Fixed-effect modelling

Significant fixed effects were identified separately for each genotype using linear mixed model procedures of SAS (SAS Institute, Cary, NC, USA) or GENSTAT

Table 5-1 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

(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. 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 5-2 lists the traits included in the analyses, the abbreviated codes used in the text and a brief description of trait measurement.

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 5-3.

Table 5-2 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 (oC)	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 EMA15	Rump fat thickness (mm) Eye-muscle area (cm2)	Subcutaneous fat thickness at the rump P8 site measured using ultrasonography at 15 months of age 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

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 5-4. 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 5-5 to 5-7. 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.

Table 5-3 Unadjusted means ± s.d. and ranges for hormone and production traits measured on Brahman and Tropical Composite bulls

See Table 5-2 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 (^{O}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 (^{O}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
H15 (cm)	2099	125 ± 4.9	105	139
SH18 (score)	2104	7 ± 1.7	1	9
EV18 (mm)	2104	10 ± 20.9	0	120

Table 5-4 Unadjusted means ± s.d. and ranges for scrotal circumference and semen quality traits measured on Brahman and Tropical Composite bulls

See Table 5-2 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

Heritability of hormone traits

The heritability estimate for LH4 was moderate but for IN4 was high and consistently so for both genotypes (Table 5-5). 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 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 5-5) 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.

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 5-6). 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 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 at 18 months of age in BRAH and at 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.

Table 5-5 Additive variance (σ^2_a), phenotypic variance (σ^2_p) and heritability (h^2) of blood hormone levels and production traits of Brahman and Tropical Composite bulls

See Table 5-2 for trait description; approximate standard error shown in parentheses

Trait	Brahman			Tropical Composite		
	σ^2_a	σ^2_p	h^2	σ^2_a	σ^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 5-6 Additive variance (σ^2_a), phenotypic variance (σ^2_p) and heritability (h^2) of scrotal circumference of Brahman and Tropical Composite bulls

See Table 5-2 for trait description; approximate standard error shown in parentheses

Trait	Brahman			Tropical Composite		
	σ^2_a	σ^2_p	h^2	σ^2_a	σ^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 5-7 Additive variance (σ^2_a), phenotypic variance (σ^2_p) and heritability (h^2) of semen quality traits of Brahman and Tropical Composite bulls

See Table 5-2 for trait description; approximate standard error shown in parentheses

Trait	Brahman			Tropical Composite		
	σ^2_a	σ^2_p	h^2	σ^2_a	σ^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)

Table 5-8 Genetic and phenotypic correlations among hormone and production traits for Brahman bulls

See Table 5-2 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	–	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	0.1	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	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	0.1	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	–0.03	0.08	0.07	0	0.2	–	0.37 (0.17)	0.57 (0.16)	–0.48 (0.15)	–0.22 (0.20)	0.30 (0.21)
P815	–0.05	0	–0.08	0.04	–0.06	0.1	0.25	–	–0.11 (0.16)	–0.30 (0.14)	0.17 (0.17)	–0.08 (0.17)
EMA15	0.1	0.04	0.19	0	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	–0.04	0.64	–0.06	–0.03	0.27	–	–0.28 (0.16)	0.13 (0.16)
SH18	0.1	0.03	0.03	0	–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 5-9 Genetic and phenotypic correlations among hormone and production traits for Tropical Composite bulls

See Table 5-2 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	–	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	0.1	0	–	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	–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	0.1	0.11	0	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	0.2	–	0.30 (0.20)	0.35 (0.13)	–0.46 (0.15)	0.17 (0.16)	0.00 (0.17)
P815	–0.06	0	–0.02	–0.01	–0.06	0.1	0.21	–	–0.24 (0.18)	–0.29 (0.15)	–0.07 (0.21)	0.32 (0.21)
EMA15	0.1	0	0.2	–0.04	0.03	0.5	0.26	0.02	–	0.34 (0.14)	0.21 (0.13)	–0.06 (0.14)
HH15	–0.02	0.1	–0.01	0	0	0.6	–0.07	–0.03	0.27	–	–0.29 (0.16)	0.11 (0.16)
SH18	0.1	–0.16	0.09	–0.02	–0.03	–0.11	0.06	–0.02	0.1	–0.05	–	–0.93 (0.03)
EV18	–0.10	0.1	–0.06	0	0.02	0.1	–0.04	0.03	–0.03	0.07	–0.55	–

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 5-6 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 5-7). 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 5-8 and 5-9 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.

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 5.10, 5.11). With the exception of

Table 5-10 Genetic and phenotypic correlations among scrotal circumference and semen quality traits for Brahman bulls

See Table 5-2 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	0.16 (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^A													
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)	.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	0.2	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	0.4	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	0.16	0.11	0.12		0.25	0.3	0.27	0.2	0.24		1.00 (0.13)	0.42 (0.30)
MOT24	0.02	0.1	0.06	0.07		0.19	0.21	0.24	0.12	0.2	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	

Table 5-11 Genetic and phenotypic correlations among scrotal circumference and semen quality traits for Tropical Composite bulls

See Table 5-2 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	0.5	–	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	0.1	0.4	–	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	0.1	0.4	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	0.1	0.3	0.52	0.6	–	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	0.5	0.9	0.28	0.3	0.1	–	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	0.1	0.3	0.28	0.3	0.2	0.3	–	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	0.1	0.2	0.23	0.3	0.2	0.2	0.78	–	0.80 (0.12)	0.24 (0.16)	0.97 (0.17)	0.95 (0.12)	0.61 (0.14)
PNS18	0.1	0.2	0.28	0.3	0.4	0.2	0.32	0.4	–	0.04 (0.16)	0.80 (0.23)	0.83 (0.15)	0.98 (0.05)
SC24	0.5	0.8	0.17	0.2	0	0.9	0.19	0.2	0.1	–	0.55 (0.20)	0.33 (0.18)	0.20 (0.14)
MASS24	0.1	0.2	0.23	0.2	0.1	0.2	0.27	0.3	0.2	0.2	–	0.98 (0.08)	0.80 (0.18)
MOT24	0.1	0.2	0.19	0.2	0.1	0.2	0.25	0.3	0.3	0.2	0.8	–	0.76 (0.12)
PNS24	0.1	0.2	0.2	0.2	0.4	0.2	0.25	0.3	0.6	0.1	0.34	0.5	–

Table 5-12 Genetic correlations of hormone and production traits with scrotal circumference and semen quality traits for Brahman bulls

See Table 5-2 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	–0.11 (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		0.00 (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)

Table 5-13 Genetic correlations of hormone and production traits with scrotal circumference and semen quality traits for Tropical Composite bulls

See Table 5-2 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)

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 ± 0.13) and at 12 months in TCOMP (0.55 ± 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 5-7) 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 5-12 for BRAH and Table 5-13 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 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 5-12 and 5-13. 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.

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Chapter 6. Genetic correlations between Male and Female traits

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

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

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Introduction

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

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

Materials and methods

Data were from a single large beef breeding experiment in northern Australia that investigated the genetics of whole-herd profitability (Burrow *et al*. 2003). Animal ethics approval was provided by CSIRO Rendel Laboratory AEC under RH198/04 and RH198/04.

The experimental design associated with each aspect of the study are described by Barwick *et al*. (2009*a*, 2009*b*), Burns *et al*. (2013) and Johnston *et al.* (2014). In brief, Brahman (BRAH) and Tropical Composite (TCOMP) steers (n = 2216) and

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

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

Statistical analyses

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

All analyses used a relationship matrix constructed for the full population as three generations of pedigree where known. Data used in analyses between bull and female traits, were edited to remove any bull records of dam-offspring pairs where the bull was the resultant progeny of the female trait being analysed. Editing was done to remove any contributions to the genetic covariance generated from an environmental covariance between the dam-offspring for the pairs of traits.

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Table 6-1 Trait description of bull, heifer and female reproduction traits

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

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

For example, when analysing female traits associated with mating 1, records were removed for bulls that were the resultant progeny from this first mating. Analyses involving lifetime female traits, the records were removed for bulls that were the only progeny of a cow.

Results

Heifer puberty and female reproduction

Genetic correlations of heifer puberty traits with female reproduction traits at mating 1, mating 2 and lifetime are presented in Tables 6-2 and 6-3. For BRAH moderate to high correlations existed between all heifer puberty traits and mating 1 female reproductive traits. However, the correlations were lower for weaning rate at mating 1 with age at puberty (= –0.39) and weight at puberty (= –0.11), and for calving rate with heifer weight at puberty (–0.27). The negative genetic correlations of weight and fatness at puberty suggested possible antagonisms with reproduction output traits at mating 1. Similar trends were observed for TCOMP but the magnitudes of the correlations were lower. The higher standard errors for TCOMP estimates reflect the greater number of TCOMP heifers pubertal before mating (Johnston *et al*. 2009) and the very low heritabilities of TCOMP reproduction traits at the first mating, as reported by Johnston *et al*. (2014).

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

Genetic correlations between heifer puberty traits and female lifetime reproduction had high standard errors. The directions of the correlations in both genotypes generally reflected the association seen between heifer age at puberty and performance at mating 1 and 2. In both genotypes, younger age at puberty tended to be genetically associated with increased lifetime reproductive performance.

Young bull traits and heifer puberty

Genetic correlations between bull traits and heifer age at puberty traits are presented in Tables 6-4 and 6-5. For BRAH, correlations were generally low across the male hormone traits. The exception was insulin-like growth factor-I (IGF-I) with moderate correlations with age at puberty,

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

Table 6-2 Genetic correlations between heifer puberty traits and female mating 1, mating 2 and lifetime reproduction in Brahman

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

[A]Estimate exceeded bounds.

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

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

Genetic correlations between bull and female traits at mating 2 are presented in Tables 6-8 and 6-9. For BRAH the genetic correlations with the bull hormone traits were low. For TCOMP, luteinizing hormone (LH) was moderately to highly correlated with mating 2 reproduction traits (e.g. 0.59 with lactation anoestrus interval and –0.66 with calving rate). Semen quality traits in BRAH and TCOMP at 18 and 24 months showed consistent correlations with mating 2 traits in both genotypes. Genetic correlations of mass activity and motility at 18 months with mating 2 traits were moderate to high, albeit with high standard errors in TCOMP. Percent normal sperm at 12 and 18 months in TCOMP were also correlated with the mating 2 traits. However, at 24 months the correlations were lower and not significantly different from zero. In BRAH, percent normal sperm at 18 months was lowly to moderately to highly correlated with mating 2 traits. At 24 months, the correlations were moderate to high across the mating 2 traits.

Scrotal circumference in BRAH was lowly to moderately correlated with mating 2 traits, with slightly higher correlations when measured at 18 months (Table 6-8). In TCOMP, correlations with scrotal circumference were low and with no consistent trends in the correlations at the different measurement ages (Table 6-9).

Preputial eversion score and sheath score in TCOMP were correlated with lactation anoestrus traits (e.g. –0.58 and 0.41 correlations with lactation cyclicity

rate, respectively), but less with other reproductive traits, while in BRAH, they were not significantly correlated with female reproduction traits at mating 2.

Young bull traits and lifetime female reproduction

Genetic correlations of bull traits with female lifetime traits are presented in Tables 6-10 and 6-11. All estimates had large standard errors but some general trends were apparent. Bull hormone traits were generally lowly correlated with female lifetime traits. Mass activity and motility at 18 months were highly correlated (0.70 and 0.75, respectively), with lifetime annual calving rate. These correlations reduced in the magnitude with lifetime traits recorded only in cows still present at mating 6. Scrotal circumference showed no consistent relationships with lifetime reproduction traits in BRAH, and in TCOMP there was a tendency for the correlations to be negative. Preputial eversion was genetically correlated with lifetime calving rate (–0.59 in BRAH and TCOMP) and weaning rate (–0.71 in BRAH; –0.88 in TCOMP). In BRAH, these correlations were reduced in magnitude for lifetime traits recorded only in cows present at mating 6.

Table 6-3 Genetic correlations between heifer puberty traits and female mating 1, mating 2 and lifetime reproduction in Tropical Composite

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

[A]Estimate exceeded bounds.

Table 6-4 Genetic correlations between bull reproduction traits and heifer puberty traits in Brahman

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

Table 6-5 Genetic correlations between bull reproduction traits and heifer puberty traits in Tropical Composite

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

Discussion

Earlier work by others suggested male traits were useful genetic predictors of female reproductive performance (Land 1973; Smith *et al*. 1989) including studies in tropical beef genotypes (Mackinnon *et al*. 1990; Meyer *et al*. 1991). Brinks *et al*. (1978) and Martin *et al*. (1992) suggested scrotal circumference at 12 months was effectively the same trait as heifer age at puberty in beef cattle.

However, results from the present study showed only low to moderate correlations, ranging from –0.06 to –0.41. Morris *et al*. (2000) reported a similar correlation (–0.25) in Angus cattle and Martinez-Velazquez *et al*. (2003) found genetic correlations of –0.15 and 0.23 for scrotal circumference with heifer age at puberty and first mating weaning rate, respectively in pooled *Bos taurus* breeds. Perry *et al*. (1990), in tropical breeds similar to this study, reported no evidence of a relationship between heifer age at puberty and bull scrotal circumference in small half-sib families. Our results showed the magnitude of relationships was influenced by the age of the bulls at scrotal measurement. In both genotypes, correlations between heifer age at puberty and scrotal circumference were higher at younger ages (i.e. 12 months BRAH; 6 months in TCOMP). They were reduced in magnitude at 18 months, and by 24 months there was no significant association of scrotal circumference with heifer age at puberty in either genotype.

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

The relationships between scrotal circumference and mating 2 and lifetime reproduction traits were generally low.

Table 6-6 Genetic correlations between bull reproduction traits and female mating 1 reproduction traits in Brahman

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

Table 6-7 Genetic correlations between bull reproduction traits and female mating 1 reproduction traits in Tropical Composite

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

However, the –0.35 genetic correlation of scrotal circumference at 18 months with days to calving in BRAH was similar to the –0.30 correlation reported by Meyer and

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

Semen quality traits had similar, or higher, correlations than scrotal circumference with heifer age at puberty and moderate correlations with mating 1 traits. For mating 2 traits, in particular lactation anoestrus traits, the correlations with semen quality traits were consistently higher than the correlations with scrotal circumference. Semen mass activity and motility were genetically related to female mating 2 traits, particularly when measured at 18 months. These two measures can be recorded crush-side but requires a trained technician.

The semen morphology trait, percent normal sperm, was also moderately to highly correlated with mating 2 traits, though differences in the magnitudes of the correlations were observed across genotypes for different measurement times. Recording of percent normal sperm is a more costly measure than crush-side semen trait requiring a sample sent for analysis by an accredited morphologist. Percent normal sperm at 24 months was identified as a genetic predictor of all female traits at mating 2 in BRAH, whereas for TCOMP, by this age, the correlations were close to zero.

Lifetime female reproduction traits were also correlated with semen quality traits. In BRAH, measures at 18 months, particularly mass activity and motility, were highly correlated with the lifetime traits. In TCOMP, estimates for measures at 18 month had large standard errors but

Table 6-8 Genetic correlations between bull reproduction traits and female mating 2 reproduction traits in Brahman

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

Table 6-9 Genetic correlations between bull reproduction traits and female mating 2 reproduction traits in Tropical Composite

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

Table 6-10 Genetic correlations between bull reproduction traits and female lifetime reproduction traits in Brahman

See Table 6-1 for description of traits, approximate standard errors in parentheses

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

Table 6-11 Genetic correlations between bull reproduction traits female lifetime reproduction traits in Tropical Composite

See Table 6-1 for description of traits, approximate standard errors in parentheses

Bull traits	Age (months)	Female lifetime reproduction traits			
		LACR	LAWR	ARC6	AWR6
		Hormones			
Inhibin	4	0.49 (0.45)	0.17 (0.27)	–0.02 (0.15)	–0.08 (0.13)
Luteinising hormone	4	–0.64 (0.55)	0.03 (0.33)	–0.39 (0.25)	–0.06 (0.18)
IGF-I	6	0.73 (0.39)	0.18 (0.33)	0.24 (0.20)	–0.02 (0.17)
		Semen quality			
Mass activity	12	–0.15 (0.38)	–0.20 (0.31)	0.01 (0.19)	0.14 (0.17)
	18	0.20 (0.55)	–0.36 (0.44)	0.20 (0.29)	0.21 (0.25)
Motility	12	0.06 (0.38)	0.08 (0.30)	–0.03 (0.20)	0.14 (0.18)
	18	0.37 (0.51)	–0.05 (0.39)	0.27 (0.27)	0.29 (0.24)
Percent normal sperm	12	0.31 (0.44)	–0.07 (0.38)	0.24 (0.25)	0.23 (0.22)
	18	0.37 (0.46)	–0.02 (0.38)	0.43 (0.24)	0.41 (0.22)
	24	0.22 (0.40)	0.24 (0.33)	0.09 (0.21)	0.17 (0.19)
		Scrotal and sheath			
Scrotal circumference	6	–0.62 (0.39)	–0.46 (0.25)	–0.06 (0.18)	–0.06 (0.16)
	12	–0.26 (0.37)	–0.29 (0.29)	0.11 (0.17)	0.16 (0.15)
	18	–0.26 (0.36)	–0.28 (0.27)	0.07 (0.17)	0.14 (0.16)
	24	–0.45 (0.37)	–0.33 (0.27)	–0.15 (0.17)	–0.01 (0.16)
Sheath score	18	0.26 (0.42)	0.57 (0.28)	0.32 (0.19)	0.42 (0.17)
Preputial eversion	18	–0.59 (0.44)	–0.88 (0.33)	–0.56 (0.23)	–0.43 (0.22)

tended to show moderate correlations with lifetime calving rate.

No literature estimates were found for genetic correlations between these groups of traits. Phenotypic associations have been reported (Holroyd *et al*. 2002) between semen quality traits and a bull's calf output under multiple-sire mating in tropical beef cattle breeds. Holroyd *et al*. (2002) found significant associations between a bull's percent normal sperm and subsequent calf output but no association with motility from a multiple regression analysis. However, the bulls used were considerably older (2–4 years) than those in the present study.

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

No published estimates of relationships of sheath and preputial eversion with female reproduction were found. There are publications (e.g. NSW Agriculture 2005) that described the physiological basis of a protruding prepuce (i.e. eversion) and its associated increased risk of prolapse. It is also reported to have increased occurrence in polled bulls (NSW Agriculture 2005). Our result suggests that bulls with greater preputial eversion (and more pendulous sheaths) were genetically related to lower female reproductive performance. Further, the reduction in the magnitude of the correlations in the subset of cows still present at the sixth mating for BRAH suggests that these traits may be related to

an increased chance of culling due to consecutive reproductive failures. Burns *et al*. (2010) in a review postulated that cervix shape and size may affect pregnancy rate in cattle; and Finch *et al*. (2003) reported a high heritability estimate for cervical size in a small sample of Santa Gertrudis. The possibility of there being a genetic link between sheath and preputial eversion and structural aspects of the female reproductive tract warrants further investigation.

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

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

Gargantini *et al*. (2005) reported lower correlations with heifer age at puberty and pregnancy rate for scrotal circumference at 12 versus 15 months but standard errors for the estimates were not given.

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

Conclusions

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

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the male reproduction studies, previously acknowledged in Johnston *et al*. (2014) and Corbet *et al*. (2013), respectively.

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Chapter 7. Deriving New Reproductive Traits Using Ultrasound

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Using ultrasound to derive new reproductive traits in tropical beef breeds: implications for genetic evaluation

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Abstract. Key components of female fertility in tropically adapted beef breeds are age at puberty and interval from calving to conception. Presence of an ovarian *corpus luteum* or stage of pregnancy were recorded using trans-rectal ultrasonography in 4649 heifers and 2925 first-lactation cows in seven herds of either Brahman, Droughtmaster or Santa Gertrudis tropical beef cattle breeds in northern Australia. The traits derived from a single ultrasonographic examination were incidence of *corpus luteum* at ~600 days of age in heifers, and weeks pregnant 5 weeks post-mating in heifers at ~2.5 years of age and in first-lactation cows at either 2.5 or 3.5 years of age. At 600 days of age, the bodyweight of heifers averaged 340 kg and 40% had a *corpus luteum*. At 2.5 years of age bodyweight of heifers averaged 452 kg and 80% were pregnant. First-lactation cows averaged 473 kg and 64% were pregnant. Considerable between-herd variation in traits reflected differences in climate and management at each site. However, estimates of heritability of incidence of *corpus luteum* at 600 days (0.18–0.32) and weeks pregnant in lactating cows (0.11–0.20) suggested that a significant proportion of the variation was due to additive gene action. Small to moderate genetic correlations with other economically important traits and the range in estimated breeding values indicate substantial opportunity for genetic improvement of the traits. The study provided evidence to accept the hypothesis that strategically timed ultrasound examinations can be adopted to derive useful traits for genetic evaluation.

Additional keywords: cattle, fertility, puberty.

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Introduction

A major challenge for north Australian beef enterprises is to improve reproduction rate in the tropically adapted beef breeds. While environmental factors influenced by climate and herd- management practices account for a proportion of the variation in reproduction rate (Entwistle 1983), genetic factors also explain individual animal differences (Mackinnon *et al*. 1989; Martin *et al*. 1992). As herd reproduction rate is a major driver of beef enterprise productivity and profitability (McGowan *et al*. 2014), genetic improvement of fertility traits in conjunction with sound breeding-herd management offer a sustainable solution to the challenge.

Ultrasonography has been used in cattle since the early 1980s, providing knowledge of ovarian function (Pierson and Ginther 1984), which has implications for reproduction research (Ginther 2014), genetic evaluation (Carthy *et al*. 2014; Johnston *et al*. 2014*a*), genomic studies (Hawken *et al*. 2012; Fortes *et al*. 2012, 2016) and breeding management (Adams and Singh 2014; Holm *et al*. 2016). Detection of an ovarian *corpus luteum* (CL) using ultrasound allows accurate determination of key component traits of female reproductive performance, such as age at first CL in heifers (Johnston *et al*. 2009) and postpartum anoestrus interval in first-lactation cows (Johnston *et al*. 2014*a*). Heritability of age at first CL in Brahman and Tropical Composite breed females was estimated to be 0.57 and 0.52 respectively (Johnston *et al*. 2009). Heritability of postpartum anoestrus interval in the same breeds was estimated at 0.51 and 0.26 respectively (Johnston *et al*. 2014*a*). Age at first CL and postpartum anoestrus interval were also shown respectively, to be moderately and strongly associated with lifetime reproductive performance (Johnston *et al*. 2014*a*, 2014*b*). However, to accurately derive age at first CL and postpartum anoestrus interval, multiple trans-rectal examinations were required. Such intensity of measurement was necessary for rigorously designed research programs but may not be practical for most commercial beef-producing enterprises.

The extensive beef herds of northern Australia need a robust but simple system of trait recording to identify superior animals for these fertility traits so they can accelerate genetic improvement. The aim of the current research project was to test the practicality of using ultrasound to determine the presence of a CL in peri-pubertal heifers and pregnancy in heifers and lactating cows in Australian seed-stock herds and to evaluate the strength of inheritance of these traits. An additional objective was to estimate the phenotypic

and genetic relationships between reproductive and body composition traits. The hypothesis was that a single ultrasound examination of heifers at 600 days of age, and one of heifers and lactating cows 5 weeks post- mating, will provide useful traits for genetic evaluation to aid improvement of herd reproduction.

Materials and methods

Ethics

Animal ethics approval was provided by The University of Queensland Production and Companion Animal Ethics Committee as Approval QAAFI\050\13\Smart Futures.

Animals

The cattle were located in seven seed-stock herds across Queensland; their numbers and location within breed are shown in Table 7-1. The collaborating herds were engaged in a research project funded by the Queensland Smart Futures Fund (Burns *et al*. 2016) and represented Brahman, Droughtmaster and Santa Gertrudis beef cattle breeds, each being widely used for beef production in the subtropical and tropical regions of northern Australia. The cattle were born and raised as contemporaries in their cohorts within locations. Females were mated for approximately 3–4 months each year to bulls that had met the standards of bull breeding soundness (Beggs *et al*. 2013). Heifers in some herds were first mated as yearlings so a proportion of females in those herds presented as first-lactation cows at 2 years of age. Heifers in the remaining herds were first mated at 2 years of age.

Table 7-1 Numbers of heifers scanned by breed, herd and location

Breed	Herd	Location; latitude, longitude	Number of heifers
Brahman	ALC	Valkyrie, central Queensland; –22.32, 148.93	576
	ELR	Roundstone, central Queensland; –24.81, 149.74	863
	SCC	May Downs, central Queensland; –22.72, 149.16	275
Droughtmaster	COM	Canoona, central Queensland; –23.12, 150.17	346
	LIS	Gumlu, northern Queensland; –19.82, 147.61	741
Santa Gertrudis	GYR	Cracow, central Queensland; –25.26, 150.19	1042
	ROS	Diamondy, south-eastern Queensland; –26.71, 151.30	806
Total			4649

At all locations, the breeding females were managed on grass- based pasture containing native and introduced species. Diets were supplemented with protein and minerals in the form of a ‘dry lick’ during periods of poor pasture quality to avoid loss of bodyweight and condition.

Animals were vaccinated against endemic diseases (mainly *Clostridium* sp.) and strategically treated to reduce tick

(*Rhipicephalus microplus*) and buffalo fly (*Haemotobia irritans exigua*) infestation. In total, 4649 heifers and 2925 first-lactation cows were included in the study from September 2012 through to July 2015. In total, 180 Brahman, 69 Droughtmaster and 116 Santa Gertrudis sires were represented and on average (±s.d.) they sired 9 (±10.0), 15 (±16.6) and 16 (±15.8) daughters respectively, with an overall range of 2–68 daughters per sire.

Trait measurement

Ovarian activity was assessed in heifers at ~600 days of age by real-time ultrasound scanning. Previous studies reported that average age at puberty in tropically adapted Composite breeds occurred between 580 and 650 days (Burns *et al.* 1992; Johnston *et al.* 2009), at which time sire variation for pubertal rate of their daughters would likely be greatest. The timing of 600 days coincided with the recording of other performance traits submitted for genetic evaluation (e.g. ultrasound-scanned carcass traits) and also with post-joining pregnancy scanning in the older breeding females.

At scanning, the ovaries and uterus of each female were examined trans-rectally by ultrasound imaging with a Honda HS-2000V or HS-2100V (Honda Electronics Co., Ltd, Toyohashi, Japan) using a 10MHz linear array transducer to derive the fertility traits described in Table 7-2. For each animal, the same transducer was used to provide a cross-sectional image at the P8 rump site (Johnson 1987) and to measure thickness of the subcutaneous fat layer; additional records of liveweight and body condition score (BCS; 1–5 scale) were also kept.

In addition to the traits recorded in the present study, previously calculated estimated breeding values (EBVs) for the ultrasound-scan measures of subcutaneous fat depth, intra- muscular fat percentage (IMF%) and cross-sectional area of the eye-muscle (EMA; *M. longissimus thoracis pars lumborum*) were made available by the Australian Agricultural Business Research Institute, to provide associated body composition data. EBVs for the trait days to calving were also provided. Days to calving was calculated as the period from the start of mating to the date of calving (Johnston and Bunter 1996) and is currently included in BREEDPLAN genetic evaluation for Brahman and Santa Gertrudis, but not for Droughtmaster breeds. Pedigree files spanning several generations were available for each breed and, in total, contained 24 598, 10 339 and 46 815 identities for Brahman, Droughtmaster and Santa Gertrudis respectively.

Statistical analyses

Fixed-effect modelling

Significant fixed effects were identified separately for each breed using linear mixed model procedures in Genstat (16th Edition, VSN International, Hemel Hempstead, UK). Models included the fixed effects of year (2012–2015), herd (2 or 3 herds per breed), birth month, dam age (2–12 years), management group, their interactions and sire as a random effect. The effect of animal age was included as a covariate for all traits. BCS and P8 fat depth were tested as discrete variables in initial models to ascertain co-variability with CL score. Birth month of the individual was included in heifer trait models to account for differences in environmental conditions experienced across the calving period. Calving periods generally started in August and ended in late January, but there were differences in the start and end calving month across herds and years. Within herd–cohort subclasses, adjacent birth months with fewer than five animals were combined. Calving birth month was included in lactating- cow trait models to account for any effects that the age of their suckling calf might have on their ability to reconceive before bull removal. Non-significant ($P > 0.05$) terms were sequentially removed from the models to yield the final model for each trait. Final models for heifer traits generally consisted of a concatenated term for Herd + Year + Birth month and the age covariate. For cow traits, final models generally included terms for herd, year, management group (or paddock mated) and calving birth month.

Variance component estimation

Additive genetic variance and heritability for each trait were estimated in univariate analyses separately for each breed, using restricted maximum-likelihood procedures in ASRemL (Gilmour *et al*. 2009). The binary traits (CL rate and pregnancy rate) were analysed using sire models with a logit-link function. Trait heritability on the observed binomial scale was approximated by multiplying the underlying logit-scale heritability by $p\ (1 - p)$, where p is the mean trait incidence (Gilmour *et al*. 2009). Heritability for binary traits was also derived with a linear model for comparison. The linear traits (CL score and weeks pregnant) were analysed by fitting an additive genetic effect for the animal, assuming a linear model. Both sire and animal models included the final fixed effects identified for each trait. Genetic correlations among pairwise combinations of 600d CL score with body condition score and P8 fat depth were estimated in a series of bivariate analyses for each breed separately.

Estimated breeding values were generated for the linear traits as solutions

for the random effect of animal. Genetic associations between 600d CL score, weeks pregnant, body composition traits and days to calving were estimated by simple correlations between the EBVs of each trait for all individuals in the pedigree with EBV accuracy greater than 40% for all traits (including days to calving for the Brahman and Santa Gertrudis herds). From the available data, 4207 Brahman, 1516 Droughtmaster and 2339 Santa Gertrudis females had EBV accuracy greater than 40% for all traits and were included in the simple correlation matrices.

Table 7-2 Description of derived fertility traits

CA, corpus albicans; *CL*, corpus luteum

Trait	Description
CL rate	Presence (= 1) or absence (= 0) of CL or CA on either ovary observed by ultrasound imagery of all heifers in the cohort at ~600 days of age
CL score	Scored using ultrasound imagery of the reproductive tract at 600 days of age as: 0 = infantile tract, inactive or undetectable ovaries; 1 = ovarian follicles 10 mm; 2 = ovarian follicles >10 mm; 3 = presence of CL or CA
Pregnancy rate	Presence (= 1) or absence (= 0) of conceptus observed by ultrasound imagery of the reproductive tract ~5 weeks after completion of mating in heifers and first-lactation cows
Weeks pregnant	Weeks pregnant as determined by fetal size using ultrasound imagery 5 weeks after completion of mating in heifers and first-lactation cows; animals with no visible pregnancy but with detectable CL were given a value of 1 week, otherwise a zero; values ranged from 0 to 20 weeks

Results

Trait means

The numbers of females, their mean liveweight, body condition, fatness and scanned reproductive-trait measures within breed are presented in Table 7-3. The scanning of heifers at 600 days of age over 3 years and across seven herds captured an overall mean incidence of CL of 0.39 (±0.49). The differences in CL rate among breeds was confounded by herd and, therefore, prevailing seasonal conditions at the various locations. As females from each of the breeds were not kept together and raised as contemporaries, a valid breed comparison cannot be made.

Trait heritability and EBVs

Heritability of the scanned reproductive traits measured at different ages within breed are presented in Table 7-4. Heritability estimates for binary traits on the logit scale were higher than those on the observed scale and the latter were generally similar to the linear-model estimates. The heritability of 600-day CL rate (0.22–0.33) was higher than that of pregnancy rate measured in heifers (0.04–0.18) and lactating cows (0.01–0.08), particularly in the Droughtmaster herds.

Converting CL rate to CL score resulted in no appreciable change to the magnitude of heritability estimates, but generally

reduced the standard error of the estimates. Conversion of heifer pregnancy rate to weeks pregnant did not affect either magnitude or standard error of the heritability estimates. However, converting pregnancy rate to weeks pregnant in first-lactation cows improved heritability estimates. The heritability of 2.5-year-old heifer pregnancy traits in Droughtmaster and Santa Gertrudis breeds was low or zero, reflecting high incidence (0.84 and 0.85 respectively) and little or no additive variance for the traits. However, in Brahman females, the incidence of heifer pregnancy was lower at 0.76 and the heritability of 0.18 was significantly greater than zero.

Estimated breeding values for 600-day CL score (0–3) ranged from +0.91 to –0.88 in Brahman, from +0.73 to –0.64 in Droughtmaster and from +1.3 to –0.9 in Santa Gertrudis cattle. The range of EBVs for first-lactation weeks pregnant was highest in Brahman at +4.1 to –4.4 weeks, intermediate in Santa Gertrudis at +3.0 to –2.3 and lowest in Droughtmaster cattle at +1.8 to –2.2 weeks. Further work is required to collate Droughtmaster animal records so that days to calving can be genetically evaluated and EBVs assigned.

Correlation among traits

Correlations between EBVs for the female scanned traits and EBVs for days to calving, a trait currently recorded for BREEDPLAN analyses in Brahman and Santa Gertrudis cattle, are presented in Table 7-5. Accuracy of EBVs for Santa Gertrudis and Droughtmaster heifer pregnancy rate could not be estimated as additive variance was close to zero and, hence, not shown in the correlation matrix in Table 7-5.

In Brahman females, 600-day CL score was moderately correlated with heifer pregnancy, but had low correlation with weeks pregnant in first-lactation cows and days to calving. Weeks pregnant in Brahman heifers and first-lactation cows had small to moderate favourable correlations with each other and with days to calving. In Santa Gertrudis females, there was moderate favourable correlation among all reproductive measures assessed. Genetic and phenotypic correlations among 600d CL score, BCS and P8 fat depth in heifers measured at the time of 600-day ultrasonic examination of reproductive tracts are shown in Table 7-6.

Table 7-3 Descriptive statistics of age, weight, body condition, fatness and reproductive scan data recorded on females at 600 days, 2.5 years and 3.5 years within breed

Table values are given as a variable mean ± s.d.; n, number of animals scanned. 600d, heifers scanned at 600 days of age; 2yH, heifers scanned at 2.5 years of age; 2yL and 3yL, lactating cows scanned at 2.5 and 3.5 years of age; Santa Gertrudis herds mated a proportion of heifers at yearling so that some 2.5-year-olds are first-lactation cows (2yL) and 3yL will include first- and second-lactation cows in that breed. For CL or preg (incidence), tract scan variable at 600 days is shown as incidence of corpus luteum (CL); at other ages it is incidence of pregnancy. BCS, body condition score

Cohort	*n*	Age (days)	Weight (kg)	BCS (1–5)	P8 fat (mm)	CL or preg (incidence)	Weeks pregnant
				Brahman			
600d	1714	627 ± 74.6	336 ± 35.0	3.1 ± 0.52	5 ± 3.0	0.39 ± 0.49	
2yH	1605	930 ± 96.0	930 ± 96.0	3.6 ± 0.48	8 ± 4.2	0.76 ± 0.43	11 ± 7.1
3yL	875	1285 ± 44.9	461 ± 50.6	2.9 ± 0.69	5 ± 4.6	0.63 ± 0.48	9 ± 7.5
				Droughtmaster			
600d	1087	591 ± 47.2	342 ± 38.4	3.0 ± 0.48	4 ± 1.9	0.17 ± 0.38	
2yH	754	894 ± 50.0	466 ± 37.6	3.8 ± 0.44	11 ± 4.0	0.84 ± 0.36	11 ± 5.5
3yL	595	1283 ± 38.1	476 ± 47.3	2.9 ± 0.53	5 ± 3.9	0.66 ± 0.48	8 ± 6.7
				Santa Gertrudis			
600d	1848	521 ± 62.3	361 ± 39.7	3.1 ± 0.46	4 ± 2.6	0.53 ± 0.50	
2yH	535	862 ± 48.0	482 ± 39.5	3.9 ± 0.40	10 ± 4.1	0.85 ± 0.35	11 ± 5.7
2yL	581	923 ± 34.5	488 ± 52.2	2.9 ± 0.57	4 ± 4.0	0.64 ± 0.48	8 ± 6.7
3yL	874	1291 ± 41.9	551 ± 69.1	2.9 ± 0.61	6 ± 4.8	0.82 ± 0.39	11 ± 7.1

Genetic correlations were moderate between CL score and BCS and low between CL score and P8 fat depth. Genetic correlations between BCS and P8 fat depth were moderate to high. Genetic correlations were generally associated with a high standard error.

The correlations between reproductive trait EBVs and carcass trait EBVs are presented in Table 7-7. The correlations were generally low for most pair-wise combinations; the few exceptions were low to moderate correlation between 600-day CL and rump fat (–0.28) and the moderate correlations of weeks pregnant with EMA (–0.30) and IMF% (0.41) in Santa Gertrudis females.

Discussion

This study used ultrasound imagery of reproductive tracts in tropically adapted heifers and cows in Australian seed-stock herds to demonstrate genetic variation in and derive estimates of genetic merit for presence of an ovarian CL or stage of pregnancy. These unique measures have previously been reported only by Johnston *et al*. (2009, 2014*a*, 2014*b*). Measuring the ability of heifers to mature sexually earlier in life and for first-lactation cows to reconceive earlier in the breeding season are principal components to determining lifetime reproductive performance of beef-producing cows

Table 7-4 Heritability of reproductive traits at 600 days, 2.5 years and 3.5 years in Brahman, Droughtmaster and Santa Gertrudis females

600d, heifers scanned at 600 days of age; 2yH, heifers scanned at 2.5 years of age; 2yL and 3yL, lactating cows scanned at 2.5 and 3.5 years of age; Santa Gertrudis herds mated a proportion of heifers at yearling so that some 2.5-year-olds are first-lactation cows (2yL) and 3yL will include first- and second-lactation cows in that breed. Logit model shows estimates for binary traits using a sire model with a logit-link function; p, trait incidence; s2A =4·s2S; h2L, heritability on the logit scale; h2, heritability on the observed binomial scale approximated by h2L p(1–p). Linear model, estimates for binary traits from linear sire models, estimates for linear traits from animal models. Standard errors are shown in parentheses. ne, inestimable. See Table 7-2 for trait definition

Trait	Logit model			Linear model		
	p	σ^2_A	h^2_L	h^2	σ^2_A	h^2
			Brahman			
600d CL rate	0.39	1.581	1.13 (0.29)	0.27	0.033	0.23 (0.07)
600d CL score	–	–	–	–	0.201	0.21 (0.06)
2yH pregnancy rate	0.76	1.310	0.99 (0.29)	0.18	0.027	0.18 (0.06)
2yH weeks pregnant	–	–	–	–	5.907	0.15 (0.05)
3yL pregnancy rate	0.65	0.906	0.74 (0.50)	0.17	0.011	0.08 (0.09)
3yL weeks pregnant	–	–	–	–	5.722	0.17 (0.10)
			Droughtmaster			
600d CL rate	0.17	2.836	1.66 (0.37)	0.23	0.043	0.35 (0.11)
600d CL score	–	–	–	–	0.169	0.33 (0.09)
2yH pregnancy rate	0.84	0.274	0.26 (0.42)	0.03	0.005	0.04 (0.06)
2yH weeks pregnant	–	–	–	–	0.052	0.00 (0.04)
3yL pregnancy rate	0.66	0.404	0.37 (0.52)	0.08	0.008	0.05 (0.09)
3yL weeks pregnant	–	–	–	–	2.529	0.10 (0.09)
			Santa Gertrudis			
600d CL rate	0.53	1.115	0.87 (0.24)	0.22	0.042	0.22 (0.07)
600d CL score	–	–	–	–	0.269	0.21 (0.05)
2yH pregnancy rate	0.85	0.000	ne	ne	0.000	ne
2yH weeks pregnant	–	–	–	–	0.000	ne
2yL pregnancy rate	0.64	0.301	0.28 (0.48)	0.06	0.009	0.05 (0.10)
2yL weeks pregnant	–	–	–	–	3.630	0.13 (0.10)
3yL pregnancy rate	0.82	0.254	0.24 (0.46)	0.04	0.002	0.01 (0.06)
3yL weeks pregnant	–	–	–	–	1.107	0.03 (0.06)

(Johnston *et al*. 2014*a*, 2014*b*). Obtaining measurements of reproductive capability at these two critical periods in the breeding time-line of bovine females will enable selection of genetically superior individuals to parent the next generation.

Johnston *et al*. (2009) reported the mean age of heifers at the time of detection of their first CL to be ~750 days in Brahman and 650 days in Tropical Composite breeds. In the current study, 40% of the Brahman heifers had, on average, a CL at 630 days, showing a tendency to earlier age at first CL than that reported in Brahman research herds by Johnston *et al*. (2009), where 50% had a CL by ~750 days. However, the Droughtmaster heifers in the current study, despite having weight and body fatness similar to the Brahmans, had only 17% with a CL at an average 590 days. Approximately 50% of Santa Gertrudis heifers had CL by 520 days and weighed

~20–25 kg more than did heifers from the Brahman and Droughtmaster herds at approximately the same ages, which is likely reflecting better nutritional conditions at the locations of Santa Gertrudis herds. The results provided evidence to suggest substantial breed and environmental influences on the incidence of CL at 600 days of age.

Despite environmental effects, ultrasound scanning of ovaries to ascertain presence of an ovarian CL in heifers at 600 days provided a trait with heritability of between 0.21 and 0.33. In a review, Martin *et al*. (1992) reported a pooled heritability estimate of 0.40 for age at puberty. These estimates were moderate, compared with the higher heritability of the trait age at first CL (0.51–0.57) estimated by Johnston *et al*. (2009). However, 600-day CL in the current study was derived from a single scan and poses a viable alternative to monthly scanning of heifers to ascertain age at first CL. No other literature estimates of heritability were found for pubertal traits in beef cattle, determined using ultrasound scans for presence of CL.

Fetal ageing of first-lactation cows 5 weeks after the completion of the joining period provided a continuous measure of reconception with a normal distribution and a higher heritability estimate than the binary trait of pregnancy rate (0.17 versus 0.08 in Brahman cows, 0.10 versus 0.05 in Droughtmaster cows and 0.13 versus 0.05 in Santa Gertrudis cows). Johnston *et al*. (2014*a*) estimated the heritability of pregnancy rate, anoestrus interval and days to calving in the first-lactation Tropical Composite cows to be 0.05, 0.26 and 0.35 respectively; and in the first-lactation Brahman cows to be 0.25, 0.51 and 0.49 respectively.

Table 7-5 Simple correlations among estimated breeding values (EBVs) for reproductive traits in Brahman and Santa Gertrudis breeds

600d, heifers scanned at 600 days of age; 2yH, heifers scanned at 2.5 years of age; 2yL and 3yL, lactating cows scanned at 2.5 and 3.5 years of age; Santa Gertrudis herds mated a proportion of heifers at yearling so that some 2.5-year-olds are first-lactation cows (2yL) and 3yL will include first- and second-lactation cows in that breed. n = number of individuals with EBVs >40%accuracy included in the correlation matrix. EBVs for Santa Gertrudis 2yH not included due to low additive variance and zero accuracy; Droughtmaster had few EBVs with >40% accuracy for 2yH weeks pregnant and no days to calving EBVs so not included

Trait	2yH weeks pregnant	3yL weeks pregnant	Days to calving
	Brahman (n = 4207)		
600d CL score	0.39	0.06	–0.08
2yH weeks pregnant	–	0.25	–0.23
3yL weeks pregnant		–	0.25
	Santa Gertrudis (n = 2339)		
600d CL score	–	0.31	–0.38
2yL weeks pregnant	–	0.34	–0.41
3yL weeks pregnant		–	0.58

Table 7-6 Genetic and phenotypic correlations among heifer corpus luteum (CL) score, body condition score (BCS) and rump fat (P8 fat) at 600 days

Genetic correlations above diagonal, phenotypic below, estimates from bivariate analyses; standard errors are shown in parentheses; 600d, heifers scanned at 600 days

Trait	600d CL score	BCS	P8 fat
	Brahman		
600d CL score		0.36 (0.18)	0.29 (0.18)
BCS	0.19 (0.03)		0.85 (0.07)
P8 fat	0.19 (0.02)	0.58 (0.02)	
	Droughtmaster		
600d CL score		0.31 (0.20)	0.25 (0.18)
BCS	0.17 (0.03)		0.43 (0.16)
P8 Fat	0.20 (0.03)	0.44 (0.02)	
	Santa Gertrudis		
600d CL score		0.49 (0.19)	0.10 (0.18)
BCS	0.30 (0.02)		0.74 (0.11)
P8 fat	0.31 (0.02)	0.55 (0.02)	

Table 7-7 Simple correlations of female reproduction-trait estimated breeding values (EBVs) with carcass-trait EBVs for Brahman, Droughtmaster and Santa Gertrudis breeds

600d, heifers scanned at 600 days; 2yL and 3yL, first-lactation cows scanned at 2.5 and 3.5 years respectively. n = number of individuals with EBVs >40%accuracy included in the correlation matrix; EBVs for intramuscular fat (IMF%) were not available for Brahman

Trait	Rump fat	Rib fat	EMA	IMF%
	Brahman (n = 4207)			
600d CL score	0.12	0.09	-0.11	
3yL weeks pregnant	0.15	0.08	0.10	
	Droughtmaster (n = 1516)			
600d CL score	0.10	0.10	0.12	0.10
3yL weeks pregnant	0.012	0.00	-0.11	0.41
	Santa Gertrudis (n = 2339)			
600d CL score	-0.28	-0.21	-0.11	0.11
2yL weeks pregnant	0.00	0.04	-0.30	0.41

The heritability estimates for first-lactation pregnancy from the current study were generally similar (Cavani *et al*. 2015; Terakado *et al*. 2015) or greater (Cammack *et al*. 2009; Berry *et al*. 2014) than were those reported from studies of other breeds internationally. The heritability estimates for first-lactation anoestrus from the study of Johnston *et al*. (2014*a*) were moderate to high and a key finding of that study. The strong estimated heritability may be resultant of the robust experimental design in the research herds and the ability of regular ultrasound scans to more precisely determine when the cows returned to oestrus post-calving. The heritability estimates of Johnston *et al*. (2014*a*) in Brahman cows were associated with a considerably higher standard error (0.19) than that for the Tropical

Composite cows (0.09) and those estimated for weeks pregnant in the current study (0.06–0.10). Nonetheless, the results signify marked differences among heritability estimates for related traits measured across breeds and herds. The differences emphasise the need for breed-specific genetic variances and for strong genetic linkage among herds contributing performance data to within-breed genetic evaluation programs.

The simple correlation between EBVs for 600-day CL score in heifers and weeks pregnant in first-lactation cows was low in Brahman herds (0.06) and moderate in Santa Gertrudis herds (0.31). Johnston *et al*. (2014*b*) estimated genetic correlations between age at first CL and pregnancy rate in first-lactation cows to be considerably stronger for Brahman (–0.14) and for Tropical Composite (–0.68) females in the rigidly controlled research herds. The genetic relationship between 600-day CL score and days to calving, estimated in the current study by simple correlation of the trait EBVs, was low in Brahman herds (–0.08) and moderate in Santa Gertrudis herds (–0.38), but favourable. The genetic correlation between age at first CL and days to calving in first-lactation cows estimated by Johnston *et al*. (2014*a*) was 0.08 in Brahman and 0.43 in Tropical Composite females, similar in magnitude to the seed-stock herd estimates, and also favourable. The results indicated that selection for earlier age at first CL, or for increased incidence of CL in heifers at 600 days will have correlated responses in pregnancy rate and days to calving in first-lactation cows, particularly in Santa Gertrudis and Tropical Composite breeds.

Correlation between EBVs for weeks pregnant in first-lactation cows and days to calving EBVs in the seed-stock herds was moderate for both Brahman (–0.23) and Santa Gertrudis (–0.41) breeds. In the research herds, Johnston *et al*. (2014*a*) estimated genetic correlations among the reconception traits measured in first-lactation cows (pregnancy rate, anoestrus interval and days to calving) to be close to unity in both Brahman and Tropical Composite herds, suggesting that the traits may be controlled by the same genes. Johnston *et al*. (2014*a*, 2014*b*) also reported that age at first CL and reconception traits were genetically associated with lifetime reproductive performance (genetic correlations ranged from 0.30 to 0.55).

Genetic correlation estimates of 600-day CL score were stronger with BCS than with P8 fat depth, particularly in Santa Gertrudis heifers. Johnston *et al*. (2009) and Wolcott *et al*. (2014*a*) reported

genetic correlations of age at first CL with BCS and P8 fat depth at 600 days to have similar trends in Brahman heifers, but not in Tropical Composite heifers. The Santa Gertrudis heifers at 600 days in the current study were heavier, leaner and less variable in P8 fat than were the Brahman heifers. The results suggested that body mass and overall body condition could be more important than subcutaneous fat reserves for the attainment of puberty in some breeds.

Correlations of EBVs for 600-day CL score and weeks pregnant in first-lactation cows with body composition trait EBVs within Brahman and Droughtmaster breeds were generally low and showed no consistent trends or antagonisms. These results suggest that selection for increased fertility would have no adverse effects on fatness or muscling in those breeds. However, the correlations between reproduction and body- composition traits in Santa Gertrudis cattle indicated that selection for increased early pregnancy in first-lactation cows may be associated with a higher IMF% and a lower EMA. Wolcott *et al*. (2014*b*) also reported contrasting genetic associations between EMA and first-lactation pregnancy rate in Brahman (–0.03) and Tropical Composite (0.50) breeds. In Brahman cattle, Johnston *et al*. (2009) found moderate genetic correlation between age at first CL and fatness in heifers (–0.35) but not in their steer siblings (0.04). The genetic correlations reported by Johnston *et al*. (2009) indicated that selection for increased heifer fatness at 600 days would reduce age at CL in both Brahman and Tropical Composite breeds. By contrast, the correlation between rump fat and 600-day CL score EBVs (–0.28) in Santa Gertrudis in the current study suggested that selection for increased fatness in heifers would be associated with reduced incidence of CL at 600 days, or, at best, that presence of CL in Santa Gertrudis heifers is not dependent on fat cover at the rump. As discussed previously, bodyweight and condition may be more important for attainment of a CL at 600 days than is fatness recorded at the rump P8 site in Santa Gertrudis heifers.

Developments in genomic technologies aim to improve the accuracy of selection, particularly for the difficult-to-measure reproductive traits (Hawken *et al*. 2012; Zhang *et al*. 2014; Fortes *et al*. 2016; Reverter *et al*. 2016). However, collection of phenotypes will still be needed, in resource populations at least, to refine genomic predictions. Further work is required to determine the genetic relationship of these single-scan reproductive traits with measures of whole-herd productivity and how they might be

implemented into the genetic evaluation process of BREEDPLAN. However, heritability, relationships with days to calving and the range of EBVs provided evidence to suggest that 600-day CL score and weeks pregnant traits might add value to the current genetic evaluation, possibly by contributing to an index for reproductive capability.

Conclusions

The use of ultrasound provides a practical means of detection of early sexual maturity and pregnancy in heifers and lactating cows. These attributes of fertility provide information to derive heritable traits that should prove useful in genetic evaluation programs. For this form of reproductive-trait recording to become widely implemented in Australian seed-stock herds, the cost of scanning replacement heifers at 600 days of age has to be perceptibly outweighed by the proven benefits of selecting superior individuals.

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Chapter 8. Using Temporal Associations to Measure Reproductive Traits

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Using temporal associations to determine postpartum oestrus in tropical beef cows

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Abstract. The radio frequency identification (RFID) technology introduced with the National Livestock Identification System has increased the precision of livestock management. Tag readers incorporated in walk-over-weighing systems have enabled automated collection of daily RFID sequential data as cattle access water. The temporal sequence of individuals accessing a watering point in a rangeland grazing system could potentially provide knowledge of key aspects of animal behaviour. The current study investigated the use of the shortest daily average interval of time from cow to bull (TTB) coming to water over a 29-day period to predict postpartum oestrus events. Fifteen Brahman and 15 Belmont Red cows mated to bulls of the same breed in separate paddocks were fitted with proximity loggers, heat-mount detectors and were ovarian-scanned with ultrasonics to determine the timing of postpartum oestrus. The data collected from these devices were compared with RFID sequence data of the bulls following cows to water to evaluate whether TTB alone could predict oestrus activity. At the start of the experimental period, mean (±s.d.) weight and days postpartum of the Brahman cows were 527 (±43.4) kg and 89 (±18.4) days respectively, and of the Belmont Red cows 513 (±54.1) kg and averaged 66 (±19.6) days postpartum. Six of the 15 Brahman cows and 9 of the 15 Belmont Red cows displayed oestrus activity, as indicated by increased contact with the bull, an activated heat-mount detector and the presence of an ovarian *corpus luteum*. The sensitivity and specificity of TTB as an indicator of oestrus events across the groups were 0.65 and 0.60 respectively. Temporal sequence data have the potential to contribute to the determination of oestrus and date of conception.

Additional keywords: anoestrus, behavior, behaviour, estrus, reproduction.

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Introduction

The National Livestock Identification System (NLIS) was introduced in Australia in 1999 to meet the requirements of some export red-meat markets and enable individual animals to be traced for the purpose of food safety. The system became mandatory in most states by 2005 and the radio frequency identification (RFID) technology that came with the NLIS system has increased the precision of livestock management. RFID-tag readers incorporated in walk-over-weighing (WoW) systems, for example, have enabled automated collection of daily weights and RFID sequential data as cattle access water. The temporal sequence of individuals accessing a watering point in a rangeland grazing system has been proven by Menzies *et al*. (2018) to determine maternal parentage with 97% accuracy and has the potential to provide knowledge of other key aspects of reproductive behaviour in cattle.

Postpartum anoestrus is recognised as a key contributor to poor reproductive performance in tropical beef cattle (Burns *et al*. 2010). Recent research in northern Australia has shown that the interval from calving to first postpartum oestrus is heritable, indicating the potential for genetic improvement of reproductive efficiency (Johnston *et al*. 2014*a*). However, adoption of genetic evaluation and breeding strategies by beef producers is slow and a major barrier to adoption is the perceived challenge of collecting accurate pedigree and performance data (ABRI 2015). Developing automated methods of recording to achieve precise measures of reproductive events (e.g. oestrus, conception, calving, re-conception) in livestock populations may help increase adoption of genetic technologies by beef producers.

Recent studies using UHF proximity loggers have shown that associations between cattle in tropical beef production systems can provide a reliable indicator of oestrus (O'Neill et al. 2014). The current study used RFID readers to monitor cattle movement to determine whether the temporal sequence of individuals accessing a watering point in a rangeland grazing system can identify cows in oestrus. The shortest daily interval of time from cow to bull (TTB) coming to water was used to predict the day of postpartum oestrus in tropical beef cows.

Materials and methods

Animals

Animal ethics approval to conduct the experimentation was provided by the CQUniversity Animal Ethics Committee (Approval number 20244). Two groups of

40 lactating cows, one Belmont Red and the other Brahman, and their calves were located in separate paddocks at Belmont Research Station (23.22°S, 150.38°E), ~26 km north of Rockhampton, central Queensland, Australia. The Belmont Red cows were mated to a single bull, while the Brahman cows were mated with two bulls of the same breed. The experimental period ran from 6 February 2017 through to 6 March 2017, during which 15 cows and the bulls in each group were fitted with devices (described in the following sections) to record oestrus behaviour.

At the start of the experimental period, the mean weight (±s.d.) of the Belmont Red cows was 513 (±54.1) kg and they were an average 66 (±19.6) days postpartum; the Brahman cows averaged 527 (±43.4) kg and 89 (±18.4) days postpartum. The Belmont Red group grazed 50 ha and the Brahman group grazed 65 ha of open woodland containing mostly improved pasture species (predominately *Chloris gayana* and *Panicum maximum*). Water in both paddocks was provided in a trough fed by underground bore water. The trough was the only water source and was enclosed so that the cattle accessed the water via a race and a one-way spear gate integrated in a WoW system (Menzies *et al*. 2018).

Data collection

Ultrasound scans were conducted at the beginning and end of the 4-week experimental period to monitor cyclic ovarian activity and identify the presence or absence of a *corpus luteum* (CL) to indicate that ovulation had occurred. A further scan was conducted 8 weeks later to determine fetal age and approximate time of conception in pregnant cows. The cows and bulls in each group were fitted with collars incorporating proximity loggers (Sirtrack, Havelock North, New Zealand) pre-set to record cow–bull contact within a range of 4 m. The cows were also fitted with heat-mount detectors (Kamar®, Kamar Products Inc., Zionsville, USA) for visual validation of standing oestrus behaviour. Telemetry components of the WoW allowed 24-h remote monitoring of RFID sequence and digital images of heat-mount detectors as the cattle accessed the single watering point. Cameras mounted above the WoW were triggered by the RFID reader (either Tru-Test XRP2, Tru-Test, Auckland, NZ or Aleis 8051, Aleis, Capalaba, Australia) using Raspberry Pi (Raspberry Pi Foundation, Cambridge, UK) technology to take an image as the animal stepped onto the weigh platform (see Fig. 1).

Data processing and analysis

RFID data files and digital images were streamed wirelessly via the Telstra Next G™ telecommunications network directly to a server for downloading to a personal computer. Cow–bull contact data recorded by the proximity loggers were manually downloaded from the devices at the end of the study period, using the Sirtrack administration tool v1.1.06 (Sirtrack, Havelock North, New Zealand) and stored in CSV format. Daily cow–bull contacts were plotted over time (see Fig. 2) and significant differences between peak daily contacts of cows exhibiting oestrus during the study period and peak daily contacts of anoestrus cows were determined using the two-sample Student's *t*-test of sample means and standard deviations. RFID sequence was used to calculate an average of time between cows and the bull moving through the WoW system. Code was written in R v3.2.3 (R Foundation, Vienna, Austria) to develop an algorithm that initially compared the time that individual cows and bulls passed the RFID reader and identified the shortest time interval between the bull and each individual cow on each day. A moving average of the shortest time interval was then calculated over 3 days using data from either side of a central daily value. The moving average aimed to reduce the impact of short-term fluctuations and identify periods when a bull and cow consistently (over a 3-day period) accessed water in close proximity. The sensitivity and specificity of TTB as a test for cows in oestrus were calculated as the true positive rate and the true negative rate respectively.

Results

Ultrasound scanning

Ultrasonography of the cow reproductive tracts identified the presence of an ovarian CL in six of the Brahman cows and nine of the Belmont Red cows, indicating that these 15 cows had ovulated during the 29-day observation period.

Figure 8-1 A cow with activated heat-mount detector is closely followed through a walk-over-weighing (WoW) system by a bull.

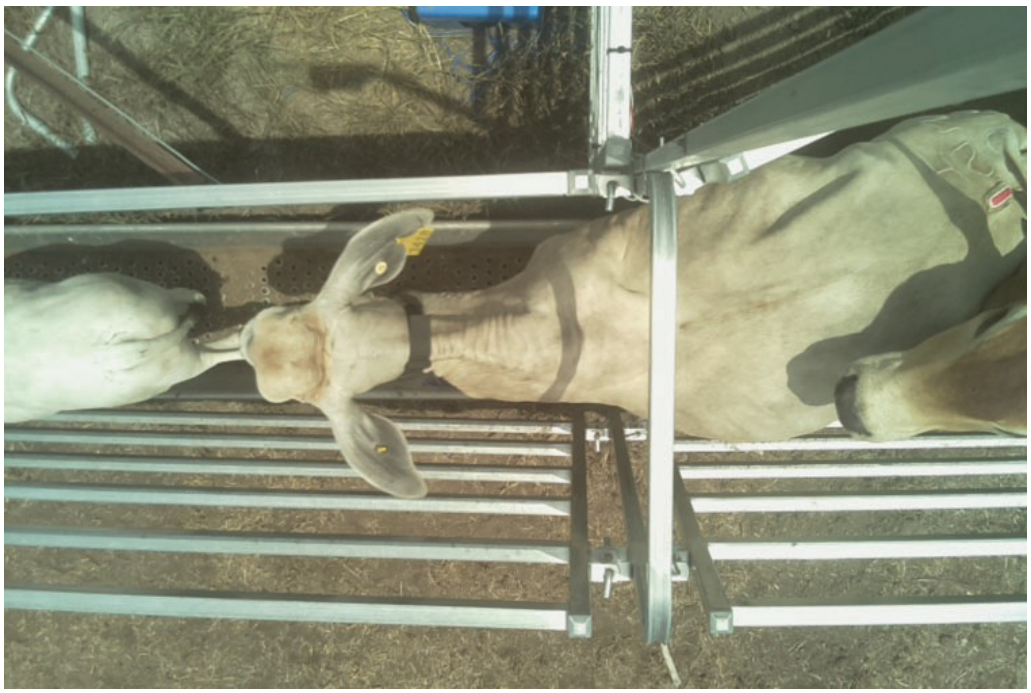
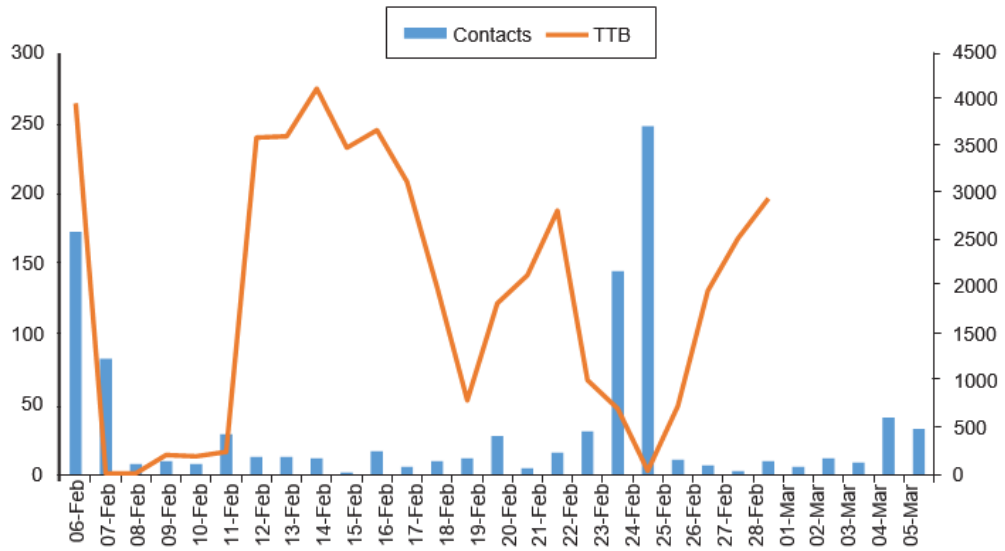


Figure 8-2 Graph showing typical distribution of daily contacts (bar plot; left y-axis) of a cow in oestrus with the bull and a rolling average of time (line plot in s; right y-axis) to the bull following her through a walk-over-weighing (WoW) system



The remaining 15 cows either had not returned to cyclic oestrus activity postpartum or had a CL and an early pregnancy, so had cycled and conceived before the start of the study period and, hence, did not ovulate during the study period. For the purpose of definition in the present study, the cows that did not ovulate were termed 'anoestrus' or 'acyclic'. Oestrus or cyclic cows were defined as those that ovulated during the study period and were determined by a combination of CL presence, a peak in daily contact with the bull and an activated heat-mount detector. Fetal aging indicated that of the 15 cows that had ovulated, 13 had also conceived during the study period.

Proximity loggers and heat-mount detectors

In the Brahman group, activation of heat-mount detectors coincided with the peak in cow–bull daily contact of all six cows exhibiting oestrus. In the Belmont Red group, activated heat-mount detectors aligned with peaks in daily bull contact for seven of the nine cyclic cows. One detector was not fully activated and a second was not seen activated but noticed missing just after the peak in bull contact. Across the groups, the activated heat-mount detectors reliably aligned with peaks in cow–bull contact in 87% of individuals.

In each breed group, peaks in daily cow–bull contact were greater ($P < 0.001$) for the cows in oestrus than for anoestrus cows. Peak daily contact with the bull at the time of oestrus for the six cyclic Brahman cows averaged (±s.d.) 174 (±58.2) contacts per day, while the nine acyclic Brahman cows averaged a maximum of 57 (±18.9) daily contacts during the study period. Peak daily contact in the nine cyclic and the six acyclic Belmont Red cows averaged 104 (±35.6) and 44 (±19.8) respectively. For two of the Brahman cows, daily bull contact peaked twice during the 29-day study period, indicating that they each had two oestrus events 18 or 19 days apart. Figure 2 shows the number of daily contacts of a cow with the bull (bar plot), with peaks 19 days apart indicating two oestrus periods. Fetal aging confirmed that this cow conceived at the time of the second oestrus event.

RFID sequence (time to bull)

Average time to bull following cows in oestrus was typically less than 240 s, with an average (±s.d.) of 115 (±74.7) seconds in the Brahman group and 178 (±126.2) seconds in the Belmont Red group. When cows were not in oestrus, TTB was longer ($P < 0.01$) and averaged 2988 (±2734.5) seconds in the Brahman group and 2413 (±1758.6) seconds in the Belmont Red

group. The line plot in Fig. 2 gives an example of TTB dropping to below 240 s during oestrus events, signified by peaks in daily bull contact (bar plot).

The number of oestrus events and the number of true positive and falsely predicted oestrus events across cow groups is presented in Table 8-1. Sensitivity was 0.65 and represents the probability that TTB was short (<240 s) when the cow was in oestrus (true positive rate). Specificity was 0.60 and represents the probability that TTB was longer (>240 s) when cows were not in oestrus (true negative rate).

Short TTB reliably predicted oestrus in six of the eight (75%) oestrus events observed in the Brahman cows and in five of the nine (56%) oestrus events in the Belmont Red group. Two bulls were used in the Brahman group, which is likely to have added to the sensitivity of RFID sequence to determine cows in oestrus in that group.

Table 8-1 Number of true positive and true negative oestrus events detected by the shortest interval of time from cow to bull accessing a watering point (TTB)

Sensitivity: 0.65 (95% CI: 0.38–0.86). Specificity: 0.60 (95% CI: 0.32–0.84)

Test (TTB)	Oestrus event		
	Present	Absent	Total
Positive (short TTB)	11	6	17
Negative (long TTB)	6	9	15
Total	17	15	

It was observed that while the more dominant bull was engaging with cows away from the WoW compound, his subordinate followed oestrus cows as they accessed the watering point.

Discussion

Monitoring RFID sequence allowed an evaluation of temporal associations of bulls engaging with cows in oestrus as they moved through a one-way race to access water. The bulls typically followed closely behind cows in oestrus and a simple algorithm of a daily moving average of time from cow to following bull was developed to automatically identify the day of postpartum oestrus and, hence, determine postpartum anoestrus interval. The accuracy of the test was reduced by false negative and false positive cases. False negative cases were oestrus events not detected by the algorithm and these may be moderated with the introduction of more bulls to the herd. However, the presence of more bulls may also result in an unfavourable increase in false positive cases. The latter represent anoestrus cows falsely flagged as having engaged with the bull and were generally chance associations with pregnant cows. These coincidental contacts may be tempered with knowledge of the full postpartum oestrus behaviour profile of the cows rather than just the 29-day window monitored in the current study.

Further work is warranted to improve the accuracy of predicting oestrus events using RFID sequence to detect bull proximity.

Previous studies have evaluated the use of proximity loggers to explore changes in temporal associations between cattle pairs (O'Neill *et al*. 2010; and 2014; Patison *et al*. 2010; Swain and Bishop-Hurley 2007). Similar to the findings of the current study, O'Neill *et al*. (2014) found that peak daily contacts with the bull were significantly higher in cows exhibiting oestrus. Peaks in daily cow–bull contacts tended to be higher in the Brahman group, but may be a result of individual differences in bull experience rather than differences in breed. The bull used in the Belmont Red group was a 2-year old in his first breeding season compared with the more experienced 4- and 5-year old bulls in the Brahman group, which were in their second and third breeding seasons respectively. A difference was also seen in RFID sequence where the older bulls tended to more closely follow cows in oestrus as they accessed the WoW. It was observed that the Belmont Red bull tended to visit the WoW less frequently than did the Brahman bulls and appeared to prefer to engage with cows in oestrus while in the paddock. These observations also indicated that identification of cows in oestrus using temporal associations (RFID sequence) should be more complete in multi-sire mating groups, as bulls in competition tend to follow cows in oestrus more frequently than a single bull without rivals.

Menzies *et al*. (2018) applied a half-weight association index to RFID sequence data between cows and calves to reliably determine maternal parentage. It is also feasible that the technology could be developed to similarly determine age at first oestrus (puberty) in peri-pubertal heifers (O'Neill *et al*. 2010), removing the need for regular ovarian scanning. Such a suite of tools would enable producers to automatically record maternal parentage and performance data, both essential for identification of genetically superior individuals. The advantage of using RFID sequence to study temporal associations compared with logged contact data is that the RFID sequence data could be streamed live via telecommunications networks and relied only on an RFID ear- tag, rather than fitting and removing collar-mounted sensors.

The RFID sequence technology as it exists cannot replace per rectal pregnancy testing and fetal aging to assess mating success or failure and needs to be tested on a larger number of animals over consecutive breeding seasons, but advancements in the technologies could feasibly provide a combination of sensing

devices to continually and autonomously monitor reproductive behaviour. The knowledge gained offers increased precision of determining oestrus events, which should assist early culling decisions and enhance genetic improvement of reproductive efficiency.

Conclusions

The study used RFID sequence data to develop an effective tool that producers could use to identify cows with extended postpartum anoestrus intervals. Further investigation is warranted to develop the technology using larger numbers of animals and to measure other key reproductive traits, such as pubertal age in heifers, with the aim of providing producers with capabilities to identify early indicators of lifetime reproductive performance.

Conflicts of interest

The authors declare no conflicts of interest.

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Chapter 9. Discussion

Discussion

Lifetime reproductive performance of a cow is only established at the end of her breeding life, hence measurement and selection for that trait alone can only promote genetic improvement retrospectively. Component traits related to female and male fertility, however, can be measured earlier in life and pose as alternative selection criteria for genetic improvement of reproductive performance. Lifetime reproductive performance here is defined as the average weaning rate of the cows over six years of study. The experimentation conducted here aimed to examine the usefulness of a range of male and female fertility traits as candidates for indirect selection criteria. The specifics of trait description, estimated genetic parameters and methods used to refine trait measurement are discussed in relevant sections of each chapter. Although it was beyond the scope of this research to investigate the potential of all possible new and developing technologies to measure aspects of fertility, insight into refining and automating the collection of data is provided. The objective of this chapter is to provide a summary of the key findings of the research, compare the results with contemporary literature reports and make suggestions for future research direction.

9.1 Key component traits

The results of research presented in this thesis identified age at puberty, scrotal circumference, percent normal sperm, heifer pregnancy rate, days to calving and post-partum anoestrus as key components of reproduction. These traits have a combination of moderate to high heritability, genetic correlation with lifetime reproductive performance and the ability to be measured early in life. Breeding strategies that include selection for these key component traits of reproductive performance would be well advised. Tables 9-1 and 9-2 provide a summary of the genetic parameters reported world-wide for a range of female and male fertility traits in tropical beef breeds over the last decade and are compared with those obtained in the present study in the following sections.

9.1.1 Female reproductive traits

Heifer age at puberty (measured as age at first CL) in the tropically adapted breeds studied here was highly heritable (0.52 to 0.57) and favourably associated with lifetime reproductive performance (-0.36 to -0.51). These attributes were a key finding of our research and promote age at puberty as a useful selection criterion to not only reduce age at puberty but also to genetically improve lifetime reproduction rate. The estimates of heritability of age at puberty reported here were higher than the estimate of 0.42 reported by Vargas *et al*. (1998) in a study

of Brahman cattle in Florida, USA. No other studies reporting estimates of genetic parameters for age at puberty in tropical beef cattle breeds were found. Our studies used ultrasonography to determine the presence of an ovarian CL, providing absolute evidence that ovulation has occurred. Determining presence of an ovarian CL as opposed to visual observation of standing heat may likely be a more accurate determination of first pubertal oestrus.

Table 9-1 Studies reporting genetic parameters for female reproductive traits in tropical cattle breeds

LRP = Lifetime reproductive performance measured as weaning rate over 6 years or stayability in the Brazilian studies; n = number of animals included in the study

Trait	Heritability	Correlation with LRP	Country, breed (n)	Source
Age at puberty	0.57	-0.36	Australia, Brahman (1,007)	Johnston *et al*. (2009)
	0.52	-0.29	Australia, Composite (1,108)	Johnston *et al*. (2009)
Heifer pregnancy rate	0.42	0.51	Australia, Brahman (1,020)	Johnston *et al*. (2014*a*)
	0.10	0.65	Australia, Composite (1,117)	Johnston *et al*. (2014*a*)
	0.57		Brazil, Nellore (28,887)	Eler *et al*. (2014)
	0.46	0.59	Brazil, Nellore (18,063)	Santana *et al*. (2015)
Age at first calving	0.18	-0.60	Brazil, Nellore (12,883)	Eler *et al*. (2014)
	0.19		Columbia, Brahman (19,991)	Martinez *et al*. (2016)
	0.13	-0.06	Brazil, Nellore (12,161)	Schmidt *et al*. (2018)
Calving interval	0.06		Brazil, Canchim (10,871)	Buzanskas *et al*. (2013)
	0.02 to 0.06	-0.16 to -0.40	Brazil, Nellore (5,724)	Grossi *et al*. (2016)
	0.06		Columbia, Brahman (42,491)	Martinez *et al*. (2016)
Days to calving	0.22	-0.54	Australia, Brahman (1,020)	Johnston *et al*. (2014*a*)
	0.13	-0.57	Australia, Composite (1,117)	Johnston *et al*. (2014*a*)
	0.12		Brazil, Nellore (33,500)	Schmidt *et al*. (2019)
Post-partum anoestrus interval	0.51	-0.62	Australia, Brahman (1,020)	Johnston *et al*. (2014*a*)
	0.26	-0.87	Australia, Composite (1,117)	Johnston *et al*. (2014*a*)

Johnston *et al*. (2014*a*) reported that heifer pregnancy rate and post-partum anoestrus interval (PPAI), respectively, were moderately (0.42) to highly (0.51) heritable in Brahman females but only low (0.10) to moderate (0.26) for the tropical Composite females. Lower heritability of heifer pregnancy rate may reflect the higher incidence and less variation expressed for that trait in the Composite breed studied. Studies in Brazilian Nellore cattle also report moderate (0.46) to high (0.57) heritability for heifer pregnancy rate (Eler *et al*. 2014; Santana *et al*. 2015). The implications of low heritability in the tropical Composite breed might be that heifer pregnancy rate is not suitable for use in genetic evaluation programs for that breed.

No other studies reporting genetic parameters for PPAI were found. Genetic correlation of heifer pregnancy rate and PPAI with lifetime reproduction in the current study was high (0.51 and -0.87, respectively). Similar high genetic correlation (0.59) with lifetime reproductive performance was reported for heifer pregnancy rate in Nellore cattle (Santana *et al*. 2015). Heifer pregnancy rate records her first mating outcome and PPAI records her ability to re-conceive after her first calf. Together these traits provide an indication of the reproductive capability of the young breeding female. Strong genetic correlation of heifer pregnancy rate and PPAI with lifetime reproduction provides evidence that the traits are controlled by many of the same genes. Using breeding strategies that include heifer pregnancy rate and PPAI as selection criteria would engender a favourable response in lifetime reproductive performance.

Table 9-2 Studies reporting genetic parameters for male reproductive traits in tropical cattle breeds

LRP = Lifetime reproductive performance measured as weaning rate over 6 years or stayability in the Brazilan studies; the parameters presented by Raidan *et al*. (2019) are genomic estimates using data from Corbet *et al*. (2013), post-partum anoestrus interval substituted as the LRP trait in that study; the genetic correlation with LRP for Australian Brahman and Composites were sourced from Johnston *et al*. (2014*b*).

Trait	Heritability	Correlation with LRP	Country, breed (n)	Source
Scrotal circumference	0.65	0.14	Australia, Brahman (1,639)	Corbet *et al*. (2013)
	0.46	0.16	Australia, Composite (2,424)	Corbet *et al*. (2013)
	0.40		Brazil, Nellore (8,443)	Terakado *et al*. (2015)
	0.50	0.29	Brazil, Nellore (49,283)	Santana *et al*. (2015)
	0.52	0.50	Brazil, Nellore (27,675)	Kluska *et al*. (2018)
	0.44		Brazil, Nellore (135,862)	Schmidt *et al*. (2019)
Percent normal sperm	0.08		Brazil, Nellore (2,284)	Siqueira *et al*. (2012)
	0.15		Brazil, Nellore (17,648)	Silva *et al*. (2011)
	0.19		Brazil, Nellore (5,903)	Silveira *et al*. (2012)
	0.25	0.43	Australia, Brahman (1,639)	Corbet *et al*. (2013)
	0.20	0.41	Australia, Composite (2,424)	Corbet *et al*. (2013)
	0.13	-0.66*	Australia, Brahman (1,116)	Raidan *et al*. (2019)*

Heritability of days to calving (DTC) in the Australian Brahman (0.22) and Composite breeds (0.13) studied here were moderate to low (Johnston *et al*. 2014*a*) and higher than earlier estimates reported for Angus (0.11; Johnston and Bunter 1996) and Brahman (0.09; Meyer *et al*. 1990) herds in Australia. The estimate of heritability for DTC reported by Johnston *et al*. (2014*a*) for an Australian Composite breed (0.13) was similar to that reported for Brazilian Canchim (Mucari *et al*. 2007) and Nellore (Forni *et al*. 2005; Schmidt *et al*. 2019) breeds. Although DTC has a lower heritability than other fertility traits (e.g. age at puberty), estimates of strong genetic correlation with lifetime performance (-0.54 to -0.57) presented in the current study indicate the usefulness of DTC as an indirect selection criteria. DTC has the advantage

of being uncomplicated to measure; simply requiring records of bull exposure date and calving date for calculation. Hence the recommendation by Meyer *et al*. (1990) for the inclusion of days to calving in genetic evaluation programs.

The measurement of other female reproductive traits has been reported for tropical beef cattle breeds and include age at first calving (AFC) and calving interval (Table 9-1). AFC was not measured in the current study mainly due to differences across Australian breeds and herds in age at first exposure to bulls; some herds have the ability to mate heifers as yearlings while many mate heifers as 2-year olds. When mated at 2-year old, the majority of heifers have commenced cycling, so the record of AFC poorly reflects the genetics of earlier sexual maturation. Calving interval was not measured in the current study due to a combination of trait measurement not being possible until later in life and previous reports of low heritability (e.g. 0.05; Forni *et al*. 2005). Recent reports of heritability (Table 9-1) were low for both AFC (<0.20) and calving interval (<0.10) in South American tropically adapted beef breeds. Estimates of genetic correlation of AFC with lifetime reproductive performance in Brazilian Nellore (Table 9-1) varied from -0.15 and -0.60. The reasons for such variation were not clear but may reflect differences in statistical models used (e.g. Bayesian versus classical statistics) in data analyses. Estimates of genetic correlation of calving interval with lifetime performance in Nellore cattle (Grossi *et al*. 2016) were low to moderate (-0.16 to -0.40) depending on whether the trait was measured as first, second or average calving interval.

9.1.2 Male reproductive traits

It has previously been established in temperate *Bos taurus* breeds that scrotal circumference is moderately heritable and genetically related to measures of female reproductive performance (Toelle and Robinson 1985; Martinez-Velázquez *et al*. 2003). Scrotal circumference (SC) is relatively easy to measure on peri-pubertal bulls and included as a male fertility trait for genetic evaluation in BREEDPLAN (Graser *et al*. 2005). The estimated heritability of SC measured in the tropically adapted breeds studied here was generally high for Brahman (0.65) and moderate for tropical Composite (0.45) bulls. Genetic correlation of yearling SC with age at puberty in females was moderate in both breeds (-0.21 in Composite bulls to -0.41 in Brahman bulls). In addition, yearling measurements of SC had stronger genetic correlation with heifer age at puberty than SC measured at 18 or 24 months of age. Bonamy *et al*. (2018) reported similar results of earlier measures of SC better reflecting female precocity in a South American Angus herd.

Genetic correlation of SC with lifetime reproduction was generally low but favourable for both breeds (~0.15). The low genetic correlation suggests that SC is not a good predictor of female lifetime reproductive performance. Recent studies of genetic parameters for scrotal circumference in the tropically adapted Nellore breed, however, report moderate to high heritability (~0.50) and moderate genetic correlation (0.29 to 0.50) with lifetime reproductive performance. The Brazilian studies included a much larger sample of the population with higher accuracy of parameter estimation. Further study is warranted on larger samples of Australian breeds to update estimates of genetic correlation between scrotal circumference and lifetime reproduction.

The data reported in the results chapters of this thesis confirm that aspects of semen quality are moderately heritable and genetically related to female reproductive traits but varied with breed and age of measurement. The heritability of percent morphologically normal sperm (PNS) collected at 12, 18 and 24 months of age was generally moderate. For Brahman bulls, heritability of PNS was highest when measured at 18 months of age (0.25) and for Composite bulls when measured at 12 months (0.41). Genetic correlation of PNS with female lifetime weaning rate was highest in Brahman when measured at 24 months (0.49) and highest in Composite bulls when measured at 18 months (0.41). The breed difference is likely a function of earlier age at puberty with Composite bulls able to produce higher quality semen at a younger age and implies that measurement of PNS for genetic evaluation programs could be made earlier in Composite bulls. Despite the relatively higher cost to measure PNS (compared to measuring SC), some seed-stock breeders are making the investment to record PNS on their bull progeny prior to 24mths of age for inclusion in sale catalogues. Percent normal sperm is potentially a useful genetic predictor of lifetime weaning rate and is now included in the genetic evaluation programs for Australian Brahman and Santa Gertrudis breeds run by BREEDPLAN. Research by Hagiya *et al*. (2017) in Japanese dairy cattle similarly showed favourable genetic correlation between semen quality and PPAI suggesting that selection for better semen quality will have a correlated response in reproductive efficiency. Additionally, research by Schatz *et al*. (2010) has demonstrated that the inclusion of percent normal sperm in a balanced selection index improved heifer pregnancy rates by greater than 35% over 10 years.

Despite the moderate to high heritability of the circulating blood hormones in young males studied here (LH, inhibin and IGF-1), genetic correlation with other male traits and measures of lifetime reproductive performance were generally low and inconsistent. Measurement of blood hormone levels was costly and required specialist skills for blood sampling and

laboratory assays. Subsequently, these blood hormone traits could not be recommended as useful indicators of lifetime reproductive performance.

9.1.3 Maternal effects

Maternal genetic effects (additive variance due to dam, V_m) on the traits were not partitioned in our studies. Without dams having their own records and also progeny with records, the partitioning of V_m to estimate the contribution of the dam to trait heritability will be inaccurate. For sex limited traits especially (e.g. age of first CL in females and scrotal size in males), repeat progeny records for each dam were sparse and, in some cases, non-existent. To accurately estimate maternal heritability for the traits studied the data structure would need to include generations of daughters, dams, grand dams etc. with records to allow V_m to be modeled well. No estimates of V_m were found for sex limited traits in other studies of cattle breeds. Recording maternal pedigree, however, is important to allow contributions of maternal grandsires to be made to trait heritability estimates via the relationship matrix.

The analyses presented in the experimental chapters of this thesis were performed with and without a random maternal common environmental effect to determine the best fitting model. Additionally, dam age, lactational status and management group were included in the analytical models to appropriately account for these non-genetic effects of dam on the traits studied.

9.2 Trait measurement

Aspects of fertility trait measurement and estimates of genetic parameters had implications for genetic evaluation of the component traits of reproduction. The identification of suitable traits for inclusion in the BREEDPLAN genetic evaluation scheme, to support days to calving and scrotal size, concentrates on heritable traits measurable early in life, particularly pubertal traits, and traits conducive to automated forms of measurement.

9.2.1 Using ultrasound technology

A unique feature of the research presented in this thesis, was that a schedule of repeated ultrasound scans was developed in beef cattle herds to determine time of first ovarian CL and estimate the genetic parameters of the trait. The trait described as age at first CL, determined the age at first pubertal oestrus and was highly heritable in both breeds studied (~0.55). Trait description advocated monthly data recording which may, however, not be practical for most commercial beef operations. Further research determined that the schedule could be reduced to a single ultrasound scan at an age when approximately 50% of the females in the group are

pubertal. The single scan, rather than providing a continuous variable of age at puberty, provided a binomial trait (recording CL present or not at 600d) with moderate heritability (0.21 to 0.33). The single scan strategy enabled the identification of sires with higher proportions of daughters cycling by the time of scanning.

No other published information on the use of ultrasound to establish traits for genetic evaluation in other breeds internationally was found. In a related study, however, Johnston *et al*. (2014*a*) used monthly ultrasound scanning to determine the presence of the first ovarian CL in cows post-partum and establish PPAI. As previously discussed, the PPAI trait was estimated to have moderate to high heritability and strong genetic correlation with lifetime weaning rate. These attributes support the use of age at first CL and PPAI in selection strategies to genetically improve reproductive performance in Australian beef herds.

The phenotypes developed in our research using ultrasound scanning have been examined further in genomics studies. The research of Hawken *et al*. (2012) and Fortes *et al*. (2012 and 2016) explored the association of genomic regions with the age at first CL phenotype in Brahman and tropical Composite breeds of beef cattle. Related studies by Engle *et al*. (2019) and Hayes *et al*. (2019) have investigated the accuracy of genomic predictions of fertility using both the age at CL and 600d CL score phenotypes developed by the research presented in this thesis. Genomic prediction has the potential to improve the accuracy of selection, particularly for the more difficult to measure traits such as age at puberty and PPAI. Continued measurement of these traits requiring serial ultrasound scans could continue in research herds to provide phenotypes for genomic prediction and enhanced genetic evaluation.

9.2.2 Automated trait measurement

Walk-over-weigh (WoW) systems incorporate an RFID reader which can provide the sequence of individuals accessing a watering point. The results of experimentation presented in this thesis, although preliminary, indicate the potential to use RFID sequence data to detect cows in oestrus when followed closely by a bull through a WoW system. The data presented here was recorded on only a small sample of cows and the technology needs to be tested on larger herds grazed extensively. The temporal association algorithms developed could, however, provide a means of automatically detecting oestrus in heifers and cows.

There was no other published information on using temporal associations to determine oestrus in cattle. Temporal associations of cows and calves passing through a WoW system, however, have been used to accurately determine maternal parentage. Menzies *et al*. (2018*a*)

developed an algorithm using RFID sequence data to accurately assign cow-calf pairs. The current study also used proximity loggers to reliably confirm cows in oestrus as those with increased contact with the bull. Previous studies have advocated the use of proximity loggers to identify oestrus (O'Neill *et al*. 2014) and to assign maternal parentage (Swain and Bishop-Hurley 2007) in cattle. The utility of proximity loggers is currently limited as the devices are collar-mounted and require removal every 1 to 2 months to download the logged contact data. Additionally, battery life is limited to approximately 18 months. To gain commercial application in the beef industry, future development of proximity loggers would need to include the ability to download data without device removal and extending battery life beyond 3 years to capture pubertal oestrus and first post-partum anoestrus interval.

Although further research is required to examine the effects of herd and paddock sizes, both RFID sequence and logged contact data could be used to automate oestrus detection. Automated means of detecting oestrus would greatly reduce the time and expense currently required to determine first oestrus in heifers to establish age at puberty and to determine time of first post-partum oestrus in cows to establish PPAI.

9.3 Future research direction

In extensive beef cattle herds, behavioural information can potentially be converted to data to quantitatively assess production parameters. Additionally, if the sensing devices are linked to a telemetry system, the information could be used to continuously monitor animal health, welfare and security. On-animal devices, such as accelerometers and global positioning system (GPS) trackers have been used to provide information on social interactions between individuals in the herd. These social interaction data can provide quantitative information to potentially define time of oestrus and hence determine age at puberty and post-partum anoestrus interval. The use of on-animal devices to automate the determination of oestrus activity and reproductive performance is worthy of further research.

Accelerometers measure the rate of change of velocity on 3 axes (heave, surge and sway). In livestock, important behavioural patterns studied using accelerometers include grazing (Rayas-Amor *et al*. 2017), mating (Abell *et al*. 2017), birth (Fogarty *et al*. 2018) and suckling (Kour *et al*. 2018). Accelerometers have recently been developed in ear-tag form to remotely monitor the movement of free-ranging cattle, and by automated analysis of animal biometrics provide information on grazing activity, reproductive status, health, welfare and security. Ear-tags with accelerometers are currently marketed as HerdDogg™ (HerdDogg Inc., Ashland,

Oregon, USA), CowManager™ (CowManger BV, Harmelen, Netherlands) and eSense™ (Allflex, Capalaba, Queensland). There is, however, a paucity of published information on the use of these devices to automatically determine oestrus and time of birth to establish traits for genetic evaluation and improvement of reproductive performance.

GPS-enabled devices allow the movement of livestock to be tracked in near real time and provide information on the location of individuals with accuracies to around 4 metres (Anderson *et al*. 2013). In cattle herds, geo-location may provide information on reproductive behaviour, such as the location of birth-sites, date of birth and oestrus, inferred from unusual activity. Fogarty *et al*. (2015) used tracking devices on sheep to demonstrate that oestrus in ewes can be identified as a peak in activity and concluded that tracking devices could facilitate improved reproductive management in extensively grazed flocks. Tracking devices could similarly be used to identify reproductive behaviour in cattle but could potentially be more effective if combined with other sensors, such as accelerometers, to provide accurate data on behavioural state (Guo *et al*. 2009; Swain *et al*. 2011). GPS devices for cattle have traditionally been mounted on a collar. Recent developments by CSIRO and Ceres-Tag™, co-funded by MLA Donor Company (https://www.csiro.au/en/Research/AF/Areas/Livestock/Ceres-Tag), aim to manufacture a solar powered ear-tag lasting the life of the animal. Further research is required to test the utility of GPS devices to record reproductive component traits in extensive herds for the estimation of genetic parameters.

Widespread use of RFID and WoW systems already sets in place a framework for remotely recording production traits (Menzies *et al*. 2018*a*). Automation of recording accurate date of birth using WoW data (Menzies *et al*. 2018*b*) will have profound implications for the genetic evaluation of many traits, particularly DTC and gestation length. New and emerging technologies capable of recording reproductive traits could add to these systems to simplify the task of performance recording. The capture of digital or thermal images at WoW units and advances in vision recognition software (Chowdury *et al*. 2016), for example, has potential to provide information on health and physiology of individuals. Automatic measurements of body condition, parasite infestation, udder conformation and testes size of individuals as they voluntarily access a watering point are feasible. Further detailed research is required, however, to develop the concept of using vision recognition software to accurately identify and measure traits like scrotal circumference from digital images.

Current systems of performance recording require high levels of input (i.e. labour intensive) and may be associated with a risk to personal safety (e.g. working closely with large animals).

Biotelemetry has the potential to automatically measure and record the timing of reproductive events such as oestrus, mating, conception, parturition, lactation and re-conception in beef cattle herds grazed extensively. Further research should be directed at new and emerging technologies capable of automating reproductive trait measurement to add to herd management systems and make the task of performance recording less onerous. New technology may be associated with added infrastructure but hopefully the cost of the infrastructure is outweighed by the benefits of automated records for genetic evaluation.

Chapter 10. Conclusions

Conclusions

Measuring aspects of fertility in beef cattle is essential if the breeding objective is to improve reproductive efficiency. Unfortunately, no single measureable trait has the perfect combination of being easily measured early in life, high heritability and high genetic correlation with lifetime reproduction. Key component traits of reproductive performance, however, are moderately heritable and the traits measured in males are moderately genetically correlated with key reproductive performance traits measured in females. Favourable genetic correlation suggests potential to use the component traits as alternative selection criterion to illicit indirect genetic improvement of reproductive performance.

Genetic improvement of reproductive efficiency in north Australian beef herds is an achievable goal and part of the solution to more profitable beef enterprises. The most appropriate strategy for genetic improvement of reproduction would be to include measures of both male and female fertility to formulate estimated breeding values in a balanced selection index. The measurement of most reproductive performance traits to provide data for genetic and genomic evaluation, however, requires sizable input of time and resources. Subsequently, the challenge of data collection remains a barrier to the adoption of genetic improvement strategies by north Australian beef producers.

Automated measurement of key reproductive traits has the potential to reduce inputs and effort required for collection of data for genetic evaluation. Walk-over-weigh systems and on-animal sensors can provide the necessary information to infer reproductive events from changes in behaviour. With further research, automated trait measurement should provide a suite of tools to help reduce the challenge of recording and formatting data, thereby allowing beef producers to more readily develop strategies for genetic improvement of reproductive efficiency.

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