



final report

Project code: B.NBP.0363

Prepared by: David Johnston¹, Tim Grant², Kishore Prayaga⁴
and Jim Walkley³
Animal Genetics and Breeding Unit¹
Department of Agriculture, Fisheries and
Forestry- Queensland²
Cooperative Research Centre Cattle Beef
Quality³
CSIRO⁴

Date published: August 2013

ISBN: 9781925045307

PUBLISHED BY
Meat & Livestock Australia Limited
Locked Bag 991
NORTH SYDNEY NSW 2059

Early predictors of lifetime female reproductive performance

Meat & Livestock Australia acknowledges the matching funds provided by the Australian Government to support the research and development detailed in this publication.

This publication is published by Meat & Livestock Australia Limited ABN 39 081 678 364 (MLA). Care is taken to ensure the accuracy of the information contained in this publication. However MLA cannot accept responsibility for the accuracy or completeness of the information or opinions contained in the publication. You should make your own enquiries before making decisions concerning your interests. Reproduction in whole or in part of this publication is prohibited without prior written consent of MLA.

Abstract

Low weaning rates are common in beef herds in northern Australia. A large breeding project was established to quantify the contribution of genetics to various measures of female reproduction in two diverse tropical genotypes. Specifically the project aimed to identify early-in-life indicator traits that could be used in selection to improve lifetime reproduction rates. Weaning rates in the project were low, particularly in Brahman, and results showed it can be improved through selection by focusing recording on early-in-life female reproduction traits. Traits associated with age at puberty and lactation anoestrus in first-lactation cows were highly variable and moderately to highly heritable in both genotypes. Several male traits were identified, including semen quality traits, that could also be used as indirect selection criteria to improve female reproduction rates. The project established that it is possible to select for improved female reproduction simultaneously with selection for steer traits (growth, carcass, meat quality and feed efficiency), however improvement in both will require recording and appropriate multiple-trait selection strategies.

Executive summary

Female reproduction is an important profit driver in northern Australian beef production systems. Low weaning rates are common, and are mainly the result of extended post-partum anoestrous intervals, particularly in *Bos indicus* cattle. Estimates of heritabilities are also low for traits associated with net reproduction rate in beef cattle, commonly less than 10%. Therefore, to improve the rate of genetic progress this project investigated possible early predictors of female lifetime reproductive performance in two tropical genotypes and, importantly, established if any genetic antagonisms exist with economically important steer production traits. To achieve this, trait heritabilities, and genetic associations between traits, were estimated via a carefully designed quantitative genetics study. This required recording the performance of a large number of pedigreed animals subjected to known management. Critically, the cows were intensively recorded for reproduction from the onset of heifer puberty to the end of their 6th mating.

Key project findings included:

- Consistent with many other studies, the re-breeding rates in first lactation cows were low, particularly in Brahmans. The project has confirmed that extended lactation anoestrous intervals were the primary cause of reduced reproductive performance.
- Early-in-life female reproduction traits are heritable and there are alternative measures that can be used for capturing this genetic variation. For Brahmans, genetic variation in maiden heifer reproduction was highly correlated with differences in age at puberty.
- Traits describing re-breeding rates are heritable, and importantly, our results show that lactation anoestrus in first lactation cows was moderately to highly heritable. This presents the northern beef industry with an opportunity for improvement through selection. In Tropical Composites, genetic differences in lactation anoestrous interval were related to heifer age at puberty.
- Large differences were evident between sires for the early-in-life reproduction performance of their daughters. Generally the differences were greater in Brahmans, due to the higher trait heritabilities, compared to Tropical Composites.
- Lifetime reproduction traits were lowly heritable in both genotypes but the project established that several traits measured early-in-life were highly genetically related. This is a key result for the future development of genetic evaluation and performance recording. By focusing on these more heritable, early-in-life traits it will be possible to make significant genetic progress in lifetime reproductive rates.
- Genotype differences were observed for mean reproductive performance. Tropical Composite cows had less lactation anoestrus and higher early- and lifetime reproduction rates. These differences in reproductive performance demonstrate opportunities for breed substitution and provide a performance benchmark for Brahmans.
- The intensive recording of cow body composition over annual production cycles has generated a unique understanding of mobilisation and replenishment of body reserves, particularly in first-lactation cows. The genetic basis for these compositional differences, and their relationships with steer production traits, offers new insight into management and selection of cows to suit a given production environment.

- Male reproduction traits, especially measures of semen quality, have been identified as genetic indicator traits for improving female reproduction. Measurement protocols, including age at measurement, and genetic parameter estimates now provide the basis for developing industry performance recording standards and a genetic evaluation for these new traits.
- Few genetic antagonisms were identified between cow and steer traits and therefore it is possible to select for both sets of traits simultaneously. The low correlations between cow body composition and steer traits in Brahman suggest that opportunities exist to take advantage of this sexual dimorphism in selection.
- Significant reproductive wastage was evident in the study with an average calf loss of almost 10% over the experiment. The majority of the losses occurred in the first 48 hours after birth, with one location experiencing significantly higher losses due to Vitamin A deficiency.
- The project has identified several management factors that could be investigated further as ways of reducing calf losses. However, the opportunity for direct genetic selection is not clear, although two factors significantly associated with losses (*viz.* birth weight and teat scores) have been shown in this project to be under considerable genetic control.
- Cow longevity differences were apparent in this study but were largely influenced by the project management and culling policies, in particular culling for consecutive failure to wean a calf.
- Industry has already started to benefit from the results of this project through the identification of superior genetics via Brahman and Belmont Red BREEDPLAN evaluations for project animals. Some of the semen reserves on superior sires from the project have recently been used back in industry herds.
- The genetic parameters used in BREEDPLAN have been improved by re-estimation using the comprehensive project data. The new knowledge gained will be crucial over the next 6-12 months in the re-designing of the genetic evaluation of female reproduction traits in BREEDPLAN, in particular for tropical breeds.
- Project joining and calving data were pivotal in developing the first (trial) days to calving EBVs in the Belmont Red breed.
- All the data from this project have been assembled on a single database and will continue to be a very valuable resource for the northern beef industry to investigate future genetic and non-genetic issues. Importantly, the data and DNA samples have been extensively used by the CRC genomic group to develop genomic tests from *Bos indicus* based cattle.
- This project has established recording protocols, trait definitions and analytical methods that enable bulls and cows to be better genetically described for female reproductive performance. These improved EBVs can be used by commercial producers to identify genetically superior sires and dams, but importantly can be used by bull breeders to make genetic progress in these traits over time thus providing an ongoing means to increase weaning rates in northern Australia.

Table of Contents

1. Background.....	7
2. Project objectives.....	7
3. Methodology	8
3.1 Experimental design.....	8
3.2 Cow management and measurement	8
3.3 Statistical analyses.....	9
4. Results	9
4.1 Collection of phenotypic records	9
4.1.1 Cow phenotypic records	10
4.1.2 Cow reproduction records.....	10
4.1.3 Cow early- and lifetime reproduction records.....	11
4.1.4 Cow body composition records.....	12
4.1.5 Cow progeny records.....	13
4.1.6 Cow survival	13
4.1.7 Calf losses.....	13
4.2 Trait heritability estimates.....	13
4.2.1 Early reproduction traits	13
4.2.2 Lifetime reproduction	14
4.2.3 Cow body composition.....	16
4.2.4 Cow survival and longevity	17
4.3 Genetic correlations	17
4.3.1 Age at puberty and female reproduction	17
4.3.2 Cow early reproduction with cow lifetime reproduction.....	19
4.3.3 Cow body composition and reproduction	20
4.3.4 Male traits and female reproduction.....	22
4.4 Genetic correlations associated with whole-herd profitability	25
4.4.1 Cow body composition and steer traits.	25
4.4.2 Steer and female reproduction relationships.....	27
4.5 Genotype differences	28
4.5.1 Genotype means for female reproduction	28
4.5.2 Genotype means for cow body composition.....	29
4.6 Calf losses.....	30

4.6.1	Factors affecting calf losses.....	30
4.6.2	Genetic influences on calf losses.....	32
5.	Discussion and conclusions	32
6.	Recommendations.....	35
7.	Publications from this project	36
8.	Key Industry and stakeholder engagement.....	40
9.	Acknowledgement.....	41
10.	Appendices	42
11.	Bibliography.....	53

1. Background

There is currently a lack of data on the genetics of lifetime reproductive performance in female beef cattle and its relationships with other production traits. Although reproductive rate, in general, is a lowly heritable trait (see review of Koots *et al.* 1995), there are various underlying component traits that have been shown to be moderately to highly heritable affecting the overall reproduction rate in dairy cattle (e.g. Wall *et al.* (2003) and in tropical beef cattle for measures of puberty (Johnston *et al.* 2009). The challenge is to identify such traits, and include them in selection indices. To identify and quantify the effect of such indicator traits on female lifetime reproductive performance of beef cattle, comprehensive phenotypic measurements of component traits and lifetime reproduction are needed in a pedigreed resource population. Such a study would also pave the way for identification of genes affecting lifetime female reproductive performance of beef cattle that would have large economic effects on the productivity of beef cattle enterprises.

If early-in-life indicator traits with strong genetic relationships to lifetime reproductive performance are identified, strategies could be developed to manipulate or alter them to increase the productivity and profitability of the Australian beef herd. Existing breeding females from a former MLA Project NBP.301 were utilised to record lifetime reproductive performance and longevity to extend the range of quantitative genetic traits and to identify indicator traits early in life that can be used to improve lifetime reproduction and longevity. All the cows were given an opportunity to have at least 6 calves. The phenotypic data collected would also be extremely useful in identifying any correlated effects of the gene markers for age at puberty and post-partum re-conception (identified through Beef CRC Project 4.1.2 Gene Discovery of Program 4) and lifetime reproductive performance.

2. Project objectives

1. Phenotypic recording of the pedigreed resource population (6 calving opportunities per cow) from previous MLA project NBP.301 for various component traits of female reproductive performance such as mating and calving information, death and disposal information, continuous measures of weight and composition and linear type traits and reproductive tract and carcass ultrasound scan measurements at various stages during each year.
2. Genetic analysis of the data to identify early life indicators of life time reproductive performance and longevity, including measures of male reproduction (identified in Project B.NBP.0361: Male Indicator Traits to Improve Female Reproductive Performance)
3. Increased understanding of the genetic relationships between these identified early life indicators of lifetime female reproductive performance and other production traits.
4. Devised strategies to account for these indicator traits in the national genetic evaluation programs.

3. Methodology

3.1 Experimental design

Cows were part of a long-term project (previous MLA NBP.301). In brief, data were from a beef breeding experiment in northern Australia that investigated the genetics of whole herd profitability (Burrow *et al.* 2003). The complete experimental design has been described by Barwick *et al.* (2009a) and Johnston *et al.* (2009). In brief, Brahman (BRAH) and Tropical Composite (TCOMP) steers and heifers were generated over 4 years at 8 cooperator properties and were the progeny of 54 Brahman and 52 Tropical Composite sires. At weaning the heifer calves were allocated to one of 4 Queensland research stations, where they remained for the duration of the experiment (see Table 1 for distribution by location and cow birth year). Exceptions were made for cohorts from two of the locations that were temporarily relocated to a 4th location (Brigalow Research Station, Theodore, Queensland) due to prevailing drought conditions in different years. Genetic analyses of heifer performance have been previously reported for early growth and body composition (Barwick *et al.* 2009b), adaptation (Prayaga *et al.* 2009) and age at puberty (Johnston *et al.* 2009). A detailed description of the environment at each post-weaning location is given by Barwick *et al.* (2009b). This project reports on the lifetime reproduction of these females and the estimation of trait heritabilities and genetic associations with early-in-life measures, including measures of puberty. All cows had a DNA sample and their reproduction records were used to develop genomic prediction from 50K and 800K genome scans as part of the CRC's Gene Discovery project (MLA NBP.364 *Gene Discovery for post-partum re-conception and age at puberty in the Australian beef population*).

3.2 Cow management and measurement

Female reproduction data from the study were available for 1,020 BRAH and 1,117 TCOMP females. Heifers were first mated at an average age of 27 months, to first calve at 3 years of age. Subsequently, cows were mated for a 12 week period each year, commencing at approximately the same time of year within location. Cows were naturally mated in large multiple-sire groups with 3% bull to cow ratio. After the initial years of the project, cows were split into 2 or 3 permanent herds at each location for ease of management, and were mated in these groups. At Belmont Research Station, there were three mixed BRAH and TCOMP cow groups. All calves born in the project had individual birth details recorded. Calves were tagged, mother identified and, weighed generally within 24 hours of birth. A blood or hair sample was taken from all calves for DNA sire and dam parentage assignment. Samples were also used in genomic studies of associated projects. At branding, calves were scored for horn status and then dehorned. Male calves were not castrated and remained entire for the male reproduction study (Burns *et al.* 2012). Each year, all calves at a location were weaned on the same day at an average age of approximately 6 months. At this time calves were weighed and other recording of measures was commenced. Any deaths or missing calves were recorded with a date and a reason code, if it could be determined. All male calves were retained for the CRC's male reproduction project (MLA NBP.361 *Male indicator traits to improve female reproductive performance*).

Cows remained in the project until the weaning of calves from their 6th mating when they were approximately 8.5 years of age. The exception was cows removed from the project if they failed to wean a calf in consecutive years. This criterion was relaxed on two occasions: a cohort weaned at a young age into drought conditions and subsequently achieving very low reproduction from their maiden mating; and for females that failed to rear a calf at Toorak Research Station in 2004 when high calf losses resulted from Vitamin A deficiency.

Annual cow mortality rates were close to 1% throughout the project and culling for consecutive weaning failure averaged 2.7% per year. Date and reason, if known, for each death or culling was recorded. About 2% of cows were removed from the experiment for poor temperament or acquired physical conditions e.g. bottle teats or structurally unsound, that significantly compromised welfare or ability to reproduce or rear a calf.

3.3. Statistical analyses

All genetic analyses were performed using restricted maximum likelihood procedures in ASReml (Gilmour *et al.* 2009) with sets of fixed effects identified using SAS. Trait heritabilities were estimated using univariate analyses for BRAH and TCOMP separately. All binary reproduction traits were analysed using a sire model with a logit link function. A relationship matrix based on up to three generations of paternal and maternal (when known) pedigree was utilised for all analyses. A total of 54 BRAH and 51 TCOMP sires were represented by daughters with records in the data.

Genetic correlations were estimated between pairs of traits in a series of bivariate animal model analyses. This was done for blocks of traits, including those previously reported in project NBP.301. Appendix 1 shows the blocks of traits and the genetic correlations that were estimated as part of these two projects. The correlations across the blocks provide important estimates of the genetic relationships between steer traits, heifer pubertal traits, heifer growth and body composition traits, heifer early-in-life adaptation traits with female and male reproduction traits. These estimates are required for effective multiple-trait (i.e. whole-herd) genetic evaluation and selection, as well as informing performance recording on which traits are the most important to measure. Full list of traits and their definitions are presented in Appendices 2a-2d.

4. Results

4.1 Collection of phenotypic records

Generation of genetic parameter estimates with reasonable precision requires the collection of large numbers of records on pedigreed animals. The aim of this study was to estimate the genetic control of lifetime female reproductive performance and relate it to early measures of reproduction (including young bulls). Therefore this project focussed recording on the collection of a complete set of reproduction records on cows with up to 6 weaning opportunities (designated as “lifetime”). This included mating, scanning, calving, weaning and survival records on all cows. The number of cows that were present in the study at the start of mating 1 are shown in Table 1. Cows were allocated at weaning to one of 4 Queensland research stations where they remained and were fully recorded for up to 6 weaning opportunities. All data on cows recorded as part of this project (live measures and scores, reproductive scanning, mating details, calving outcomes, weaning outcomes, and cow and calf survival) have been loaded onto a single project database. The database also holds all the records from project NBP.301 and the records on the young bulls from project NBP.361.

Table 1. Numbers of females at the start of the mating 1 by location, genotype (BRAH= Brahman; TCOMP=Tropical Composite) and birth year

Genotype	Year	Post-weaning location				Total
		SWANS	BELMONT	TOORAK	BRIANP	
BRAH	2000		72			72
	2001	186	110	64		360
	2002	215	118	96		429
	2003	41	118			159
	Total	442	418	160	0	1020
TCOMP	2001		110	157	142	409
	2002		137	181	266	584
	2003		48		76	124
	Total	0	295	338	484	1117

4.1.1 Cow phenotypic records

All cows were regularly recorded for liveweight and body composition traits (e.g. carcass ultrasound scans) at strategic times during the year (i.e. into mating, mid-mating etc). Several scored traits were also recorded regarding traits associated with structural soundness and tropical adaptation. Cows that were still in the project at the end of the experiment (6 weaning opportunities) had over 60 weight measures. See Appendix 3 for number of records and raw trait statistics. These cows were DNA sire verified as part of project NBP.301.

All Brahman animals and Belmont Research Station Tropical Composite cows and their progeny were registered with the Brahman and Belmont Red breed Societies, respectively. As a result all animals (and their sires) have had EBVs generated and published through BREEDPLAN over the course of the experiment. Each year of the project all records associated with any BREEDPLAN traits were extracted for these animals from the CRC database and submitted to BREEDPLAN. Most importantly, these included the large amount of female reproduction data, cow weight data and progeny records.

These records generated increased levels of genetic linkage within each of the analyses through large numbers of head-to-head comparisons of different stud's genetics. The very high level of recording also allowed several genetically superior individuals to be identified in both breeds (see Appendices 9, 10, 11) and some of the sires have been re-used (with CRC semen stores) back into industry. The joining and calving data from this experiment from Belmont Research Station was pivotal in the development of the first trial days to calving EBVs for Belmont Reds.

4.1.2 Cow reproduction records

All cows in each of the breeding herds were reproductive tract scanned every 6-8 weeks throughout the year to determine resumption of cycling and pregnancies. Scanning occurred at the end of the calving period and coincided with the start of the annual mating period. Cows were scanned mid-mating, out of mating and at weaning. Any cows still not showing a CL continued to be scanned until a CL was observed. The total numbers of reproductive scanning records are presented in Appendix 4.

Cows were mated in large multiple sire groups for a 12 week period each year at all locations. The project generated a total of 13,414 individual mating records from 77

multiple-sire mating groups. At Belmont the cows were mated in mixed genotype groups to allow direct comparison of the reproductive performance. Each year, complete calving and weaning records were collected on all cows, including individual calf identification, date of birth, and birth weight. A blood or hair sample was obtained for DNA parentage assignment. All calf deaths were recorded with a date and a reason if it could be ascertained.

4.1.3 Cow early- and lifetime reproduction records

The large numbers of reproductive scanning records (described in section 4.1.2) were used to generate numerous reproduction traits. These include traits relating to reproduction rates or output (e.g. conception rate 0, 1) and also interval traits (e.g. lactation anoestrous interval) describing differences in the time period to exhibit certain reproductive states. Raw means for traits recorded at the mating 1 and 2, along with lifetime reproduction traits, are presented in Table 2 for Brahman females and Table 3 for the Tropical Composite females.

Table 2. Unadjusted trait means, standard deviations and ranges for Brahman female reproduction traits.

Trait	n	Mean	std.	Min.	Max.
<i>Mating 1</i>					
Conception rate	1020	0.77	0.42	0	1
Pregnancy rate	1020	0.75	0.43	0	1
Calving rate	1020	0.72	0.45	0	1
Days to calving (d)	1019	345.6	49.6	269	423
Weaning rate	1020	0.62	0.49	0	1
<i>Mating 2</i>					
Days to cycling (d)	1002	88.0	106.1	0	411
Lactation anoestrous interval (d)	629	133.7	109.5	0	411
Lactation cyclicity rate	631	0.53	0.50	0	1
Conception rate	1009	0.61	0.49	0	1
Pregnancy rate	1009	0.59	0.49	0	1
Calving rate	1005	0.57	0.50	0	1
Days to calving (d)	1005	363.1	51.8	260	423
Weaning rate	1009	0.50	0.50	0	1
Total calves born 1-2	1005	1.28	0.55	0	2
Total calves weaned 1-2	1005	1.12	0.57	0	2
Pregnant-and-weaned rate	1009	0.27	0.44	0	1
<i>Lifetime (1st to 6th mating)</i>					
Annual calving rate retained cows	717	0.77	0.16	0	1
Annual weaning rate retained cows	717	0.72	0.16	0	1
Lifetime annual calving rate	1020	0.70	0.24	0	1
Lifetime annual weaning rate	1020	0.60	0.28	0	1

Table 3. Unadjusted trait means, standard deviations and ranges for Tropical Composite female reproduction traits.

Trait	n	Mean	std.	Min.	Max.
<i>Mating 1</i>					
Conception rate	1117	0.95	0.21	0	1
Pregnancy rate	1117	0.92	0.27	0	1
Calving rate	1111	0.90	0.30	0	1
Days to calving (d)	1110	318.0	38.1	255	425
Weaning rate	1111	0.78	0.42	0	1
<i>Mating 2</i>					
Days to ovulation (d)	1095	68.7	103.7	0	401
Lactation anoestrous interval (d)	872	83.8	110.9	0	401
Lactation cyclicity rate	863	0.82	0.39	0	1
Conception rate	1095	0.80	0.40	0	1
Pregnancy rate	1095	0.76	0.43	0	1
Calving rate	1094	0.74	0.44	0	1
Days to calving (d)	1094	344.6	49.7	265	425
Weaning rate	1094	0.65	0.48	0	1
Total calves born 1-2	1094	1.64	0.53	0	2
Total calves weaned 1-2	1094	1.44	0.61	0	2
Pregnant-and-weaned rate	1094	0.58	0.49	0	1
<i>Lifetime (1st to 6th mating)</i>					
Annual calving rate retained cows	898	0.88	0.10	0	1
Annual weaning rate retained cows	898	0.83	0.14	0	1
Lifetime annual calving rate	1117	0.83	0.22	0	1
Lifetime annual weaning rate	1117	0.73	0.26	0	1

4.1.4 Cow body composition records

A subset of the records from Appendix 3 was identified that specifically related to the body composition of cows at the start of mating 2 (Table 4). Pre-calving and into mating measures, and the change between these times, were also examined for dry and lactating cows.

Table 4. Unadjusted trait means for cow body composition traits pre-calving and into mating 2 for Brahman and Tropical Composite cows

Trait	Brahman		Tropical Composite	
	N	Mean $\pm$ std.	N	Mean $\pm$ std.
<i>Pre-calving</i>				
AGE (days)	1016	1007.7 $\pm$ 52.2	1094	1009.7 $\pm$ 34.7
WT (kg)	974	423.1 $\pm$ 52.5	1082	463.0 $\pm$ 47.7
EMA (cm ²)	668	53.8 $\pm$ 7.1	932	55.6 $\pm$ 6.8
P8 (mm)	984	7.4 $\pm$ 3.2	1084	6.9 $\pm$ 3.6
RIB (mm)	668	4.5 $\pm$ 2.0	936	4.7 $\pm$ 2.0
BCS (score)	1016	3.2 $\pm$ 0.4	1094	3.0 $\pm$ 0.5
HH (cm)	815	137.7 $\pm$ 4.5	932	134.1 $\pm$ 4.9
<i>Into Mating</i>				
AGE (days)	1009	1110.6 $\pm$ 50.5	1094	1123.0 $\pm$ 34.2
WT (kg)	973	390.3 $\pm$ 48.9	1082	405.7 $\pm$ 50.6
EMA (cm ²)	985	46.1 $\pm$ 10.4	1079	44.0 $\pm$ 10.2
P8 (mm)	981	4.2 $\pm$ 3.1	1084	2.7 $\pm$ 2.4
RIB (mm)	985	2.3 $\pm$ 1.6	1084	2.0 $\pm$ 1.5
BCS (score)	1009	2.6 $\pm$ 0.8	1094	2.3 $\pm$ 0.5
HH (cm)	949	138.6 $\pm$ 4.7	1077	136.1 $\pm$ 5.3

4.1.5 Cow progeny records

Over the course of the experiment a total of 9,296 progeny were generated from our females (see Appendix 5 for numbers by location and year). These were sired by a total of 136 bulls sourced from industry. Calves were recorded up to weaning, at which stage the heifers were sold and the bulls entered the male reproduction project. The records available are shown in Appendix 6.

4.1.6 Cow survival

All cows which left the project were recorded with an exit date and a reason code if known. The frequency of disposal codes over the 6 weaning opportunities is presented in Appendix 7. The codes were also used to determine the longevity of each cow in the project and are presented in Appendix 7 as the length of time each cow survived in the project (in years). Cows still in the project at the end (i.e. weaning of 6th possible calf) had a longevity (or productive life) of 7 years.

4.1.7 Calf losses

Full calf birth and survival data was collected as a routine part of the experiment. This allowed accurate assessment of calf weaning rates but also additional analyses of calf survival. Phenotypic analyses were conducted to determine factors associated with calf losses and preliminary genetic analyses were also performed (see section 4.6) for calf loss and component traits (e.g. teat and udder scores and birth weight).

4.2 Trait heritability estimates

The project has generated a very large number of estimates of trait heritabilities and genetic correlations between traits. A reduced set of key estimates is presented in the next sections these data will also be published in a series of refereed published journal articles. Publication in peer reviewed journals is an important prerequisite for the inclusion new or updated traits or parameters in BREEDPLAN.

4.2.1 Early reproduction traits

Genetic estimates from several early reproduction traits from this study have been reported earlier in the MLA NBP.301 Final Report but additional traits have been examined as part of this project, particularly new traits associated with conception, pregnancy and conception rates with lactation anoestrus in first-lactation cows. Presented in Table 1 are the heritability estimates from the mating 1 in BRAH and TCOMP. In general estimates on the underlying (logit) scale were moderate to large but when transformed to the observed scale were lower and reflect the high incidence level for these traits, particularly in TCOMP.

Table 6. Heritabilities (h^2) and additive variances (σ_A^2) for reproductive traits at mating 1 in Brahman and Tropical Composite cows (standard errors in parentheses)

Trait	p^*	σ_A^2	h_L^2 #	h^2
<i>Brahman</i>				
Conception rate	0.77	2.38	0.61 (0.22)	0.11
Pregnancy rate	0.76	2.42	0.62 (0.22)	0.11
Calving rate	0.72	1.18	0.33 (0.15)	0.07
Weaning rate	0.62	0.53	0.15 (0.10)	0.04
Days to calving		434	-	0.22 (0.09)
<i>Tropical Composite</i>				
Conception rate	0.95	0.98	0.28 (0.27)	0.01
Pregnancy rate	0.92	1.24	0.34 (0.21)	0.03
Calving rate	0.90	1.03	0.29 (0.16)	0.03
Weaning rate	0.78	0.52	0.15 (0.10)	0.03
Days to calving		183	-	0.13 (0.06)

* trait level h^2 heritability on the logit scale; estimates from subset of data with sire known; $\sigma_A^2 = 4\sigma^2_s$; residual variance = $\pi^2/3$; h^2 approximated by $h_L^2 \times p(1-p)$

Heritability estimates for traits recorded at 2nd breeding were computed for all cows and for the sub-set of lactating cows (see Table 7). Estimates were generally larger than those observed previously for mating 1 traits, especially for traits associated with lactation anoestrus i.e. days to calving, pregnant and weaned, lactation anoestrous interval and lactation cycling rate.

4.2.2 Lifetime reproduction

Cows remained in the project at their assigned location for up to 7 matings and 6 weaning opportunities. Cows were culled if they failed to wean a calf in 2 consecutive years. Lifetime reproduction for each cow was constructed by summing the numbers of calves (born and weaned), divided by the number of opportunities to give a rate. Table 8 presents heritabilities for the lifetime traits in both genotypes and includes estimates for all cows and also for cows that were retained for the whole 6 opportunities.

Table 7. Heritabilities (h^2) and additive variances (σ^2_A) for reproductive traits at mating 2 in Brahman and Tropical Composite cows (standard errors in parentheses)

Trait	p^*	σ^2_A	$h^2_{L\#}$	h^2
<i>Brahman - All cows</i>				
Days to cycling		2689		0.41 (0.12)
Conception rate	0.61	2.74	0.69 (0.21)	0.16
Pregnancy rate	0.59	2.42	0.62 (0.19)	0.15
Calving rate	0.56	1.98	0.52 (0.18)	0.13
Weaning rate [†]	0.49	1.43	0.39 (0.15)	0.10
Days to calving		374		0.20 (0.08)
Pregnant-and-weaned	0.27	3.32	0.80 (0.22)	0.16
Total calves born 1&2		0.039		0.15 (0.07)
Total calves weaned 1&2		0.062		0.21 (0.08)
<i>Brahman - lactating cows only</i>				
Lactation anoestrous interval		5238		0.51 (0.18)
Lactation cyclicity rate	0.53	4.01	0.93 (0.25)	0.28
Conception rate	0.45	4.12	0.96 (0.26)	0.24
Pregnancy rate	0.43	4.46	1.01 (0.27)	0.25
Calving rate	0.41	3.70	0.88 (0.26)	0.21
Weaning rate [†]	0.36	3.83	0.90 (0.25)	0.21
Days to calving		915		0.49 (0.14)
<i>Tropical Composite - All cows</i>				
Days to cycling		1088		0.18 (0.08)
Conception rate	0.80	1.24	0.34 (0.18)	0.05
Pregnancy rate	0.76	0.51	0.15 (0.12)	0.03
Calving rate	0.74	0.90	0.26 (0.14)	0.05
Weaning rate [†]	0.66	0.55	0.16 (0.10)	0.04
Days to calving		320		0.17 (0.08)
Pregnant-and-weaned	0.58	0.67	0.19 (0.09)	0.05
Total calves born 1&2		0.038		0.14 (0.07)
Total calves weaned 1&2		0.055		0.16 (0.07)
<i>Tropical Composite – lactating cows only</i>				
Lactation anoestrous interval		1965		0.26 (0.11)
Lactation cyclicity rate	0.82	2.16	0.56 (0.25)	0.08
Conception rate	0.77	1.92	0.50 (0.19)	0.09
Pregnancy rate	0.73	0.82	0.23 (0.14)	0.05
Calving rate	0.71	1.35	0.37 (0.16)	0.08
Weaning rate [†]	0.64	0.73	0.21 (0.13)	0.05
Days to calving		679		0.35 (0.13)

* p = trait level # heritability on the logit scale; estimates from subset of data with sire known; $\sigma^2_A = 4\alpha\sigma^2_s$; residual variance = $\pi^2/3$; h^2 approximated by $h^2_{L\#} \times p(1-p)^{\dagger}$ models ignoring calf effects

Heritability estimates were generally low, however considerable variance existed in these traits, and the estimates were higher when only considering those cows still present at the end of the experiment.

Table 8. Heritabilities (h^2) and additive variances (σ_A^2) for lifetime annual reproduction traits for Brahman and Tropical Composite (standard errors in parentheses)

trait	Brahman		Tropical Composite	
	σ_A^2	h^2	σ_A^2	h^2
Calving rate retained cows	0.0061	0.30 (0.11)	0.0021	0.15 (0.09)
Weaning rate retained cows	0.0069	0.31 (0.12)	0.0045	0.24 (0.11)
Lifetime annual calving rate	0.0080	0.16 (0.08)	0.0018	0.04 (0.05)
Lifetime annual weaning rate	0.0077	0.11 (0.06)	0.0042	0.07 (0.06)

4.2.3 Cow body composition

The body weight and composition of cows at the start of mating 2 was considered potentially important given the large differences in reproductive performance that occurred at this mating. Heritabilities are presented in Table 9 for both genotypes for measures at both pre-calving, into mating and the change between those two periods (on average 100 days). All traits were moderately to highly heritable and show that genetics are contributing to the differences observed in cow body composition at these production stages. The change traits were also heritable and indicate some genetics (i.e. sire's daughters) are changing composition differently.

Table 9. Additive (σ_A^2) and phenotypic (σ_p^2) variances and heritabilities (h^2) for cow body composition traits at pre-calving and mating, and for the change from pre-calving to mating 2, in Brahman and Tropical Composite cows (standard errors in parentheses)

Trait	BRAH			TCOMP		
	σ_A^2	σ_p^2	h^2	σ_A^2	σ_p^2	h^2
<i>Pre-calving</i>						
LWT (kg)	663	1084	0.61 (0.12)	1074	1544	0.70 (0.13)
EMA (cm ²)	10.7	32.1	0.33 (0.14)	18.9	37.0	0.51 (0.14)
P8 (mm)	4.00	7.41	0.54 (0.11)	2.39	7.26	0.33 (0.12)
RIB (mm)	1.62	3.06	0.53 (0.15)	1.40	2.96	0.47 (0.14)
BCS (score)	0.03	0.11	0.31 (0.10)	0.04	0.11	0.32 (0.11)
HH (cm)	7.6	17.1	0.44 (0.14)	16.4	20.6	0.80 (0.14)
<i>Into mating 2 (wet cows only)</i>						
LWT (kg)	728	1112	0.65 (0.16)	980	1349	0.73 (0.16)
EMA (cm ²)	16.1	38.3	0.42 (0.15)	25.0	42.9	0.58 (0.14)
P8 (mm)	1.65	2.47	0.67 (0.17)	0.61	1.40	0.43 (0.16)
RIB (mm)	0.43	0.79	0.54 (0.17)	0.38	0.76	0.50 (0.18)
BCS (score)	0.08	0.17	0.48 (0.14)	0.03	0.10	0.27 (0.12)
HH (cm)	11.9	19.0	0.62 (0.16)	17.9	22.1	0.81 (0.14)
<i>Change from pre-calving to mating 2</i>						
LWT (kg)	203	377	0.54 (0.15)	215	441	0.49 (0.13)
EMA (cm ²)	8.1	40.1	0.20 (0.14)	9.8	39.5	0.25 (0.10)
P8 (mm)	1.95	3.66	0.53 (0.15)	1.53	4.70	0.33 (0.13)
RIB (mm)	0.94	2.49	0.38 (0.16)	0.87	2.30	0.38 (0.12)
BCS (score)	0.02	0.14	0.17 (0.10)	0.03	0.13	0.24 (0.10)
HH (cm)	0.00	4.39	0.00 (0.00)	0.64	6.32	0.10 (0.18)

4.2.4 Cow survival and longevity

Given the low incidence of cow deaths and the impact of management decisions and culling practices it was difficult to determine any genetic differences for cow survival. Preliminary estimates for longevity in TCOMP were all close to zero and for BRAH ranged from 0.01 to 0.08, but all estimates had large standard errors but in general reflect differences in culling levels for reproductive failure. Given these low heritability estimates it was not possible to estimate genetic correlations with other blocks of traits.

4.3 Genetic correlations

To determine the degree to which traits are related the project has estimated a very large number of genetic correlations between pairs of traits. This is critical to determine likely correlated response to selection (i.e. select on one trait what affect is expected on another) but also provides an insight into the opportunity for indirect selection. Of particular interest to this project were early indicators of lifetime female reproductive performance and any possible consequences for whole-herd profitability (i.e. genetic correlations with steer traits). Note, the sign (i.e. positive or negative) of correlations needs to be interpreted with knowledge of the measurement scale of each trait. For example estimates with the trait days to calving or lactation anoestrous interval often have opposite signs to the other reproductive traits because shorter intervals (i.e. negative) are generally associated with increased reproductive performance.

4.3.1 Age at puberty and female reproduction

The first set of early-in-life reproductive measures were those associated with heifer puberty (reported in NBP.301). These traits were moderately to highly heritable in both genotypes. The genetic correlations with early- and lifetime reproduction are presented in Table 10 (Brahman) and Table 11 (Tropical Composite).

For Brahman, both age at puberty (i.e. age at first *corpus luteum* (CL); AGECL) and pubertal at commencement of mating (CLJOIN) were highly genetically correlated with mating 1 reproductive performance, but less so for mating 2 traits, resulting in only moderate correlations with lifetime reproductive performance. Overall the correlations show selection for reduced age at puberty will result in increased reproductive performance at both the early and lifetime stages.

Table 10. Genetic correlations between heifer puberty traits and female reproduction traits in Brahman (standard errors in parentheses)

Female reproduction traits [#]	AGECL	WTCL	FATCL	CLJOIN
<i>Mating 1</i>				
Conception rate	-0.70 (0.12)	-0.49 (0.16)	-0.54 (0.17)	0.87 (0.17)
Pregnancy rate	-0.71 (0.11)	-0.49 (0.15)	-0.55 (0.16)	0.80 (0.18)
Calving rate	-0.61 (0.16)	-0.27 (0.21)	-0.55 (0.19)	0.81 (0.20)
Weaning rate	-0.39 (0.26)	-0.11 (0.28)	-0.55 (0.25)	0.70 (0.29)
Days to calving	0.79 (0.14)	0.52 (0.19)	0.54 (0.20)	-1.0* (0.16)
<i>Mating 2</i>				
L. anoestrous interval	0.31 (0.18)	0.32 (0.18)	0.28 (0.20)	-0.43 (0.24)
Lactation cyclicity rate	-0.26 (0.18)	-0.24 (0.18)	-0.19 (0.20)	0.41 (0.23)
Conception rate	-0.21 (0.19)	-0.15 (0.19)	-0.26 (0.20)	0.11 (0.27)
Pregnancy rate	-0.14 (0.20)	0.00 (0.20)	-0.17 (0.21)	0.12 (0.28)
Calving rate	-0.12 (0.22)	-0.01 (0.22)	-0.09 (0.23)	0.07 (0.30)
Weaning rate	-0.28 (0.23)	-0.07 (0.24)	0.03 (0.25)	0.20 (0.31)
Days to calving	0.08 (0.24)	-0.06 (0.23)	-0.01 (0.24)	-0.04 (0.32)
Calves born 1&2	-0.38 (0.23)	-0.24 (0.24)	-0.42 (0.24)	0.51 (0.27)
Calves weaned 1&2	-0.27 (0.22)	-0.09 (0.22)	-0.18 (0.24)	0.43 (0.26)
Pregnant-and-weaned rate	-0.30 (0.18)	-0.25 (0.18)	-0.41 (0.19)	0.40 (0.23)
<i>Lifetime</i>				
Lifetime annual calving rate	-0.40 (0.20)	-0.39 (0.21)	-0.47 (0.22)	0.47 (0.27)
Lifetime annual weaning rate	-0.36 (0.21)	-0.03 (0.22)	-0.06 (0.24)	0.42 (0.27)

[#]AGECL=age at first CL; WTCL=live weight at first CL; FATCL= P8 fat depth at first CL; CLJOIN=pubertal prior to commencement of maiden mating * estimate exceeded bounds

For Tropical Composite, the genetic correlations between age at puberty (AGECL) or pubertal at commencement of mating (CLJOIN) were moderately correlated with mating1 traits but more highly correlated with mating 2 traits, and resulting in low to moderate correlations with lifetime traits. As seen for Brahmans, these results show that selection for reduced age at first CL would increase reproduction rates.

Table 11. Genetic correlations between heifer puberty traits and female reproduction traits in TCOMP (standard errors in parentheses)

Female reproduction traits [#]	AGECL	WTCL	FATCL	CLJOIN
<i>Mating 1</i>				
Conception rate	-0.41 (0.35)	-0.14 (0.36)	0.05 (0.39)	0.58 (0.44)
Pregnancy rate	-0.23 (0.27)	-0.39 (0.26)	-0.23 (0.29)	0.68 (0.31)
Calving rate	-0.17 (0.28)	-0.15 (0.28)	-0.12 (0.29)	0.70 (0.33)
Weaning rate	-0.49 (0.30)	-0.34 (0.31)	0.03 (0.33)	1.0* (0.41)
Days to calving	0.10 (0.27)	0.12 (0.27)	0.22 (0.27)	-0.80 (0.28)
<i>Mating 2</i>				
Lactation anoestrous interval	0.72 (0.17)	0.69 (0.18)	0.61 (0.22)	-0.89 (0.23)
Lactation cyclicity rate	-0.64 (0.19)	-0.59 (0.20)	-0.61 (0.22)	0.49 (0.30)
Conception rate	-0.37 (0.28)	-0.20 (0.29)	-0.38 (0.30)	0.39 (0.36)
Pregnancy rate	-0.68 (0.40)	-0.19 (0.38)	-0.45 (0.40)	0.47 (0.48)
Calving rate	-0.58 (0.32)	-0.21 (0.31)	-0.15 (0.32)	0.22 (0.39)
Weaning rate	-0.63 (0.38)	-0.17 (0.35)	-0.09 (0.36)	0.22 (0.45)
Days to calving	0.43 (0.26)	0.03 (0.27)	0.25 (0.27)	0.04 (0.35)
Calves born 1&2	-0.22 (0.28)	-0.06 (0.27)	-0.09 (0.28)	0.30 (0.36)
Calves weaned 1&2	-0.39 (0.25)	-0.18 (0.26)	0.00 (0.26)	0.51 (0.33)
Pregnant-and-weaned rate	-0.55 (0.21)	-0.39 (0.23)	-0.17 (0.25)	0.85 (0.25)
<i>Lifetime</i>				
Lifetime annual calving rate	-0.33 (0.28)	-0.22 (0.28)	-0.20 (0.32)	0.59 (0.30)
Lifetime annual weaning rate	-0.29 (0.23)	-0.05 (0.25)	-0.07 (0.27)	0.66 (0.25)

[#] see Table 10 * estimate exceeded bounds

4.3.2 Cow early reproduction with cow lifetime reproduction

The genetic relationship between early measures and lifetime are presented in Tables 12 and 13. These are key estimates to determine how selection for early reproductive performance will impact on lifetime rates. For both Brahman and Tropical Composite the genetic correlations were high to very high, indicating that selection for these early measures will be associated with improvements in lifetime reproductive rates. Some differences exist in the initial mating in the magnitude of correlations between traits for calving versus weaning rates which reflect the influence of calf losses on the estimates.

Table 12. Brahman estimates of the genetic correlations between early- and lifetime reproduction traits (standard errors in parentheses)

trait	Lifetime annual calving rate	Lifetime annual weaning rate
<i>Mating 1</i>		
Conception rate	0.61 (0.20)	0.47 (0.26)
Pregnancy rate	0.60 (0.20)	0.51 (0.25)
Calving rate	0.50 (0.25)	0.44 (0.29)
Days to calving	-0.46 (0.26)	-0.54 (0.27)
Weaning rate	0.98 (0.21)	0.99 (0.18)
<i>Mating 2</i>		
Conception rate	0.90 (0.13)	0.76 (0.20)
Pregnancy rate	0.75 (0.17)	0.69 (0.22)
Calving rate	0.89 (0.14)	0.81 (0.19)
Days to calving	-1.0* (0.11)	-0.96 (0.17)
Weaning rate	0.86 (0.19)	0.81 (0.18)
Days to cycling	-0.55 (0.25)	-0.60 (0.25)
Lactation anoestrous interval	-0.71 (0.21)	-0.62 (0.24)
Lactation cyclicity rate	0.59 (0.23)	0.53 (0.26)

* estimate exceeded bounds

Table 13. Tropical Composite estimates of the genetic correlations between early- and lifetime reproduction traits (standard errors in parentheses)

trait	Lifetime annual calving rate	Lifetime annual weaning rate
<i>Mating 2</i>		
Conception rate	0.56 (0.53)	0.54 (0.45)
Pregnancy rate	1.0* (0.26)	0.65 (0.30)
Calving rate	0.78 (0.33)	0.56 (0.32)
Day to calving	-0.75(0.30)	-0.57 (0.30)
Weaning rate	0.89 (0.48)	0.86 (0.28)
<i>Mating 2</i>		
Conception rate	1.0* (0.45)	1.0* (0.34)
Pregnancy rate	1.0* (0.32)	1.0* (0.34)
Calving rate	0.96 (0.25)	0.91 (0.29)
Day to calving	-0.97 (0.20)	-0.76 (0.25)
Weaning rate	1.0* (0.35)	0.85 (0.28)
Days to cycling	-0.91 (0.46)	-0.99 (0.34)
Lactation anoestrous interval	-1.0* (0.46)	-0.87 (0.32)
Lactation cyclicity rate	1.0* (0.56)	0.66 (0.36)

* estimate exceeded bounds

4.3.3 Cow body composition and reproduction

Genetic correlations between the cow body composition measures and cow reproduction at mating 2 and lifetime are presented in Tables 14 and 15. In general the correlations were low, with the exceptions of moderate correlations for EMA and BCS in BRAH. These estimates suggest that cow body composition measures are not strong genetic indicators of female reproduction.

Table 14. Genetic correlations for BRAH cow body composition and cow reproduction at mating 2 and lifetime performance (standard errors in parentheses)

Cow traits	Lactation anoestrous interval	Day to calving 2	Pregnancy rate 2	Lifetime annual calving rate	Lifetime annual weaning rate
<i>Into mating</i>					
LWT	-0.05 (0.21)	-0.15 (0.25)	0.20 (0.22)	0.06 (0.29)	0.40 (0.27)
EMA	-0.38 (0.23)	-0.42 (0.27)	0.39 (0.24)	0.18 (0.33)	0.41 (0.31)
P8	-0.15 (0.22)	-0.30 (0.26)	0.12 (0.24)	0.39 (0.30)	0.06 (0.32)
BCS	-0.22 (0.21)	-0.38 (0.24)	0.31 (0.22)	0.43 (0.27)	0.12 (0.30)
HH	0.07 (0.20)	-0.11 (0.25)	0.05 (0.22)	0.14 (0.28)	0.40 (0.29)
<i>Change (Into mating minus precalving)</i>					
LWT	-0.04 (0.22)	-0.46 (0.25)	0.37 (0.23)	0.47 (0.28)	0.11 (0.31)
EMA	-0.45 (0.29)	-0.32 (0.37)	0.27 (0.33)	0.03 (0.43)	0.16 (0.44)
P8	0.20 (0.21)	0.12 (0.27)	-0.09 (0.23)	-0.17 (0.30)	-0.40 (0.29)
BCS	-0.12 (0.30)	-0.21 (0.36)	0.10 (0.32)	-0.02 (0.41)	-0.26 (0.41)

Table 15. Genetic correlations for TCOMP cow body composition and cow reproduction at mating 2 and lifetime performance (standard errors in parentheses)

Cow traits	Lactation anoestrous interval	Day to calving 2	Pregnancy rate 2	Lifetime annual calving rate	Lifetime annual weaning rate
<i>Into mating</i>					
LWT	0.11 (0.26)	-0.11 (0.25)	-0.31 (0.26)	0.23 (0.37)	-0.34 (0.46)
EMA	0.17 (0.29)	-0.01 (0.27)	-0.26 (0.26)	0.02 (0.41)	-0.02 (0.45)
P8	0.20 (0.31)	-0.17 (0.31)	0.19 (0.34)	-0.34 (0.50)	-0.09 (0.55)
BCS	0.25 (0.31)	-0.19 (0.30)	0.01 (0.31)	-0.15 (0.45)	-0.22 (0.56)
HH	0.00 (0.23)	0.14 (0.23)	-0.33 (0.24)	0.47 (0.36)	-0.17 (0.38)
<i>Change (Into mating minus precalving)</i>					
LWT	0.02 (0.26)	0.15 (0.26)	0.22 (0.27)	-0.07 (0.40)	0.55 (0.43)
EMA	-0.14 (0.31)	0.30 (0.30)	-0.01 (0.35)	-0.44 (0.50)	0.21 (0.49)
P8	-0.03 (0.26)	0.37 (0.26)	-0.09 (0.29)	0.33 (0.41)	0.10 (0.43)
BCS	-0.35 (0.27)	0.60 (0.24)	-0.55 (0.27)	0.63 (0.38)	0.41 (0.46)

4.3.4 Male traits and female reproduction

The completed genetic analyses of all male reproduction traits are presented in the MLA NBP.363 Final Report. Presented here are the genetic correlations between the male traits and a sub-set of the female traits. Note: the estimates with large standard errors are a function of the low heritabilities of some of the male and female traits. However the focus of this part of the project was to identify if there are potential male reproductive measures that could be used as indirect measures of female reproductive performance.

Tables 16 and 17 present the genetic correlations between the bull measures and mating 1 female reproduction traits. No strong relationships existed for either genotype however IGF-I showed consistent and low to moderate relationships and scrotal circumference and the semen traits were generally in the same direction.

The genetic correlations between bull traits and key mating 2 traits are presented in Tables 18 and 19. For the hormone traits, LH in Tropical Composite was the only trait with a clear relationship with lactation anoestrous interval and the calving outcome traits. The semen traits in both genotypes showed moderate to high genetic correlations with female reproduction, however the time of measuring the bulls appears to be influencing the relationships. Genetic correlations with scrotal circumference in Brahmans measured after 6 months tended to be favourably related, but this was less clear in Tropical Composites. For TCOMP, there was a moderate correlation between preputial eversion and lactation anoestrous interval.

Table 16. Genetic correlations between bull traits and female reproduction at mating 1 in BRAH (standard errors in parentheses)

Bull trait	Age (mths)	Pregnancy rate 1	Calving rate1	Day to calving 1
<i>Hormones</i>				
Inhibin	4	0.14 (0.12)	0.23 (0.15)	-0.27 (0.15)
Luteinising hormone	4	-0.01 (0.17)	0.10 (0.21)	-0.05 (0.21)
IGF-I	6	0.29 (0.16)	0.44 (0.20)	-0.34 (0.21)
<i>Semen Quality</i>				
Mass activity	12	0.14 (0.14)	0.16 (0.18)	-0.25 (0.18)
	18	0.42 (0.23)	0.12 (0.26)	-0.15 (0.27)
	24	0.53 (0.38)	0.36 (0.42)	-0.39 (0.43)
Motility	12	0.25 (0.16)	0.21 (0.19)	-0.32 (0.20)
	18	0.18 (0.22)	-0.04 (0.27)	-0.03 (0.27)
	24	0.34 (0.40)	0.32 (0.45)	-0.37 (0.48)
%normal sperm	12	.	.	.
	18	0.26 (0.23)	-0.02 (0.27)	-0.04 (0.28)
	24	-0.08 (0.27)	-0.26 (0.34)	0.44 (0.34)
<i>Scrotal and sheath</i>				
Scrotal circumference	6	0.12 (0.14)	0.35 (0.17)	-0.36 (0.17)
	12	0.16 (0.14)	0.25 (0.17)	-0.30 (0.18)
	18	0.14 (0.13)	0.24 (0.17)	-0.34 (0.17)
	24	0.14 (0.13)	0.25 (0.17)	-0.25 (0.17)
Sheath score	18	0.29 (0.19)	0.11 (0.22)	-0.12 (0.23)
Preputial eversion	18	-0.13 (0.17)	0.03 (0.20)	0.09 (0.20)

Table 17. Genetic correlations between bull traits and female reproduction at mating 1 in TCOMP (standard errors in parentheses)

Bull trait	Age (mths)	Pregnancy rate 1	Calving rate1	Day to calving 1
<i>Hormones</i>				
Inhibin	4	0.24 (0.21)	0.24 (0.21)	-0.13 (0.19)
Luteinising hormone	4	-0.14 (0.25)	-0.20 (0.25)	0.51 (0.24)
IGF-I	6	0.15 (0.24)	-0.01 (0.25)	-0.11 (0.23)
<i>Semen Quality</i>				
Mass activity	12	0.12 (0.22)	-0.01 (0.23)	-0.08 (0.21)
	18	0.20 (0.34)	0.42 (0.31)	-0.38 (0.30)
	24	-0.66 (0.40)	-0.22 (0.41)	0.04 (0.38)
Motility	12	0.12 (0.22)	0.02 (0.23)	-0.10 (0.21)
	18	0.21 (0.30)	0.32 (0.29)	-0.22 (0.28)
	24	-0.63 (0.42)	-0.26 (0.45)	-0.04 (0.43)
%normal sperm	12	0.01 (0.31)	-0.13 (0.30)	0.10 (0.28)
	18	0.45 (0.30)	0.43 (0.30)	-0.50 (0.27)
	24	0.26 (0.28)	0.50 (0.29)	-0.43 (0.28)
<i>Scrotal and sheath</i>				
Scrotal circumference	6	-0.03 (0.23)	0.07 (0.24)	0.00 (0.22)
	12	0.19 (0.21)	0.11 (0.22)	-0.18 (0.20)
	18	0.08 (0.22)	0.18 (0.22)	-0.15 (0.21)
	24	-0.06 (0.22)	0.17 (0.23)	-0.11 (0.21)
Sheath score	18	-0.13 (0.31)	-0.57 (0.36)	0.48 (0.38)
Preputial eversion	18	-0.19 (0.31)	0.30 (0.35)	0.15 (0.29)

Table 18. Genetic correlations between bull traits and female reproduction at mating 2 in BRAH (standard errors in parentheses)

Bull trait	Age (mths)	L. Anoestrous interval	Calving rate 2	Days to calving 2
<i>Hormones</i>				
Inhibin	4	-0.08 (0.13)	0.14 (0.15)	-0.19 (0.16)
Luteinising hormone	4	-0.29 (0.18)	0.33 (0.21)	-0.29 (0.23)
IGF-I	6	-0.21 (0.15)	0.20 (0.17)	-0.24 (0.18)
<i>Semen Quality</i>				
Mass activity	12	-0.17 (0.14)	0.14 (0.17)	-0.24 (0.18)
	18	-0.27 (0.18)	0.55 (0.23)	-0.65 (0.24)
	24	-0.76 (0.30)	0.88 (0.37)	-0.81 (0.41)
Motility	12	-0.12 (0.14)	0.03 (0.17)	-0.11 (0.19)
	18	-0.37 (0.22)	0.72 (0.26)	-0.77 (0.28)
	24	-0.61 (0.32)	0.88 (0.36)	-0.84 (0.39)
%normal sperm	12	.	.	.
	18	-0.52 (0.31)	0.29 (0.35)	-0.21 (0.37)
	24	-0.65 (0.24)	0.63 (0.26)	-0.69 (0.28)
<i>Scrotal and sheath</i>				
Scrotal circumference	6	-0.04 (0.14)	0.01 (0.18)	0.18 (0.21)
	12	-0.19 (0.13)	0.15 (0.16)	-0.19 (0.17)
	18	-0.27 (0.13)	0.27 (0.15)	-0.35 (0.16)
	24	-0.09 (0.12)	0.10 (0.15)	-0.12 (0.17)
Sheath score	18	-0.12 (0.16)	0.11 (0.20)	-0.18 (0.22)
Preputial eversion	18	0.13 (0.16)	-0.12 (0.20)	0.20 (0.22)

Table 19. Genetic correlations a between bull traits and female reproduction at mating 2 in TCOMP (standard errors in parentheses)

Bull trait	Age (mths)	L. Anoestrous interval	Calving rate 2	Days to calving 2
<i>Hormones</i>				
Inhibin	4	-0.09 (0.16)	-0.02 (0.22)	0.08 (0.17)
Luteinising hormone	4	0.59 (0.23)	-0.66 (0.30)	0.46 (0.23)
IGF-I	6	-0.10 (0.18)	0.14 (0.24)	0.03 (0.20)
<i>Semen Quality</i>				
Mass activity	12	-0.12 (0.19)	0.09 (0.25)	0.03 (0.21)
	18	-0.68 (0.36)	0.91 (0.53)	-0.62 (0.40)
	24	-0.22 (0.36)	0.53 (0.52)	-0.40 (0.46)
Motility	12	-0.11 (0.19)	0.00 (0.26)	0.01 (0.21)
	18	-0.73 (0.35)	1.0* (0.58)	-0.64 (0.38)
	24	-0.05 (0.38)	0.49 (0.53)	-0.26 (0.45)
%normal sperm	12	-0.34 (0.25)	0.55 (0.33)	-0.47 (0.28)
	18	-0.30 (0.25)	0.31 (0.33)	-0.16 (0.27)
	24	0.05 (0.20)	0.26 (0.29)	-0.04 (0.23)
<i>Scrotal and sheath</i>				
Scrotal circumference	6	0.15 (0.16)	-0.03 (0.24)	-0.06 (0.20)
	12	0.14 (0.16)	0.15 (0.23)	-0.14 (0.19)
	18	0.13 (0.16)	0.14 (0.24)	-0.07 (0.20)
	24	0.23 (0.16)	-0.04 (0.23)	0.06 (0.19)
Sheath score	18	-0.30 (0.19)	0.08 (0.26)	-0.15 (0.22)
Preputial eversion	18	0.52 (0.25)	-0.26 (0.32)	0.34 (0.26)

Table 20. Genetic correlations between bull traits and lifetime female reproduction in BRAH (standard errors in parentheses)

Bull trait	Age (mths)	Lifetime annual calving rate	Lifetime annual weaning rate
<i>Hormones</i>			
Inhibin	4	0.32 (0.22)	0.26 (0.24)
Luteinising hormone	4	0.29 (0.32)	0.42 (0.32)
IGF-I	6	-0.14 (0.25)	0.02 (0.26)
<i>Semen Quality</i>			
Mass activity	12	-0.34 (0.25)	-0.28 (0.27)
	18	0.70 (0.34)	0.61 (0.33)
	24	0.92 (0.64)	0.77 (0.62)
Motility	12	-0.07 (0.27)	-0.22 (0.28)
	18	0.75 (0.36)	0.79 (0.36)
	24	1.0* (0.60)	1.00 (0.64)
%normal sperm	12	.	.
	18	0.09 (0.41)	-0.12 (0.42)
	24	-0.25 (0.46)	0.13 (0.46)
<i>Scrotal and sheath</i>			
Scrotal circumference	6	-0.25 (0.27)	-0.32 (0.28)
	12	0.03 (0.24)	-0.21 (0.24)
	18	0.12 (0.22)	0.14 (0.23)
	24	0.04 (0.22)	-0.03 (0.23)
Sheath score	18	0.33 (0.31)	0.28 (0.33)
Preputial eversion	18	-0.59 (0.28)	-0.71 (0.27)

* estimate exceeded bounds

Table 21. Genetic correlations a between bull traits and lifetime female reproduction in TCOMP (standard errors in parentheses)

Bull trait	Age (mths)	Lifetime annual calving rate	Lifetime annual weaning rate
<i>Hormones</i>			
Inhibin	4	0.49 (0.45)	0.17 (0.27)
Luteinising hormone	4	-0.64 (0.55)	0.03 (0.33)
IGF-I	6	0.73 (0.39)	0.18 (0.33)
<i>Semen Quality</i>			
Mass activity	12	-0.15 (0.38)	-0.20 (0.31)
	18	0.20 (0.55)	-0.36 (0.44)
	24	-0.26 (0.68)	0.01 (0.57)
Motility	12	0.06 (0.38)	0.08 (0.30)
	18	0.37 (0.51)	-0.05 (0.39)
	24	-0.07 (0.75)	-0.12 (0.61)
%normal sperm	12	0.31 (0.44)	-0.07 (0.38)
	18	0.37 (0.46)	-0.02 (0.38)
	24	0.22 (0.40)	0.24 (0.33)
<i>Scrotal and sheath</i>			
Scrotal circumference	6	-0.62 (0.39)	-0.46 (0.25)
	12	-0.26 (0.37)	-0.29 (0.29)
	18	-0.26 (0.36)	-0.28 (0.27)
	24	-0.45 (0.37)	-0.33 (0.27)
Sheath score	18	0.26 (0.42)	0.57 (0.28)
Preputial eversion	18	-0.59 (0.44)	-0.88 (0.33)

The genetic correlations between bull traits and female lifetime traits are presented in Tables 20 and 21. The correlations generally reflect the observations from the previous results. For Brahman no clear relationships were apparent for the hormone or scrotal traits but high to very high correlations were observed for the semen traits measured at 18 and 24 months (albeit with very large standards errors).

For TCOMP, all estimates had large standard errors but here are indications of genetic relationships with hormone traits (e.g. IGF-I) with lifetime calving rates. Genetic correlations with scrotal tended to be negative. Preputial eversion was correlated with lifetime traits, with similar magnitude of estimates in both genotypes.

4.4 Genetic correlations associated with whole-herd profitability

Estimates of the genetic correlations between traits measured in females and traits in steers provides understanding of how these traits are related and the likely impact on multiple trait selection (i.e. selection for whole herd profitability). The estimates also highlight what traits may need to be recorded if antagonisms exist. In this work the very large environmental and physiological state differences between the steers (i.e. feedlot) and the cows (lactating in northern production environments) will contribute to the estimated genetic correlation.

4.4.1 Cow body composition and steer traits.

The genetic relationship between similar measures on steers and cows is presented in Tables 22 and 23. Steers were recorded after an average of 120 days on a high energy

feedlot ration. Cows were recorded pre-calving (PC) at the start of the 2nd mating (i.e. Mating 2; M2), as described in section 4.1.4.

In general the estimates are lower for Brahman compared to Tropical Composites and the estimates reduce in magnitude when the cow measures are recorded at the “into mating” stage as first-lactation cows. For Brahman the reduction in the magnitude of the genetic correlation between the steer trait and the cow trait (for the same measure) was greatest for weight, EMA and body condition score. In Tropical Composites, the reduction was greatest between measures of fatness. These estimates show these traits are often quite different when recorded in steers versus cows, particularly when measured in first-lactation cows. As a result, sires are expected to re-rank significantly for these traits across the sexes.

Table 22. Genetic correlations between steer and corresponding cow traits at the 3 stages in Brahman (standard errors in parentheses)

Steer trait	Pre-calving	Into Mating	Change M2– PC
LWT	0.42 (0.18)	0.17 (0.24)	-0.30 (0.24)
EMA	0.94 (0.21)	-0.03 (0.37)	-0.32 (0.44)
P8	0.69 (0.15)	0.54 (0.22)	-0.46 (0.24)
RIB	0.89 (0.12)	0.54 (0.18)	-0.78 (0.23)
BCS	0.70 (0.30)	-0.11 (0.38)	-0.16 (0.41)
HH	0.74 (0.12)	0.85 (0.12)	- -

Table 23. Genetic correlations between steer and corresponding cow traits at three stages in Tropical Composite (standard errors in parentheses)

Steer Trait	Pre-calving	Into Mating	Change M2-PC
LWT	0.82 (0.09)	0.85 (0.08)	-0.47 (0.19)
EMA	0.96 (0.14)	0.70 (0.15)	0.72 (0.14)
P8	0.92 (0.08)	0.09 (0.24)	-0.91 (0.08)
RIB	0.62 (0.16)	0.11 (0.25)	-0.84 (0.14)
BCS	0.17 (0.25)	-0.51 (0.21)	-0.54 (0.24)
HH	0.95 (0.08)	1.0*	- -

* estimate exceeded bounds

4.4.2 Steer and female reproduction relationships

Genetic correlation estimates between key steer traits and a subset of cow traits are presented in Tables 24 and 25. These are important estimates to establish the expected correlated effects of selection for steer traits on female reproduction (and vice versa). In general no major antagonisms existed however there were some indications that selection for reduced shear force (i.e. improved tenderness) may be associated with reduced reproductive performance. Also in both genotypes there were indications that increased steers fatness is genetically related to reduced female performance. Residual feed intake in Brahmans showed a changing relationship between female reproduction traits at mating 1 versus mating 2, and is most likely associated with the effects of lactation.

Table 24. Genetic correlations between key cow reproduction traits and important steer traits[#] for Brahman (standard errors in parentheses)

COW	WT	EMA	P8	RFI	OSS	RBV	IMF	SF
CR1	-0.02 (0.26)	0.60 (0.40)	-0.06 (0.26)	0.46 (0.32)	0.28 (0.23)	0.62 (0.30)	0.23 (0.30)	0.25 (0.26)
DC1	-0.13 (0.27)	-0.53 (0.41)	0.07 (0.26)	-0.50 (0.33)	-0.36 (0.22)	-0.64 (0.29)	-0.28 (0.30)	-0.27 (0.26)
LAI	-0.21 (0.22)	-0.01 (0.37)	0.53 (0.21)	0.23 (0.29)	-0.39 (0.20)	0.51 (0.30)	-0.27 (0.24)	-0.23 (0.23)
DC2	-0.11 (0.27)	0.18 (0.41)	0.42 (0.25)	0.56 (0.32)	-0.12 (0.25)	0.38 (0.40)	-0.19 (0.30)	-0.01 (0.26)
PR2	-0.21 (0.24)	-0.44 (0.35)	-0.63 (0.20)	-0.28 (0.30)	0.22 (0.22)	-0.30 (0.37)	-0.17 (0.26)	0.05 (0.24)
LCR	-0.15 (0.29)	-0.17 (0.45)	-0.28 (0.29)	0.10 (0.36)	0.13 (0.27)	0.32 (0.42)	0.26 (0.34)	0.04 (0.29)
LWR	0.09 (0.31)	-0.30 (0.46)	0.02 (0.30)	0.29 (0.37)	0.23 (0.28)	-0.71 (0.44)	0.14 (0.34)	0.27 (0.28)

[#] WT=hot carcass weight; EMA= eye muscle area; P8 = carcass P8 fat depth RFI=residual feed intake; OSS=MSA ossification score; RBV=retail beef yield %; IMF = carcass intramuscular fat; SF=shear force.

Table 25. Genetic correlations between key cow reproduction traits and important steer traits[#] for Tropical Composite (standard errors in parentheses)

COW	WT	EMA	P8	RFI	OSS	IMF	SF
CR1	0.14 (0.26)	-0.15 (0.28)	0.36 (0.24)	0.02 (0.32)	0.12 (0.28)	0.32 (0.28)	0.48 (0.27)
DC1	-0.10 (0.26)	0.24 (0.26)	-0.41 (0.23)	-0.11 (0.30)	-0.01 (0.27)	-0.33 (0.26)	-0.56 (0.25)
LAI	0.12 (0.24)	0.47 (0.25)	0.30 (0.24)	0.04 (0.29)	-0.38 (0.24)	-0.23 (0.23)	-0.09 (0.28)
DC2	-0.01 (0.26)	0.05 (0.27)	0.05 (0.26)	-0.12 (0.31)	0.17 (0.28)	-0.32 (0.24)	-0.36 (0.28)
PR2	-0.12 (0.37)	-0.12 (0.39)	-0.40 (0.40)	-0.13 (0.42)	-0.26 (0.40)	0.38 (0.33)	0.50 (0.41)
LCR	-0.37 (0.41)	-0.46 (0.45)	-0.02 (0.40)	0.37 (0.42)	-0.38 (0.44)	0.51 (0.40)	0.42 (0.40)
LWR	-0.06 (0.32)	-0.21 (0.34)	-0.19 (0.32)	-0.07 (0.38)	-0.34 (0.35)	0.32 (0.34)	0.33 (0.33)

[#] WT=hot carcass weight; EMA= eye muscle area; P8 = carcass P8 fat depth RFI=residual feed intake; OSS=MSA ossification score; IMF = carcass intramuscular fat; SF=shear force

4.5 Genotype differences

Predicted genotype means were produced for a range of traits and allowed the differences between genotypes (i.e. BRAH vs. TCOMP) to be determined. All analyses were performed using only data from cows run at the Belmont Research Station. This was because these cows have remained as contemporaries throughout the experiment and therefore their performance can be directly compared.

4.5.1 Genotype means for female reproduction

Adjusted genotype means for female reproduction traits are presented in Table 26. At the mating 1 the conception and pregnancy were not significantly different between BRAH and TCOMP. However, BRAH had significantly longer days to calving and a lower calving and weaning rate compared to TCOMP cows. At the mating 2, first-lactation BRAH cows had significantly longer lactation anoestrous intervals and a lower cycling rate compared to TCOMP. This was reflected in significantly lower reproduction rates for all traits, culminating in a 48% weaning rate for BRAH compared to 73% for TCOMP in lactating cows. In non-lactating cows at the mating 2 there were no significant differences between the genotypes for days to cycling, conception, pregnancy or calving rates. However BRAH had significantly longer days to calving (+16.6d) and a lower weaning rate (-18%) compared to TCOMP.

Significant genotype differences existed for the lifetime reproduction traits with TCOMP having higher lifetime calving and weaning rates compared to BRAH. For cows still present at the 6th mating for TCOMP both the annual calving and annual weaning rates were still significantly higher compared to BRAH. The reduction in the differences between the genotypes in the mean calving and weaning rate compared to all cows reflects the fact that a greater percentage of BRAH cows were culled or died compared to TCOMP.

Table 26. Genotype means for female reproduction traits of similarly managed Brahman and Tropical Composite cows (at Belmont Research Station)

Trait	Brahman		Tropical Composite	
	n	Mean*	n	Mean
<i>Mating 1</i>				
Conception rate	299	0.92 ^a	295	0.96 ^a
Pregnancy rate	299	0.89 ^a	295	0.92 ^a
Calving rate	299	0.83 ^a	295	0.92 ^b
Weaning rate	299	0.75 ^a	295	0.85 ^b
Days to calving (d)	299	335.5 ^a	295	315.3 ^b
<i>Mating 2 - lactating cows</i>				
Lactation anoestrous interval (d)	208	114.0 ^a	245	57.1 ^b
Lactation cyclicity rate	210	0.71 ^a	245	0.93 ^b
Conception rate	212	0.57 ^a	249	0.85 ^b
Pregnancy rate	212	0.53 ^a	249	0.81 ^b
Calving rate	211	0.53 ^a	248	0.79 ^b
Weaning rate	211	0.48 ^a	248	0.73 ^b
Days to calving (d)	211	372.8 ^a	248	341.6 ^b
<i>Mating 2 - dry cows</i>				
Days to cycling (d)	65	14.1 ^a	41	11.3 ^a
Conception rate	66	0.91 ^a	41	0.98 ^a
Pregnancy rate	66	0.88 ^a	41	0.98 ^a
Calving rate	65	0.83 ^a	41	0.95 ^a
Weaning rate	65	0.72 ^a	41	0.90 ^b
Days to calving (d)	65	329.0 ^a	41	312.6 ^b
<i>Lifetime</i>				
Annual calving rate retained cows	206	0.83 ^a	245	0.89 ^b
Annual weaning rate retained cow	206	0.80 ^a	245	0.86 ^b
Lifetime annual calving rate	299	0.76 ^a	295	0.86 ^b
Lifetime annual weaning rate	299	0.65 ^a	295	0.79 ^b

* Within a row means followed by a different letter are significantly different $P < 0.05$.

4.5.2 Genotype means for cow body composition

Adjusted genotype means for female body composition traits at mating 2 and for change in composition over the period from pre-calving to into mating (approx. 3 months) are presented in Table 27. Brahman cows were lighter but fatter into mating as lactating cows compared to Tropical Composites. However, both genotypes lost similar amounts of weight, fat and EMA during the period pre-calving and into mating. For example, Brahman and Composite cow lost on average 52 kg of body weight in this period and reduced EMA by 14 cm² and 5 mm of P8 fat.

Table 27. Genotype means for cow body composition of similarly managed Brahman and Tropical Composite cows (at Belmont Research Station)

Trait	Pregnant or lactating				Genotype s.e.d.
	BRAH		TCOMP		
	N	Mean [*]	N	Mean	
Into mating					
WT (kg)	220	399.2 ^a	245	426.4 ^b	5.6
EMA (cm ²)	221	42.6 ^a	242	41.8 ^a	1.0
P8 (mm)	221	3.2 ^b	243	2.1 ^a	0.3
RIB (mm)	221	1.9 ^b	242	1.6 ^a	0.1
BCS (score)	230	2.2 ^a	243	2.2 ^a	0.1
HH (cm)	221	138.3 ^b	243	135.9 ^a	0.8
Change (Into mating minus precalving)					
WT (kg)	220	-52.3 ^a	245	-52.2 ^a	2.9
EMA (cm ²)	221	-14.0 ^a	242	-13.9 ^a	1.1
P8 (mm)	221	-5.0 ^a	243	-4.8 ^a	0.3
RIB (mm)	221	-3.2 ^a	242	-3.6 ^a	0.3
BCS (score)	230	-0.90 ^a	243	-0.83 ^a	0.05
HH (cm)	221	0.6 ^a	243	1.2 ^a	0.4

* Within a row means followed by a different letter are significantly different $P < 0.05$.

4.6 Calf losses

A total of 9,296 calves were born during the project and a total of 906 deaths or disposals were recorded across the five locations. Table 28 lists the distribution of deaths between birth and weaning.

Table 28. Distribution of calf deaths after birth (906 from N=9296 calves)

Interval from birth	Count	% of deaths	Cumulative	% of deaths
<day 0	14	1.6	14	1.55
day 0	261	28.8	275	30.4
1-2 days	193	21.3	468	51.7
2-7 days	136	15.0	604	66.7
7-30 days	114	12.6	718	79.2
30-90 days	80	8.8	798	88.1
90+ days	108	11.9	906	100

Approximately 50% of the calf deaths occurred in the first 48 hours. Many of these deaths were associated with the large losses experienced at Toorak Research Station for the 2004 and 2005 drop calves (18% of total project losses) many were from acute Vitamin A deficiency. In subsequent years significantly higher losses also occurred at Toorak compared to the other locations even though all cow received an annual Vitamin A supplementation.

4.6.1 Factors affecting calf losses

Analyses were performed to determine the factors significantly influencing calf loss. The major variable explaining calf loss was cohort and included location and year. Other factors identified as contributing to calf loss included birth weight, twinning, cow experience, teat score, gender and horn status. Table 29 presents the odds ratios for

each factor relative to a level of 1.0. Although the level of twinning was low, the predicted chance of calf mortality up to one week (1Wk) was 10.8 times more likely than a single. Heifer calves were less likely to die compared to bull calves. For birth weight the likelihood of mortality was significantly higher for light weight calves compared to heavier calves. There was a trend (not significant) for heavy calves greater than 39kg to be more likely to die than calves in 32-39 kg range. Cow status also significantly affected calf mortality. Calves from young cows were more likely to die, especially less than 1 month of age. Also cows that had previously lost a calf had a higher chance of losing another calf. Teat and udders scores also influenced calf loss: score 5 teats (i.e. bottled) and 5 score udder (very big) were more than 2 times and up to 4 times more likely to have a calf mortality in the first month compared to score 3 cows. Finally, approximately 20% of the calf deaths occurred after 3 months of age, where the majority occurred after branding. At this time dehorning was performed but no bull castration (left entire for bull reproduction project). For calves present at branding (i.e. excluding all earlier deaths) the odds-ratio indicated that the risk of calf mortality was substantially reduced for calves that were not dehorned.

Table 29. Odds ratios (OR) for calf mortality by effect level, where the OR are expressed relative to the level (within factor) with the most data.

(OR in bold differ significantly from the reference level at $P < 0.05$)

Variable	Contrast	Cumulative mortality			
		1Wk	1Mth	3Mth	Wean
Gender	Heifer vs bull	0.57	0.56	0.52	0.53
Birth type	Twin vs single	10.8	9.09	8.10	7.22
Birth weight	1 vs 5	2.07	2.83	2.57	2.12
	2 vs 5	1.54	1.97	1.91	1.63
	3 vs 5	0.99	1.13	1.06	1.03
	4 vs 5	0.71	0.83	0.80	0.82
	5 vs 5	1.0	1.0	1.0	1.0
Cow status	1_000M	4.34	4.02	3.18	2.69
	1_000E	3.14	3.53	2.80	2.59
	1_100	5.59	4.24	3.16	2.34
	1_110	3.66	3.50	2.85	2.70
	1_111	2.31	2.09	1.88	1.77
	2_000	1.32	1.38	1.47	1.50
	2_100	0.44	0.82	1.05	0.78
	2_110	2.52	2.42	2.26	2.10
	2_111	1.0	1.0	1.0	1.0
	3_000	0.73	0.81	0.70	0.65
	3_100	1.63	1.12	0.88	0.63
	3_110	0.94	1.17	1.36	1.49
	3_111	1.11	0.99	1.06	0.97
	1 vs 3	0.15	0.40	0.53	0.61
	2 vs 3	0.37	0.64	0.69	0.74
Teat score (Back)	3 vs 3	1.0	1.0	1.0	1.0
	4 vs 3	1.00	1.34	1.43	1.35
	5 vs 3	2.08	4.54	4.30	4.15
	1 vs 3	0.52	0.43	0.47	0.55
	2 vs 3	0.91	0.81	0.79	0.78
Udder score	3 vs 3	1.0	1.0	1.0	1.0
	4 vs 3	1.10	1.04	1.04	1.08
	5 vs 3	1.78	2.08	1.75	1.52

Birth weight classes are: 1: <29kg; 2: 29.5-32kg; 3: 32.2-35kg; 4: 35.2-38.5kg; 5: 39-62kg; 6: unweighed; Cow status code denotes age of dam (in years) concatenated with previous outcome, represented as: age group outcome; M and E denote maiden and empty. Therefore,

3_000E represents a cow in age group three (7+ yo) which was empty in the previous year (000=0 pregnancy, 0 calves born, 0 calves weaned); 2_111 is a cow in age group 2 (4-7yo) that reared a calf in the previous year.

4.6.2 Genetic influences on calf losses

Preliminary genetic analyses were undertaken for calf loss and also for component factors; birth weight and teat and udder scores. While the heritability of calf mortality was very low (about 0.05 to 0.09) *per se* the heritability of teat score was 0.38 and udder score 0.49. Birth weight had a direct heritability of 0.48 and a maternal heritability of 0.13. The genetic correlation between teat score and calf mortality was 0.55 and -0.21 between teat score and the direct genetic effect of birth weight.

5. Discussion and conclusions

Large within and between genotype differences in reproduction were very apparent from this study. Extended lactation anoestrus was clearly evident, especially in first-lactation Brahman cows, and this had a large influence on reproductive performance. This result is consistent with previous studies in northern Australia (e.g. Frisch *et al.* 1987, Holroyd *et al.* 1990; O'Rourke *et al.* 1991, Fordyce *et al.* 1996; Schatz and Hearnden 2008). Heritability estimates indicate a considerable genetic contribution to lactation anoestrus, and it is expected that it could be improved by selection. This result is supported by Brahman selection line outcomes of Schatz *et al.* (2010), where a 35% difference in heifer pregnancy rates was observed between a selection line and an industry control line. Davis *et al.* (1993) also reported a 15% difference in heifer pregnancy rate between divergent Droughtmaster selection lines. Large genetic differences in heifer age at puberty, observed by Johnston *et al.* (2009), are likely to be contributing to differences in heifer reproductive performance in both these two selection experiments, and the current study.

In general, lifetime female reproductive rates were lowly heritable in both genotypes but several of the traits recorded at first and second matings were moderately to highly genetically correlated with female lifetime reproduction rates, although all estimates have large standard errors, driven primarily by the low heritabilities of the lifetime traits. However the consistent directions of the correlations suggest opportunities exist to increase rates of genetic progress in lifetime reproduction traits by selecting on these moderately to highly heritable traits earlier in life. Existing genetic evaluation of days to calving (DC) in BREEDPLAN (Graser *et al.* 2005) is modelled as a repeat measure over a number of matings (up to 6). Results from this project indicate days to calving could be improved (i.e. more accurate and earlier in life) by treating the records from matings 1 and 2 as separate traits (i.e. different heritabilities and genetic correlations). These results and recommendations are now being addressed by the MLA funded BREEDPLAN R&D Project (B.BFG.0050) as part of the redevelopment of the reproduction EBVs. The work will also incorporate outcomes from the Beef CRC genomics projects that developed prediction equations for female reproduction using these data.

The measurements that were correlated with the lifetime traits represented a range in both genotypes, from ultrasound scanning of a conception, to manual palpation for pregnancy, through to observations of a calf born and the number of days to the birth of a calf and combinations of mating 1 and 2 outcomes (e.g. pregnant-and-wet). The generally consistent sign of this range of associations is support for the genetic correlations with lifetime traits being real and also suggests there can be flexibility in

recording systems to capture this genetic variation. The results also show that days to calving was highly correlated with the other all measures, especially those associated with lactation anoestrus. Breeds currently using the trait through BREEDPLAN will be improving early- and lifetime performance by selecting on this trait. Associations of female reproduction with cow survival in this study were inconclusive given the low number of cow deaths. However, opportunities exist to follow-up this work by using the large amount of cow body composition data to develop alternative measures of cow survival, and if heritable, to estimate genetic correlations with reproduction traits from this project. It is plausible that selection for reduced lactation anoestrus may be beneficial for cow survival because it enables cow to maintain an annual calving pattern. By using bull control it should be possible to match the calving season with the time of maximum feed supply (i.e. wet season). Conversely, if weaning the calf is required to break the lactation anoestrus and trigger cycling, then under continuous mating systems, these cows will conceive and calve out of season and could be at increased risk.

Integration of these early in life reproduction traits (e.g. at mating 1 and 2) into selection should increase the rate of improvement in lifetime annual reproduction rates. Other possible correlated measures identified as potential early in life indicator traits were those associated with puberty. However these will require further consideration as to how measures of puberty could be cost effectively included in industry recording. Measures of cow body composition were not considered effective indicator traits of reproduction but may have utility as measures of cow condition. These results need to be considered in conjunction with the results and recommendations from the Beef CRC's maternal productive project from southern Australia.

The high genetic correlations of female reproduction traits with bull reproductive traits is another key outcome of the project, and offers a means to also lift rates of genetic progress in female reproduction through indirect selection on males. Measurement of scrotal circumference and, more importantly, measures of semen quality could be measured in seed-stock herds and the data used to greatly increase the accuracy of selection of female reproduction traits. Phenotypic and genetic improvements in the bull traits *per se* would increase the utility of these measures. Modifications will be required to the current genetic evaluation scheme to allow these additional traits to be analysed. Records from Bull Breeding Soundness Evaluations will need to be captured, along with necessary management group information on whole cohorts of young seedstock bulls. These results are also being follow-up in the MLA BFG.0050 project using industry recorded datasets of these bull measures, as well as computations of expected rates of gains, thus providing additional assessment of the value of these new measures.

The generally low genetic correlations between steers traits and cow reproduction traits indicates that selection for improved steer performance (i.e. early growth, carcass and meat quality and feed efficiency) can occur without any major antagonisms with female reproduction. This is important for a breeding objective focussed on whole herd profitability. However if both steer and cow reproduction traits are to be improved then they will both need to be measured, and selected appropriately according to their relative contribution to the overall breeding objective. Further work is required to establish if selection for large mature cow size (i.e. weight and frame) is antagonistic with female reproduction. This will require the development of additional traits and models that can account for culling and phenotypic effects of missing a calf on subsequent measures of cow weight and size.

Significant reproductive wastage is occurring in northern production systems. Factors contributing to these losses have been identified in this project and some can clearly be

influenced by management. In regions where Vitamin A deficiency is possible then supplementation is important to reduce calf losses. Selection against low birth weights is one means for potentially reducing calf losses but investigation of other causes, and possible solutions, is warranted. Bottle teats are also a clear risk factor for increased calf losses. Culling and bull selection are possible avenues to address this issue given the heritabilities, but other management options should be investigated further. Calf dehorning appears to be a significant risk factor and can be reduced in a herd by selection for polledness. However the rate of change will initially dependent on the gene frequency in the various tropical breeds. Outcomes from this project on calf losses need to be further examined in the context of the recently available results from the MLA's Cash Cow project, including analysis of prenatal losses at each trimester of pregnancy.

Opportunities exist, particularly in Brahman, to improve weaning rates though genetic selection. Recording of reproductive performance is the key and on-farm recording systems in seed-stock herds need to capture this data. Enhancements may be required to genetic evaluation systems to include these new female traits and potential correlated traits, along with appropriate variance components in a full multi-trait framework. Seedstock breeders can immediately begin to capture benefits from this project by initiating recording of female (and male) reproductive performance in their herds. The initial focus should be on recording the reproductive performance (i.e. mating group, mating outcome, lactation status etc) of maiden heifers and first-calf cows. It is also in these age groups, given the project results, where culling of non-pregnant cows should be most practiced. For the seedstock herd to make genetic improvements in reproduction of their herd it is important they use stud sires with above average reproduction EBVs (polled, if possible) and selection using EBVs for young home-bred bulls and replacement heifers. Culling all cows with bottle teats is also important, however, a genetic evaluation is required to increase the effectiveness of reducing this condition.

For commercial producers reproduction rates can be improved by genetically improving the herd. This can be achieved primarily through the purchasing of replacement bulls with above breed average (or herd average) EBVs for reproduction, and by not retaining replacement heifers (or bulls) from cows that missed calving as a maiden or first-calf cow (or had bottle teats). For those breeds without reproduction EBVs it is important the breeders work together to start collecting the mating and calving data to enable the future development of the EBVs for the breed. Until then, seedstock and commercial breeders should consider avoiding bulls that are the progeny of cows that missed a calf as a maiden heifer or as a first-calf cow.

Finally, improvements in reproduction rates in northern Australia are possible but will only be achieved by increased levels of recording, improved selection tools and an industry-wide commitment to making change.

6. Recommendations

- Selection can be used to increase the reproductive performance of tropical breeds however breeds not in this project require phenotypic records on these early-in-life traits (and indirect measures) to enable increased effectiveness of selection.
- Seedstock/bull breeding sector of tropical breeds need to increase their level of recording of female reproduction traits, with particular focus on maiden and 1st lactation cow performance.
- Indirect measures (including genomics) offer the opportunity to increase rates of genetic progress in improving reproduction. Further work is required to quantify the best strategies to enable this, and to develop the required genetic evaluations.
- Data from this project can be used to enhance the genetic evaluation of Brahmans and Tropical Composites, in particular the estimation of genetic parameters that underpin their genetic evaluations. The data and project outcomes can also be used to re-define traits and models used in the genetic evaluation of female reproduction.
- Advanced genetic analyses are required to further quantify the genetic differences in cow size, body composition and longevity to ensure selection for reproduction occurs without compromising cow survival.
- The comprehensive set of unique phenotypes and the existence of full genomic information should be further utilised to establish genomic selection for additional traits or genetic conditions. The data can also be used to investigate the genomic architecture of breeds which may further enhance genomic selection in multi-breed populations.
- The project data (phenotypes and genotypes) are being used to enhance the genetic evaluation of reproduction traits in Brahmans and Tropical Composites, including the development of genomic selection. However to make significant lifts in reproductive rates across the northern industry through selection requires the collection of more reproduction phenotypes on current industry genetics, coupled with strategic genotyping of influential sires, across the major tropical breeds.
- Reproductive losses were very apparent in this project and appear common across northern Australian production systems. Further work is required to gain a greater understanding of likely factors and possible strategies to reduce pre- and post natal losses.
- Need to educate producers on the role genetics plays in reproductive performance in northern Australia. But this message must coincide with increased availability of genetically described young bulls for reproductive traits generated in the bull breeding sector of the industry.

7. Publications from this project

Journal Papers

- Burns BM, Gazzola C, Holroyd RG, Crisp J and McGowan MR (2011) Male reproductive traits and their relationship to reproductive traits in their female progeny: a systematic review. *Reproduction in Domestic Animals* 46: 534-553.
- Burns BM, Fordyce G and Holroyd RG (2010) A review of factors that impact on the capacity of beef cattle to conceive, maintain a pregnancy and wean a calf – implications for reproductive efficiency in northern Australia. *Animal Reproduction Science* 122: 1-22.
- Collis E, Fortes MRS, Zhang Y, Tier B, Schutt K, Barendse W and Hawken R (2011) Genetic variants affecting meat and milk production traits appear to have effects on reproduction traits in cattle. *Animal Genetics* DOI: 10.1111/j.1365-2052.2011.02272.x
- Corbet NJ, Burns BM, Johnston DJ, Wolcott ML, Corbet DH, Venus BK, Li Y, McGowan MR and Holroyd RG (2012) Male traits and herd reproductive capability in tropical beef cattle. 2. Genetic parameters of bull traits. *Animal Production Science*, [Submitted].
- Fortes M.R.S., Lehnert SA, Burns BM, Hawken R, Boe-Hansen G, D'Atley K. and Thomas M. (2012) Genomic regions and quantitative trait loci associated with fertility traits in cattle: Advances from microsatellites to high-density chips. *Biology of Reproduction*, [In preparation]
- Fortes MRS, Lehnert SA, Bolormaa S, Reich C, Fordyce G, Corbet NJ, Whan V, Hawken RJ and Reverter A (2012) Finding genes for economically important traits: Brahman cattle puberty. *Animal Production Science* 52: 143-150.
- Fortes MRS, Reverter A, Nagaraj SH, Zhang Y, Jonsson NN, Barris W, Lehnert S, Boe-Hansen GB and Hawken RA (2011) A single nucleotide polymorphism-derived regulatory gene network underlying puberty in two tropical breeds of beef cattle. *Journal of Animal Science* 89: 1669–1683.
- Hawken RJ, Zhang Y, Fortes MRS, Collis E, Barris WC, Corbet NJ, Williams P, Fordyce G, Holroyd RG, Walkley JRW, Barendse W, Johnston DJ, Prayaga KC, Tier B, Reverter A and Lehnert SA (2012) Genome-wide association studies of female reproduction in tropically adapted beef cattle. *Journal of Animal Science* 90: 1398-1410.
- Johnston DJ and Graser H-U (2010) Estimated gene frequencies of GeneSTAR markers and their size of effects on meat tenderness, marbling, and feed efficiency in temperate and tropical beef cattle breeds across a range of production systems. *Journal of Animal Science*, 88, 1917-1935.

Refereed Conference Papers

- Fortes MRS, Bolormaa S, Porto Neto LR, Holroyd RG and Reverter A (2011) Principal component analysis in a population of Brahman bulls genotyped with 50K SNP chip revealed a genetic structure. *Proceedings Association for the Advancement of Animal Breeding and Genetics* 19: 267-270.

Fortes MRS, Li Y, Collis E, Zhang Y and Hawken RJ (2010) IGF1R: a candidate gene for cattle puberty. *Proceedings of the 32nd Conference for the International Society for Animal Genetics* Edinburgh.

Fortes MRS, Reverter A, Zhang Y, Collis E, Nagaraj SH, Jonsson NN, Barris W and Hawken RJ (2010) A new method for exploring genome-wide associations applied to cattle puberty. *Proceedings Ninth World Congress on Genetics Applied to Livestock Production*, Leipzig, Germany 9: 185.

Jeyaruban MG, Wolcott ML, Johnston DJ and Graser H-U (2011) Effect of previous reproductive status of dam on the pre-adjustment of weaning weight for genetic evaluation in tropical beef breeds. *Proceedings Association for the Advancement of Animal Breeding and Genetics* 19: 59-62.

Johnston DJ, Tier B and Graser H-U (2011) Beef cattle genetic evaluation in the genomics era. *Proceedings Association for the Advancement of Animal Breeding and Genetics* 19: 279-286.

Johnston D, Barwick S, Fordyce, G. and Holroyd R. (2010) Understanding the Genetics of Lactation Anoestrus in Brahman Beef Cattle to Enhance Genetic Evaluation of Female Reproductive Traits. *Proceedings Ninth World Congress on Genetics Applied to Livestock Production*, Leipzig, Germany 9: 923.

Wolcott ML and Johnston DJ (2009) The impact of genetic markers for tenderness on steer carcass and feedlot exit and heifer puberty traits in Brahman cattle. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics*, 18, 159-162.

Zhang Y, Tier B and Hawken R (2011) Genetic parameters of post-partum reproductive status in beef cattle from northern Australia. *Proceedings Association for the Advancement of Animal Breeding and Genetics* 19: 67-70.

Zhang YD, Tier B and Hawken R (2010) Whole genome analysis of heifer puberty in Brahman cattle. *Proceedings Ninth World Congress on Genetics Applied to Livestock Production*, Leipzig, Germany 9: 761.

Zhang YD and Tier B. (2009) Population stratification, not genotype error, causes some SNPs to depart from Hardy-Weinberg equilibrium. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics*, 18, 243-246.

Zhang Y, Tier B. and Hawken R. (2007). Fine mapping QTL with haplotypes determined from dense single nucleotide polymorphic markers. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics*, 17: 119-122.

Non-Refereed Conference Papers and Technical Reports

Burrow HM (2009) Future research agenda for northern beef genetics research. *Rendel Muster*, August 2009, *Proceedings of a Conference to mark the closure of the JM Rendel Laboratory*, Rockhampton.

Burrow HM (2009) Selection of beef cattle for harsh environments. *Proceedings 60th Annual Meeting of the European Association of Animal Production*, Barcelona, Spain

- Fordyce G, Murphy CP, Corbet NJ, and Broad K. (2011) Using ultrasound to measure carcass fat depth in live animals. *Proceedings of the Northern Beef Research Update Conference*, 2 - 5 August 2011, Darwin. p. 140.
- Fordyce G, Williams PJ, Holroyd RG, Corbet NJ, Sullivan MS and Reid A. (2008). Body condition score and rump fat depth of female beef cattle in the tropics. *Animal Production in Australia* Vol 27, 55.
- Fordyce G, Williams P, Sim WD, Young RJ and Hall RL. (2008). Correcting cattle live-weights in the tropics for weighing protocol. *Animal Production in Australia*, Vol 27, 56.
- Fordyce G, Williams PJ, Holroyd RG, Corbet NJ, Sullivan MS and Reid A. (2008) Body condition score and rump fat depth of female beef cattle in the tropics. *Proceedings Australian Society of Animal Production* Short Communication, 27: 55.
- Fordyce G, Sim WD, Young RJ and Hall RL. (2008) Correcting cattle liveweights in the tropics for weighing protocol. *Proceedings Australian Society of Animal Production* Short Communication, 27: 56.
- Fortes MRS, Hawken RJ, Zhang Y, Bolormaa S, Holroyd RG, Lehnert SA and Reverter A (2011) Finding genes for economically important traits: Brahman cattle puberty. *Proceedings Applied Genomics for Sustainable Livestock Breeding Melbourne* page 6.
- Hawken RJ, Zhang Y, Fortes MRS, Collis E, Reverter A, Barris W, Johnston D, Fordyce G, Holroyd R, Tier B, Burrow H and Lehnert SA (2011) Dissecting the genetics underlying reproduction rate in tropically adapted beef cattle. *Proceedings Applied Genomics for Sustainable Livestock Breeding Melbourne* page 4.
- Hawken RJ. (2008). Dissecting reproduction rate in Australia's tropically adapted beef cattle. 2008. *Allerton Conference 'Confronting Animal Phenotypes'* University of Champaign/Urbana, Illinois, USA, October.
- Hawken RJ, Prayaga KC, Collis E, Johnston D, Holroyd RG, Sim W, Williams P, Corbet N, Fordyce G, Tier B, Burns BM, Reverter A and Burrow HM. (2008) Gene discovery for reproduction rate in tropically adapted Australian beef cattle. *Proceedings International Society for Animal Genetics*, Amsterdam, July 2008, invited presentation.
- Johnston DJ, Tier B and Graser H-U (2011) Future opportunities and needs in beef. *Proceedings Applied Genomics for Sustainable Livestock Breeding Melbourne* page 16.
- McGowan MR, Fordyce G, and Holroyd RG. (2011) Recent advances in beef cattle reproduction – how science will improve herd performance. *Proceedings of the Northern Beef Research Update Conference*, 2-5 August, 2011, Darwin pp. 11-18.
- McGowan MR and Holroyd RG. (2008) Reproductive inefficiencies and opportunities in beef and dairy cattle. *Proceedings Australian Society of Animal Production* 27, 1-10.
- McGowan MR and Holroyd RG. (2008). Reproductive inefficiencies and opportunities in beef and dairy cattle. *Proceedings, Australian Society of Animal Production*, June 2008 Short Communication 27, 1-10.

Prayaga KC, Chan EKF, Reverter A, Johnston DJ, Hawken RJ, Barendse W, Fordyce G. and Burrow HM. (2008). Whole genome association study of adaptive traits in tropical beef cattle. *International Society of Animal Genetics Conference*, Amsterdam, The Netherlands.

Wolcott ML, Johnston DJ, Corbet NJ. and Williams PJ. (2011) The genetics of whole herd profitability. *Proceedings of the Northern Beef Research Update Conference*, 2 - 5 August 2011, Darwin. pp. 65-68.

Journal Papers in preparation

Barwick, Johnston, Wolcott (2013) Response to selection for lifetime weaning rate using combinations of early-in-life correlated measures

Bunter, Johnston, Wolcott, Fordyce (2013) Factors associated with calf mortality in tropically adapted breeds managed in extensive Australian production systems

Bunter, Johnston, Wolcott (2013) Genetic parameters for calf weights, calf mortality and maternal traits in tropically adapted breeds managed in extensive Australian production systems

Fordyce, Anderson, McCosker, Williams, Holroyd, Corbet, Sullivan (2012). Liveweight prediction from hip height, condition score, foetal age and breed in tropical female cattle

Johnston, Barwick, Fordyce Holroyd, Corbet, Williams (2013) Genetics of early- and lifetime reproductive performance in cows of two tropical beef genotypes in northern Australia

Johnston, Corbet, Wolcott, Barwick (2013) Genetic relationship between heifer puberty and male reproductive traits with female reproduction in two tropical beef genotypes.

Wolcott, Johnston, Barwick, Williams, Corbet, Fordyce (2013) Genetics of cow body composition in tropically adapted breed genotypes

Wolcott, Johnston, (2013) Genetic relationship between cow body composition and associated traits in heifers and steers.

8. Key Industry and stakeholder engagement

- MLA Meat Profit Days
- Annual NPG owners' workshop
- Presentations to company board/technical committees
- Project cooperator field days
- Industry Field day presentations (BIN, Beef2009, Beef2012)
- Beef2012, 2009 presentations
- Brahmans breeders' workshops
- Articles in industry publications (e.g. FRONTIER, Brahman News, BREEDPLAN news, CRC Beef Bulletin, rural press)
- National and international scientific presentations
- Beef CRC annual Science & Industry reviews
- BREEDPLAN breeder workshops
- Regular presentations to NBRC
- Presentations at Northern Research Update conferences
- Presentation to RBRCs and other producer groups
- Presentations to MLA workshops
- CRC industry distillation and champion workshops
- Presentations to US BIF and Genetic Prediction Committee
- Presentations to BREEDPLAN Technical Liaison Group
- SBTS/TBTS/CRC Webinar presentations

9. Acknowledgement

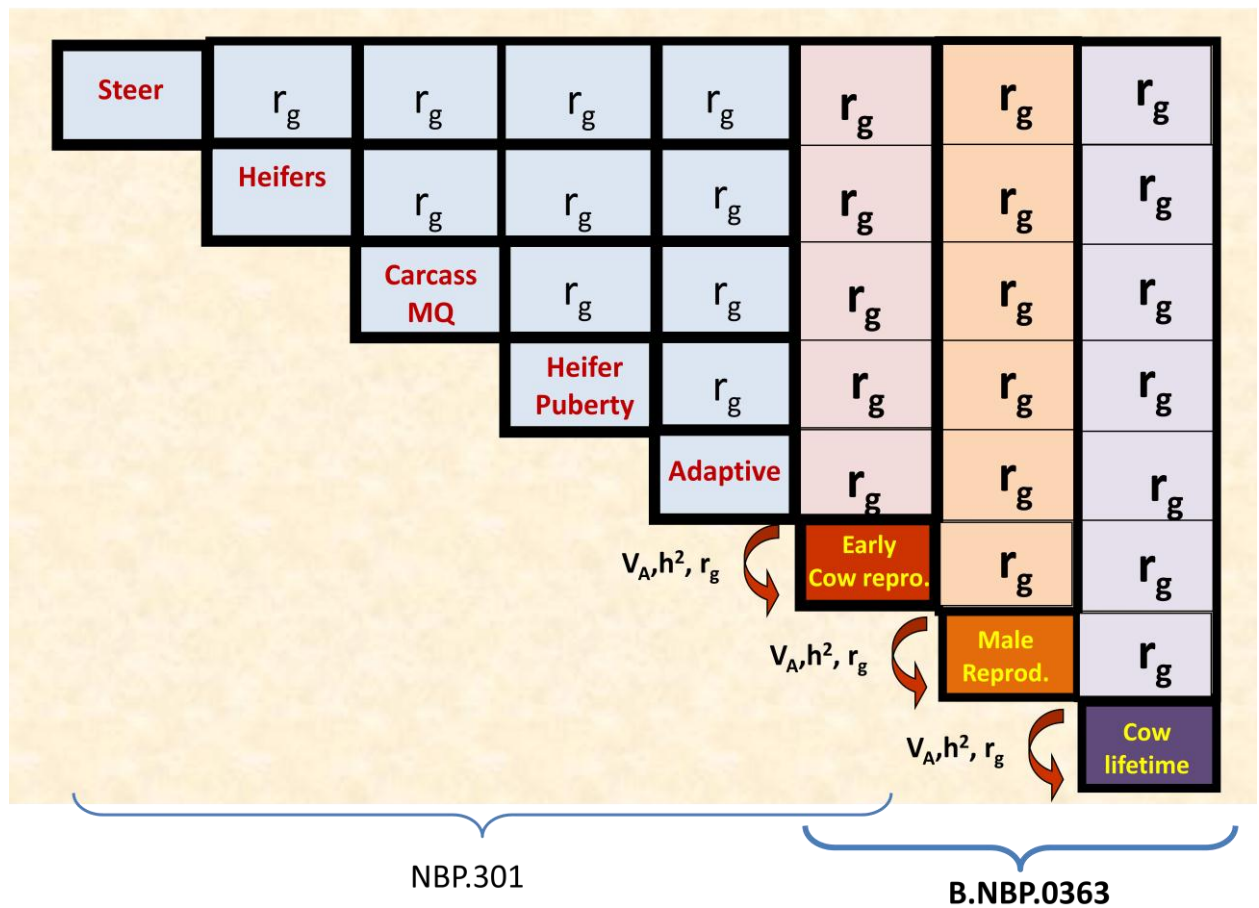
The authors acknowledge the Cooperative Research Centres for Cattle and Beef Quality and Beef Genetic technologies (and its core partners; The University of New England, NSW Department of Primary Industries, CSIRO and Queensland Department of Primary Industries and Fisheries), the Commonwealth funding through its CRC Program, and the generous financial support of Meat and Livestock Australia and the Australian Centre for International Agricultural Research (ACIAR). We acknowledge the tremendous contributions of the Australian Agricultural Company, C&R Briggs, Consolidated Pastoral Company, North Australian Pastoral Company, Stanbroke Pastoral Company, J&SM Halbersater, GE&J McCamley, S Kidman & Co, MDH Pty Ltd, and the research stations of AgForce Queensland and QDPI&F. We also gratefully acknowledge all Beef CRC participants, both scientists and technical staff, who contributed to or supported the work, including those involved in cattle management, data collection, laboratory analyses, and data handling.

Acknowledged are the contributions of Heather Burrow, Richard Holroyd, Geoffry Fordyce, Stephen Barwick, Nick Corbet, Paul Williams, Mick Sullivan, Matt Wolcott, Warren Sim, Peggy Olsson, Tracy Longhurst, Trudi Obst, Steve O'Connor, Russ Tyler, Rob Young, Dianne Vankan, and Andrew McCann and Jim Cook plus many dedicated technicians, station staff, and students.

10. Appendices

Appendix 1.

Schematic diagram of genetic analyses by trait blocks



Appendix 2a. Description of heifer pubertal traits

Code	Trait	Description
AGECL	Age at first CL (days)	Number of days from birth to the first CL ^A or CA ^B 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 first observed CL or CA
FATCL	Fat depth at the first CL (mm)	Heifer ultrasound P8 fat depth on the day (or within 7 days) of first observed CL or CA
CSCL	Condition score at first CL	Subjective score of body condition using 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 first observed CL or CA. For analysis the scores were recoded 1 to 15.
TSIZE	Reproductive tract size (mm)	Subjective diameter of the uterine horn, proximal to the bifurcation, by manual palpation. Measurements were recorded prior to 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 prior to, or on, the scanning day closest to first day of joining (i.e. 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.

^A CL = *corpus luteum*^B CA = *corpus albicans*

Appendix 2b. Description of female reproduction traits

Trait	Description
Conception rate	Conceived (=1) or not (=0) for all surviving cows, irrespective of pregnancy failure
Pregnancy rate	Pregnant (=1) or not (=0), for all surviving cows at the annual weaning, approximately 7-8 weeks after end of mating
Calving rate	Calved i.e. produced a full-term calf (dead or alive) (=1), or not (=0), for all surviving cows from the start of mating.
Weaning rate	Weaned a calf (=1) or not (=0), at the annual weaning event, for all surviving cows from the start of mating.
Days to cycling	For all surviving cows, days from start of mating to estimated date of first ovulation which was either: 12 days prior to a CL recorded; 18 days prior to a CA; or estimated date of conception from foetal ageing. To avoid reporting of negative estimates all were adjusted to zero prior to analysis.
Lactation anoestrous interval (d)	For surviving lactating cows up to the end of mating, the interval in days between the start of mating and estimated date of first ovulation.
Lactation cyclicity rate	Evidence of an ovulation (=1) (as defined above) or not (=0) prior to weaning of surviving lactating cows.
Days to calving (d)	Interval in days from the start of mating to the date of subsequent calving (Meyer <i>et al.</i> 1990), for all surviving cows from the start of mating. All cows failing to calve in a given mating were assigned a DC record based on the last valid DC record in the given mating group plus a 42 day penalty according to Johnston and Bunter (1996).
Total calves born 1-2	Total number of calves born from Matings 1 and 2, for all surviving cows from the start of mating 2.
Total calves weaned 1-2	Total number of calves weaned from Matings 1 and 2, for all surviving cows from the start of mating 2.
Pregnant-and-weaned rate	Pregnant and weaned a calf (=1) or not (=0), assessed at Mating 2 for all surviving cows from the start of mating 2
Average annual calving rate (retained cows)	Total number of calves born from the 1 st to 6 th mating divided by 6, for all surviving cows from the start of the 6 th mating.
Average annual weaning rate (retained cows)	Total number calves weaned from the 1 st to 6 th mating divided by 6, for all surviving cows from the start of the 6 th mating.
Lifetime annual calving rate	Total number of calves born from the 1 st and up to 6 th mating divided by the number of matings experienced (Meyer <i>et al.</i> 1990), for all cows from the start of the 1 st mating.
Lifetime annual weaning rate	Total number of calves weaned from the 1 st and up to 6 th mating divided by the number of matings experienced, for all cows from the start of the 1 st mating.

Appendix 2c. Description of cow body composition traits

Trait / measurement time	Trait description
<i>Measurement times</i>	
Weaning	Measured when calves were removed from their dams (~6.5 months of age).
Pre-calving (PC)	Measurements on females, taken as close as practically possible to the beginning of their first calving.
Mating	Measurements on females, taken when bulls were introduced to the cow herd for mating 2.
Change from pre-calving to mating	Change in traits from pre-calving to mating. For most traits these were negative, reflecting a loss over the period from pre-calving to mating 2.
<i>Trait definitions</i>	
WT	Liveweight (kg).
EMA	Eye muscle area measured at the 12/13 th rib site by real time ultrasound (cm ²).
P8	Fat depth (measured at the intersection of a line parallel to the spine, from the <i>tuber ischium</i> , and a line perpendicular to it, from the spinous process of the third sacral vertebra) by real time ultrasound (mm).
RIB	Fat depth measured at the 12/13 th rib, medially one quarter of the way from the lateral boundary of the eye muscle (mm).
BCS	Visually assessed body condition on a 1–5 scale to the nearest third of a point, using '+' and '-' sub-categories, where 1 is poor, 2 is backward, 3 is forward, 4 is prime, 5 is fat; and re-coded to a numeric variable 1– = 0.66 to 5+ = 5.33.
HH	Height of the animal, measured to the top of the third sacral vertebra when standing squarely on a level surface (cm).

Appendix 2d. Description of young bull traits

Code	Trait	Description
LH4	Luteinising hormone (ng/ml)	Circulating blood LH measured at ~4 months of age following GnRH challenge (Burns <i>et al.</i> 2012); plasma was assayed by the University of WA using a double-antibody radioimmunoassay procedure (Hotzel <i>et al.</i> 1998)
IN4	Inhibin (ng/ml)	Circulating blood inhibin measured at ~4 months of age; sera were assayed by Monash University using established protocols (Phillips 2005)
IGF6	Insulin-like growth factor I (ng/ml)	Circulating blood IGF-I measured at ~6 months of age; whole blood was collected on bloodspot collection cards supplied by PrimeGRO™ and assayed using a commercially available (Rivalea (Australia) Pty. Ltd.) enzyme-linked immunosorbent assay (see Moore <i>et al.</i> 2005)
FT6	Flight time (seconds)	Time taken to cover a distance of approximately 2m upon leaving weigh scales using electronic sensors
RT12	Rectal temperature (°C)	Body temperature measured using an Anritherm integrated thermometer (Anritherm HL600, Anritsu Meter Co. Ltd., Tokyo, Japan) and a rectal probe. Temperatures were taken in summer immediately prior to 12 month BBSE
WT	Body mass (kg)	Live weights were recorded between 12 and 24 months of age using electronic weigh cells; WT12 to WT24
CS15	Body condition (score)	Body condition at 15 months of age scored on the 1 (emaciated) to 5 (excessively fat) scale in 1/3 rd score increments (converted numerically to 1.0, 1.3, 1.7, 2.0,...5.0), adapted from Graham (1985)
RIB15	Rib fat thickness (mm)	Subcutaneous fat thickness at the 12 th /13 th rib site measured using ultrasonography at 15 months of age
P815	Rump fat thickness (mm)	Subcutaneous fat thickness at the rump P8 site measured using ultrasonography at 15 months of age
EMA15	Eye-muscle area (cm ²)	Area of the eye-muscle (<i>M. longissimus thoracis et lumborum</i>) at the 12 th /13 th 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 in the yard after release from weigh scales at 18 months of age
SC	Scrotal circumference (cm)	Circumference measured with a standard metal tape at the widest point of the scrotum with both testes fully distended (McGowan <i>et al.</i> 2002) at 6, 12, 18 and 24 months of age; SC6 to SC24
MASS	Mass activity (score)	Sperm mass activity was scored by examining a droplet of ejaculate under 40x magnification; scored from 0 = no activity to 5 = rapid distinct swirls at 12, 18 and 24 months of age; MASS12 to MASS24; animals failing to provide an ejaculate were assigned a zero score
MOT	Progressive motility (%)	Percent progressively motile sperm was estimated by examining a droplet of ejaculate under a cover-slip at 400x magnification at 12, 18 and 24 months of age; MOT12 to 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 examining a cover-slip preparation of ejaculate fixed in phosphate-buffered formol-saline using phase contrast microscopy at 1000x magnification; 100 spermatozoa were classified by an accredited morphologist and the percentage with normal morphology recorded at 12, 18 and 24 months of age; PNS12 to PNS24
-----	--------------------------	--

Appendix 3. Number of total records (repeats per cow) for traits recorded repeatedly over the experiment

trait	count	min	max	avg	Std_dev
Liveweight (kg)	126,540	20	916	422	127
Flight Time (secs*100)	10,608	30	700	143.7	73.7
Hip Height (cm)	39,106	87	163	135	9
Leg Structure	1,099	7	9	9	0.2
Foot Structure	1,479	6	9	8.2	0.7
Teat Score	31,704	0	5	2.4	0.8
Udder Score	31,711	1	5	2.5	0.8
Skin Inflammation Score (0-3)	5,403	0	3	0	0.2
Sheath/Navel Score (1-9)	4,037	2	9	6.7	1.8
Buffalo Fly Lesion Score (0-5)	8,887	0	5	0.9	0.9
Tooth Wear (0-4)	829	0	4	1.5	0.6
Scanned P8 (mm)	118,478	1	55	6	5.7
Scanned 12/13th Rib (mm)	52,811	1	25	3.6	3.1
Scanned Eye Muscle Area (sq cm)	52,520	10	119	55.2	14.2
Body condition score	123,518				

Appendix 4. Number of reproduction scanning records from the project COWS.

Ovarian trait	count
Left Ovary Primary Follicle Size	69,793
Left Ovary CL Size	11,369
Left Ovary Secondary Follicle Size	11,199
Right Ovary Primary Follicle Size	70,349
Right Ovary CL Size	17,766
Right Ovary Secondary Follicle Size	17,571
Pregnancy Status	81,987

Appendix 5. Number of calves born from project females at each location by year, and genotype

Breed	Location					Total
	BrianP	Brigalow	Belmont	Toorak	Swans	
BRAH	0	0	1443	631	1620	3694
TCOMP	2100	431	1174	1330	0	5035
XB	0	0	565	2	0	567
Year						
2003	0	0	61	0	0	61
2004	137	0	212	175	94	618
2005	362	0	454	402	255	1473
2006	283	134	534	262	255	1468
2007	409	131	541	227	335	1643
2008	179	166	530	375	263	1513
2009	401	0	475	344	267	1487
2010	275	0	287	178	127	867
2011	54	0	88	0	24	166
Total	2100	431	3182	1963	1620	9296

Appendix 6. Progeny records from project females (up to weaning)

trait	count	min	max	avg	std_dev
Birth weight	8,770	8	62	34.1	6
weaning weight	8,343	89	344	205.4	37
Flight Time (secs*100)	15,967	14	1700	115.9	57.2
IGF- I (ng/ml)	6,608	22	1838	521.7	290.8
Horn status	8,090				
Coat colour	10,127				
Coat score	6,750				

Appendix 7. Raw frequencies of cow survival scores in BRAH and TCOMP

Exit codes	BRAH		TCOMP	
	N	%	N	%
Died/missing	20	2.0	19	1.7
Accident	10	1.0	15	1.3
Calving related	26	2.5	25	2.2
Disease	10	1.0	24	2.1
Structural	21	2.0	7	0.6
Temperament	14	1.4	2	0.2
Twice non-weaned culled				
2 calf loss	26	2.5	26	2.3
1 abort, 1 calf loss	15	1.5	16	1.4
1 calf loss, 1 empty	88	8.5	43	3.8
2 non-pregnant	114	11.1	80	7.1
Not culled or died	684	66.5	871	77.2

Appendix 8. Raw longevity (number of years survived in the project) in BRAH and TCOMP

Years survived in the project	BRAH		TCOMP	
	N	%	N	%
2	86	8.4	51	4.5
3	80	7.8	60	5.3
4	62	6.0	37	3.3
5	65	6.3	40	3.6
6	40	3.9	47	4.2
7	684	66.5	871	77.2

Appendix 9. Genetically superior CRC Brahman cow

Identifier: BEL020402B(CR)

Sex: Female

PH No.: 020402

Birth Date: 21/11/2001

Calving Year: 2002

Status: Active

Registration Status: Calf Rec'd



Marbling (M1-0,M2-2,M3-0,M4-0) Total of 2 favourable genes

Tenderness (T1-2,T3-1,T4-1) Total of 4 favourable genes

Feed Efficiency (FE1-2,FE2-2,FE3-2,FE4-1) Total of 7 favourable genes

Sire: [* MCKELLAR RICARDO 3/840 \(IMP US\)](#)Dam: [BELMONT 980977 \(H\)](#)Breeder: [CSIRO](#)Current Owner: [CSIRO](#)

Horn: Horned

Appendix: B

Colour: Red

Progeny: [\[8 - View\]](#)Pedigree: [\[View\]](#)EBV Graph: [\[View\]](#)

June 2012 Brahman GROUP BREEDPLAN													
	Birth Wt. (kg)	200 Day Wt. (kg)	400 Day Wt. (kg)	600 Day Wt. (kg)	Mat. Cow Wt. (kg)	Milk (kg)	Scrotal Size (cm)	Days to Calving (days)	Carcass Wt. (kg)	Eye Muscle Area (sq.cm)	Rib Fat (mm)	Rump Fat (mm)	Retail Beef Yield (%)
EBV	+3.6	+25	+42	+60	+79	0	+2.8	-11.0	+28	+5.2	-1.3	-0.2	+0.9
Acc	81%	78%	80%	83%	81%	69%	56%	42%	68%	50%	47%	49%	43%
Breed Avg. EBVs for 2010 Born Calves Click for Percentiles													
EBV	+2.7	+18	+24	+33	+40	+0	+0.3	+1.4	+20	+2.3	-0.4	-0.3	+0.5

Traits Observed: BWT,200WT,400WT,600WT,MWT,EMA

Statistics: Number of Herds: 2, Progeny Analysed: 8, Scan Progeny: 1, Number of Dtrs: 2

[Hide Index Values](#)

SELECTION INDEX VALUES		
Market Target	Index Value	Breed Average
Jap Ox Index (\$)	+\$ 68	+\$ 20
Live Export Index (\$)	+\$ 63	+\$ 17

Appendix 10. Genetically superior CRC Belmont Red Cow

Identifier: BEL010308
Sex: Female
Tattoo: 0308
Birth Date: 29/11/2000
Calving Year: 2001
Status: Active
Registration Status: Registered
Breeder: [CSIRO BELMONT](#)
Current Owner: [CSIRO BELMONT](#)
Breed Composition: BR 93% BB 7%
Progeny: [\[8 - View\]](#)
EBV Graph: [\[View\]](#)

— [NARAYEN 81-440](#)
 — [NARAYEN 86/019](#)
 — [NARAYEN 82/162](#)
 — **Sire:** [NARAYEN 90-101](#)
 — [NARAYEN 81-307](#)
 — [NARAYEN 86/065](#)
 — [NARAYEN 82-710](#)

Animal: [BELMONT 01-0308](#)

— [BELMONT 84-323](#)
 — [BELMONT 87-87](#)
 — [BELMONT 84-44](#)
 — **Dam:** [BELMONT 90-194](#)
 — [COMMERCIAL](#)
 — [BELMONT 85-41](#)
 — [BELMONT 82-501](#)

2011 AUSTRALIAN COMPOSITE GROUP BREEDPLAN EBVs													
	Gest. Len. (days)	Birth Wt. (kg)	200 Day Wt. (kg)	400 Day Wt. (kg)	600 Day Wt. (kg)	Milk (kg)	Maternal Value (kg)	Scrotal Size (cm)	Carcass Wt. (kg)	Eye Muscle Area (sq.cm)	Rib Fat (mm)	Rump Fat (mm)	Retail Beef Yield (%)
EBV	-2.0	+0.8	+15	+27	+39	+8	+16	+2.4	+25	+1.2	-0.2	+0.1	+1.3
Acc	62%	86%	81%	80%	81%	76%	77%	71%	71%	58%	53%	53%	51%
Breed Avg. EBVs for 2009 Born Calves Click for Percentiles													
EBV	-0.2	+2.3	+12	+16	+22	+3	+7	+0.6	+12	+1.4	-0.4	-0.4	+0.5

Traits Observed: BWT, 200WT, 400WT, 600WT, EMA

Statistics: Number of Herds: 1, Progeny Analysed: 8, Scan Progeny: 5, Number of Dtrs: 1
[Hide Index Values](#)

SELECTION INDEX VALUES		
Market Target	Index Value	Breed Average
Domestic Index (\$)	+\$ 32	+\$ 12
Export Index (\$)	+\$ 38	+\$ 15

Appendix 11. Genetically superior CRC Young Brahman bull

Identifier: CSL09S107M(COM)
Sex: Male
PH No.: 09S107
Birth Date: 11/11/2008
Calving Year: 2009
Status: Active
Registration Status: Commercial
Sire: [CBE BEL050390 \(P\) \(COM\)](#)
Dam: [TARTRUS TAR026012 \(COM\)](#)
Breeder: CRC 2 - SWANS LAGOON
Current Owner: CRC 2 - SWANS LAGOON
Horn: Polled
Progeny: [View All](#) [View by Herd](#)
Pedigree: [View](#)
EBV Graph: [View](#)

June 2012 Brahman GROUP BREEDPLAN												
	Birth	200	400	600	Mat.				Eye			Retail
	Wt.	Day	Day	Day	Cow	Milk	Scrotal	Carcase	Muscle	Rib	Rump	Beef
	(kg)	Wt.	Wt.	Wt.	Wt.	(kg)	Size	Wt.	Area	Fat	Fat	Yield
	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(cm)	(kg)	(sq.cm)	(mm)	(mm)	(%)
EBV	+5.6	+30	+52	+75	+98	-2	+3.7	+37	+3.9	-0.4	-0.7	+1.1
Acc	73%	71%	74%	77%	70%	40%	70%	60%	42%	36%	40%	32%
Breed Avg. EBVs for 2010 Born Calves Click for Percentiles												
EBV	+2.7	+18	+24	+33	+40	+0	+0.3	+20	+2.3	-0.4	-0.3	+0.5

Traits Observed: BWT,200WT,400WT(x2),600WT,SS,EMA

[Hide Index Values](#)

SELECTION INDEX VALUES		
Market Target	Index Value	Breed Average
Jap Ox Index (\$)	+\$ 72	+\$ 20
Live Export Index (\$)	+\$ 65	+\$ 17

11. Bibliography

- Barwick SA, Wolcott ML, Johnston DJ, Burrow HM, Sullivan M (2009a) Genetics of steer daily feed intake and residual feed intake in tropical beef genotypes and relations among intake, body composition, growth and other post weaning measures. *Animal Production Science* **49**, 351-366.
- Barwick SA, Johnston DJ, Burrow HM, Holroyd RG, Fordyce G, Wolcott ML, Sim W, Sullivan M (2009b) Genetics of heifer performance in “wet” and “dry” seasons and their relationships with steer performance in two tropical beef genotypes. *Animal Production Science* **49**, 367-382.
- Burns BM, Corbet NJ, Corbet DH, Crisp JM, Venus BK, Johnston DJ, Li Y, McGowan MR, Holroyd RG (2012) Male traits and herd reproductive capability in tropical beef cattle. 1. Experimental design and animal measures. *Animal Production Science* (in press)
- Burrow HM, Johnston DJ, Barwick SA, Holroyd RG, Barendse W, Thompson JM, Griffith GR, Sullivan M (2003) Relationships between carcass and beef quality and components of herd profitability in northern Australia. *Proceedings for the Association for the Advancement of Animal Breeding and Genetics* **15**, 359-362.
- Davis GP (1993) Genetic parameters for tropical beef cattle in northern Australia: a review. *Australian Journal of Agricultural Research* **44**, 179-198.
- Entwistle KW (1983) Factors influencing reproduction in beef cattle in Australia. In *Australian Meat Research Committee Review* **43**, 1-30.
- Frisch JE, Munro RK, O'Neill CJ (1987) Some factors related to calf crops of Brahman, Brahman crossbred and HerefordxShorthorn cows in a stress tropical environment. *Animal Reproduction Science* **15**, 1-15.
- Fordyce G, Cooper NJ, Kendall IE, O'Leary BM, de Faveri J (1996) Creep feeding and pre-partum supplementation effects on growth and fertility of Brahman cross cattle in the dry tropics. *Australian Journal of Experimental Agriculture* **36**, 389-395.
- Gilmour AR, Gogel BJ, Cullis BR, Thompson R (2009) 'ASReml User Guide Release 3.0.' (VSN International: Hemel Hempstead, UK).
- Graham JF (1985) Condition scoring of beef cattle. *Victorian Department of Agriculture, Agnote* 3023/85. Agdex 420/33.
- Graser H-U, Tier B, Johnston DJ, Barwick SA (2005) Genetic evaluation for the beef industry in Australia. *Australian Journal of Agricultural Research* **45**, 913-921.
- Holroyd RG, James TA, Anderson VJ, Fordyce G, Tyler R, O'Rourke PK (1990) The performance of Brahman-Shorthorn and Sahiwal-Shorthorn beef cattle in the dry tropics of northern Queensland. 2. Reproductive rates and liveweight of F2 *et seq.* females. *Australian Journal of Experimental Agriculture* **30**, 727-733.
- Hotzel MJ, Markey CM, Walkden-Brown SW, Blackberry MA, Martin GB (1998) Morphometric and endocrine analyses of the effects of nutrition on the testis of mature Merino rams. *Journal of Reproduction and Fertility* **113**, 217-230.
- Johnston DJ, Bunter KL (1996) Days to calving in Angus cattle: genetic and environmental effects and covariances with other traits. *Livestock Production Science* **45**, 13-22.
- Johnston DJ, Barwick SA, Corbet NJ, Fordyce G, Holroyd RG, Williams PJ, Burrow HM (2009) Genetics of heifer puberty in two tropical beef genotypes in northern Australia and associations with heifer- and steer-production traits. *Animal Production Science* **49**, 399-412.

- Koots KR, Gibson JP, Smith C, Wilton JW (1995) Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Animal Breeding Abstracts* **62**, 309-338.
- McGowan MR, Bertram JD, Fordyce G, Fitzpatrick LA, Miller RG, Jayawardhana GA, Doogan VJ, DeFaveri J, Holroyd RG (2002) Bull selection and use in northern Australia. 1. Physical traits. *Animal Reproduction Science* **71**, 25-37.
- Meyer K, Hammond K, Parnell PF, Mackinnon MJ, Sivarajasingham S (1990) Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. *Livestock Production Science* **25**, 15-30.
- Moore KL, Johnston DJ, Graser HU, Herd R (2005) Genetic and phenotypic relationships between insulin-like growth factor-I (IGF-I) and net feed intake, fat, and growth traits in Angus beef cattle. *Australian Journal of Agricultural Research* **56**, 211-218.
- O'Rourke PK, Doogan VJ, Robertson DJ, Cooke D (1991) Prediction of conception rate in extensive beef herds in north-western Australia. 2. Continuous mating and minimal management. *Australian Journal of Experimental Agriculture* **31**, 9-14.
- Phillips DJ (2005) Activins, inhibins and follistatins in the large domestic species. *Domestic Animal Endocrinology* **28**, 1-16.
- Prayaga KC, Corbet NJ, Johnston DJ, Wolcott ML, Fordyce G, Burrow HM (2009) Genetics of adaptive traits in heifers and their relationship to growth, pubertal and carcass traits in two tropical beef cattle genotypes. **49**, 413-425.
- Schatz TJ, Hearnden MN (2008) Heifer fertility on commercial cattle properties in the Northern Territory. *Australian Journal of Experimental Agriculture* **48**, 940-944.
- Wall E, Brotherstone S, Woolliams JA, Banos, G, Coffey MP (2003) Genetic evaluation of fertility using direct and correlated traits. *Journal of Dairy Science* **86**, 4093-4102.