Genetics of early and lifetime annual reproductive performance in cows of two tropical beef genotypes in northern Australia

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Abstract. Reproduction records from 2137 cows first mated at 2 years of age and recorded through to 8.5 years of age were used to study the genetics of early and lifetime reproductive performance from two genotypes (1020 Brahman and 1117 Tropical Composite) in tropical Australian production systems. Regular ultrasound scanning of the reproductive tract, coupled with full recording of mating, calving and weaning histories, allowed a comprehensive evaluation of a range of reproductive traits. Results showed components traits of early reproductive performance had moderate to high heritabilities, especially in Brahmans. The heritability of lactation anoestrous interval in 3-year-old cows was 0.51 ± 0.18 and 0.26 ± 0.11 for Brahman and Tropical Composite, respectively. Heritabilities of binary reproductive output traits (conception rate, pregnancy rate, calving rate and weaning rate) from first and second matings were generally moderate to high on the underlying scale. Estimates ranged from 0.15 to 0.69 in Brahman and 0.15 to 0.34 in Tropical Composite, but were considerably lower when expressed on the observed scale, particularly for those traits with high mean levels. Heritabilities of lifetime reproduction traits were low, with estimates of 0.11 ± 0.06 and 0.07 ± 0.06 for lifetime annual weaning rate in Brahman and Tropical Composite, respectively. Significant differences in mean reproductive performance were observed between the two genotypes, especially for traits associated with anoestrus in first-lactation cows. Genetic correlations between early-in-life reproductive measures and lifetime reproduction traits were moderate to high. Genetic correlations between lactation anoestrous interval and lifetime annual weaning rate were -0.62 ± 0.24 in Brahman and -0.87 ± 0.32 in Tropical Composite. The results emphasise the substantial opportunity that exists to genetically improve weaning rates in tropical beef cattle breeds by focusing recording and selection on early-in-life female reproduction traits, particularly in Brahman for traits associated with lactation anoestrus.

Additional keywords: heritability, lactation anoestrus.

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Introduction

Female reproduction is an important profit driver in northern Australia beef production systems. However, low weaning rates are common, and are mainly the result of extended postpartum anoestrous intervals, especially in *Bos indicus* cattle (Baker 1969; Entwistle 1983). Estimates of heritabilities are low for traits associated with net reproduction rate in beef cattle (e.g. Buddenberg *et al.* 1989; Mackinnon *et al.* 1990; Burrow 2001; Martinez *et al.* 2004). These low heritabilities, coupled with longer generation intervals, low selection intensities and fewer correlated traits have contributed to low levels of reproductive

performance recording, and few genetic evaluations worldwide for female reproduction traits. They have also contributed to rates of genetic progress in female reproduction traits that are generally negligible. In dairy cattle, component traits of net reproductive rate have been shown to have higher heritabilities (Wall *et al.* 2003; Petersson *et al.* 2007; Bamber *et al.* 2009), and these may offer a means to genetically improve female reproduction.

This paper reports estimates of genetic parameters for component traits of early life female reproduction and their genetic relationships with lifetime reproduction traits in two

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tropical beef genotypes. The results are from a large breeding project, which aimed to estimate the genetics of whole-herd profitability in northern Australia, and to improve production efficiency and product quality without compromising female performance or adaptation.

Materials and methods

Data were from a beef breeding experiment in northern Australia that investigated the genetics of whole-herd profitability (Burrow *et al*. 2003). The experimental design is described by Barwick *et al*. (2009*a*) and Johnston *et al*. (2009). In brief, Brahman (BRAH) and Tropical Composite (TCOMP) steers and heifers were generated over 4 years at eight cooperator properties and were the progeny of 54 BRAH and 52 TCOMP sires. At weaning, the heifer calves were allocated to one of four Queensland research stations (Swans Lagoon, Ayr; Toorak, Julia Creek; Belmont, Rockhampton and Brian Pastures, Gayndah) that represented a range of northern Australia breeder cow herd environments (see Barwick *et al*. 2009*b*; for a full description of each research station). Table 1 presents the numbers of females at each location. Cows remained at a location for the duration of the experiment, except for cohorts from Toorak and Brian Pastures that were temporarily relocated to a fifth location (Brigalow Research station, Theodore, Queensland) in response to drought conditions. Genetic analyses of heifer performance have been previously reported for early growth and body composition (Barwick *et al*. 2009*b*), adaptation (Prayaga *et al*. 2009) and age at puberty (Johnston *et al*. 2009).

Ethics approval

Conduct of the experiment was approved for 1999–2006 and 2006–10 by the JM Rendel Laboratory Animal Experimental Ethics Committee (CSIRO, Queensland) as approvals TBC107 and RH225–06, respectively.

Animals

Reproduction data from the study were available for 1020 BRAH and 1117 TCOMP females. Heifers were managed in their year of birth group until their initial mating to first calve at 3 years of age. All matings were in natural service multiple-sire groups, and within a location, were over approximately the same 12-week period each year. After the initial years of the project, cows were allocated to two or three groups within location to facilitate management, and were maintained in these groups for the remainder of the experiment. The exception to this was Belmont Research Station, where the management groups were reformed into three mixed BRAH and TCOMP groups at the commencement of the 2005–06 mating.

Cows remained in the project until the weaning of calves from their sixth mating, at which time they were ~8.5 years of age. Exceptions were cows that were removed from the project because they failed to wean a calf in consecutive years. This culling criterion was in accord with industry practice but was relaxed on two occasions for a cohort of heifers weaned at a young age because of drought, which subsequently achieved a very low pregnancy rate from their maiden mating; and for females not rearing 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. Following industry practice, there was also culling on physical soundness. About 2% of cows were removed from the experiment for poor temperament or acquired physical conditions (e.g. bottle teats or structural unsoundness) that compromised welfare or the ability to reproduce or rear a calf.

Cow husbandry

Cows at a location were treated similarly and subject to best-practice management. Cows were monitored for parasites and nutritional deficiencies with intervention only as needed at each location. All cows were vaccinated annually against pestivirus, leptospirosis, clostridial diseases and botulism. At Swans Lagoon, Toorak and Brian Pastures, cows also received annual vaccination against camplyobacteriosis. Treatment via backrubbers for buffalo fly (*Haematobia irritans exigua*) or a synthetic pyrethroid for cattle tick (*Rhipicephalus microplus*) was carried out only at Brian Pastures, and when required.

Supplementation was responsive to the prevailing climatic and pasture conditions at each location. At Belmont, cows received 1–2 kg/head.day of a grain, molasses and urea mix in November and December 2009. At Toorak and Swans Lagoon, dry licks targeted 150–160 g/head.day from July through November each year. At Swans Lagoon, phosphorus was included in the licks fed throughout the year. Cows at Brian Pastures were fed 2.5 kg/head.day of a molasses and 4% urea mix during the dry season each year. During the drought of 2004 and 2005 the cows received additional supplementation of ~2.5/kg/head.day fortified molasses. From 2005 onwards, following calf deaths due to vitamin A deficiency, all cows at Toorak received an annual supplementation of vitamin A.

Bull management

Practices were designed to ensure that bull effects would not limit cow reproduction. All matings involved a bull to cow ratio of 3% and bulls used were required to pass a breeding soundness evaluation (Entwistle and Fordyce 2003; Fordyce *et al*. 2006) that was conducted before the breeding season each year. Exceptions occurred where a few bulls were deliberately

Table 1.   Numbers of females at start of the first breeding season by location, genotype and birth year

Genotype	Year of birth	Location				Total
		Swans Lagoon	Belmont	Toorak	Brian Pastures	
Brahman	2000	–	72	–	–	72
	2001	186	110	64	–	360
	2002	215	118	96	–	429
	2003	41	118	–	–	159
	Total	442	418	160	0	1020
Tropical Composite	2001	–	110	157	142	409
	2002	–	137	181	266	584
	2003	–	48	–	76	124
	Total	0	295	338	484	1117

re-used in an attempt to increase their number of progeny. All bulls were vaccinated annually for the same diseases as the cows.

A total of 136 bulls were used throughout the project as service sires and were sourced from industry herds, and where possible from herds enrolled in BREEDPLAN (Graser *et al.* 2005) that were recording male and female reproduction traits. Pedigree details were used to assign bulls to cow mating groups to avoid close inbreeding. Several bulls were used across years and locations to generate genetic linkage in the progeny. All progeny were DNA parentage verified, and on average the mating bulls produced 60 calves but this varied greatly due to multi-sire matings and the re-use of some bulls across years.

Calf recording and management

At each location, calving was monitored by daily inspection in smaller paddocks. All births were scored for calving ease (on a 1–5 scale) and all calf mortalities were recorded, and the cause of death noted, where possible, using a comprehensive list of reason codes. All calves were tagged, dam identified, and weighed generally within 24 h of birth. In 2005 at Swans Lagoon no birthweights were recorded. A blood or hair sample was taken from each calf for sire assignment from DNA, and for confirming dam. Calves were vaccinated against clostridial diseases (Ultravac 7in1) at branding at ~3–4 months of age, and again at weaning. Calves were scored for horn status at branding time and subsequently were dehorned. Bull calves were kept entire for a later study of male reproduction traits (Burns *et al.* 2013). All calves at each location were weaned on the same day, at an average age of ~6 months. At this time, calves were weighed and other recording of measures was commenced. Where possible, the date and reason code were also recorded for any calves that died or were missing.

Reproductive tract ultrasound scanning

Cow reproductive tracts were scanned every 4–6 weeks between the start of annual mating, when lactating cows were on average 6 weeks postpartum, and weaning, after which scanning occurred each 4–8 weeks until calving commenced (see Fig. 1). Scanning during the calving period was not performed to avoid stress to cows and their young calves.

Real-time ultrasonography was use to determine the presence and diameter of a *corpus luteum* or *corpus albicans* and the diameters of primary and secondary follicles on each ovary. Pregnancies were aged to derive estimates of conception date. Scanning was performed by one of four experienced technicians using an Aloka SSD-500 with linear array 7.5-MHz rectal transducer; or Honda HS-2000V with variable-frequency transducer set at 10 MHz.

Trait definition

The data obtained at scanning, mating, calving and weaning were used to define several reproduction traits for each annual mating (1–6), extending from the start of mating through to weaning of the resultant calves (see Fig. 1). Data were initially edited to remove any obvious inconsistencies (e.g. cows with reproductive defects preventing scanning, cows that missed a mating). Any late-term abortions or premature births that were observed were coded as calving failures. Cows having calves that were either artificially reared or fostered were considered as weaning failures. Records were checked for conformity with the expected culling practice, any non-conforming were removed from the data (e.g. cows with records that should have been culled for consecutive weaning failures). Cows that calved after the commencement of annual mating had their start of mating date re-set to their calving date. In a small number of cases, late calving cows were not moved immediately to the mating group. Their start of mating date was adjusted to the date when they rejoined the mating group.
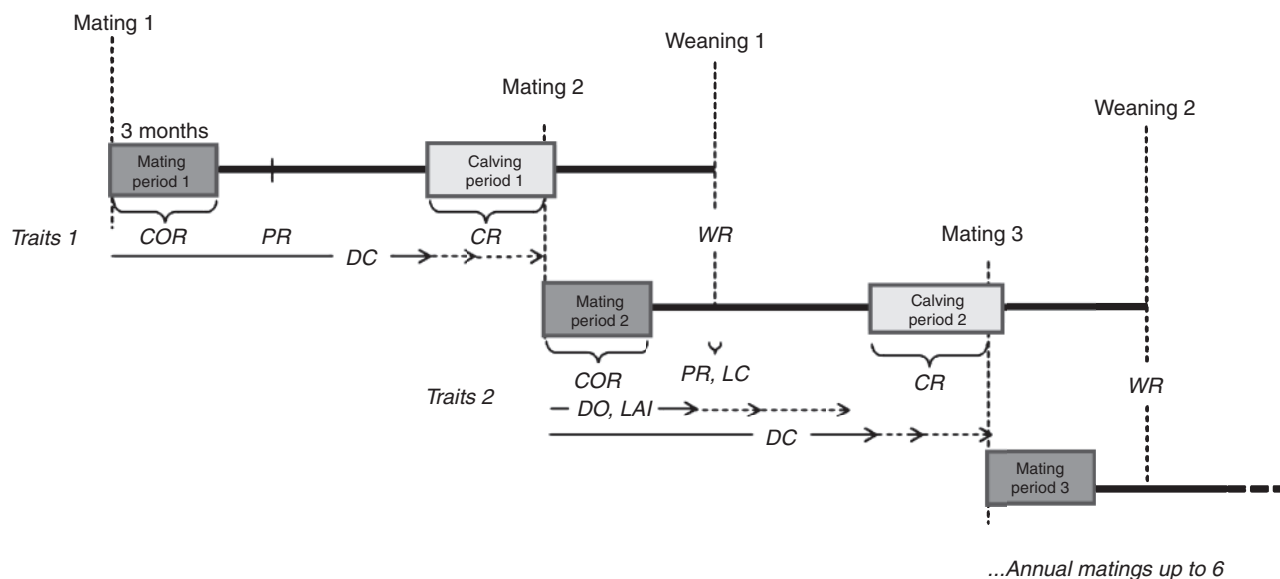
Fig. 1. Schematic representation of recording structures, times and traits recorded at each mating (COR = conception rate; PR = pregnancy rate; CR = calving rate; WR = weaning rate; DC = days to calving; DO = days to cycling; LAI = lactation anoestrous interval; LC = lactation cyclicity rate). See Table 2 for full trait descriptions.

A full description of all traits is presented in Table 2. Traits recorded at the first mating (mating 1) included conception rate, pregnancy rate, calving rate, days to calving and weaning rate. At the second mating (mating 2) similar outcome traits were recorded along with traits specifically associated with the anoestrus that followed the first calving. These included: days to cycling, lactation anoestrous interval, lactation cyclicity and days to calving in lactating cows. Cumulative reproductive outcome traits from matings 1 and 2 included: total calves born, total calves weaned and pregnant-and-weaned, the latter being the success rate of cows both weaning from mating 1 and being pregnant from mating 2. Finally, all cows had lifetime annual calving and weaning rate records calculated based on their number of mating opportunities up to six possible matings. For the subset of cows that were still present at the sixth mating, additional traits of average calving rate and average weaning rate were available. Length of productive life of cows was excluded from the computation of these lifetime reproduction rate traits as these differences will be examined separately.

Statistical analyses

Fixed effect modelling

Fixed effect modelling, for traits from all matings, except the first, involved confounded carryover effects from the cow's previous and current lactation status and effects associated with both the current calf (or missing calf) and the resultant calf, difficulties also recognised by Mackinnon *et al.* (1989). For example, for weaning rate, fitting fixed effects associated with the

resultant calf (e.g. sex, service sire, breed, and birth month) involved also fitting dummy levels of these effects for cows with no calf, which then removed the variance associated with whether or not the cow calved. To investigate the consequence of modelling previous lactation and calf effects, all traits at mating 2 therefore were analysed with both a full and a reduced set of fixed effects. Traits from subsequent matings (i.e. 3, 4, 5, 6) were not analysed separately but were included in the computation of lifetime reproduction traits and fixed effects were determined in models that ignored current and previous lactation status and all calf effects.

Significant fixed effects for each genotype and trait were determined using the MIXED procedure in SAS (SAS Institute, Cary, NC, USA) by considering both main effects and first-order interactions, with sire included as a random effect. For TCOMP, terms for sire breed group, dam breed group and their interaction (Barwick *et al.* 2009a) were also included. Initial fixed effects considered in all traits included project design variables (i.e. location, year of birth, origin, age of dam class, and cow birth month according to Johnston *et al.* 2009) and specific effects at each mating and location to account for current and previous mating group.

For mating 2 traits the initial fixed effects models included additional terms for current lactation status and calf effects. Current lactation status was determined from the weaning outcome from the first mating and was defined as either lactating (i.e. wet) during the mating period or non-lactating (i.e. dry) and included cows whose calf died before the start of the mating period. Current calf effects (i.e. resultant calf from the first mating) included sex and birth month. However, for calving

Table 2.   **Description of female reproduction traits**

Trait	Description
Conception rate 1, 2	Conceived (= 1) or not (= 0) irrespective of fetal loss for all surviving cows at start of mating 1, and at mating 2
Pregnancy rate 1, 2	Pregnant (= 1) or not (= 0), via rectal palpation for all surviving cows at the annual weaning event, ~7–8 weeks after end of the mating period for mating 1, and at mating 2
Calving rate 1, 2	Calved i.e. produced a full-term calf (dead or alive) (= 1), or not (= 0), for all surviving cows from the start of mating 1, and at mating 2
Weaning rate 1, 2	Weaned a calf (= 1) or not (= 0), at the annual weaning event, for all surviving cows from the start of mating 1, and at mating 2
Days to cycling	For all surviving cows, days from start of mating 2 to estimated date of first ovulation which was either: 12 days before a CL recorded; 18 days before a CA; or estimated date of conception from fetal ageing. To avoid reporting of negative estimates all were adjusted to zero before analysis
Lactation anoestrous interval (day)	For surviving lactating cows up to the end of mating 2, the interval in days between the start of mating and estimated date of first ovulation i.e. days to cycling for lactating cows only
Lactation cyclicity rate	Evidence of an ovulation (= 1) (as defined above) or not (= 0) before weaning of surviving lactating cows at mating 2
Days to calving 1, 2 (day)	Interval in days from the start of mating to the date of subsequent calving (Meyer *et al.* 1990), for all surviving cows from the start of mating 1, and mating 2. All cows failing to calve were assigned a days to calving record based on the days to calving record of last cow to calve 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 the 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 the 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 the mating 2
Lifetime annual calving rate	Total number of calves born from the 1st and up to sixth mating divided by the number of matings experienced (Meyer *et al.* 1990), for all cows from the start of mating 1
Lifetime annual weaning rate	Total number of calves weaned from the first and up to sixth mating divided by the number of matings experienced, for all cows from the start of mating 1
Average calving rate (retained cows)	Total number of calves born from the first to sixth mating divided by 6, for all cows surviving cows to the start of mating 6
Average weaning rate (retained cows)	Total number calves weaned from the first to sixth mating divided by 6, for all cows surviving cows to the start of mating 6

and weaning rate traits from mating 2 all fixed effects associated with the resultant calf of this mating were ignored.

For average lifetime traits, initial models included terms for project design variables and contemporary group defined as the cohort and lifetime mating group of the cow. Lifetime mating group was formed from the last mating group and all earlier mating groups, which also included the permanent cow management group at each location.

Models were stepped down removing non-significant effects ($P > 0.05$) to yield final models for each trait and genotype. Final models for all traits at mating 1 in BRAH included the effects of cohort mating group (i.e. location-birth year and mating group) and cow birth month. Origin was significant for all traits except weaning rate. Age of dam class was only significant for calving rate. Interactions between some main effects also were significant, mainly for interactions with birth month and origin. Final models for traits at mating 1 in TCOMP were generally similar across traits and included cohort-mating group and age of dam. Dam breed group was significant for weaning rate.

For analyses using the full set of fixed effects for traits at mating 2, the significant effects in BRAH included cohort-mating group (including previous mating group), current lactation status, and month of calving within lactation status for all traits. Cow birth month and origin were significant for all traits except days to cycling and lactation cyclicity rate. Sex of the current calf was significant for calving rate and weaning rate. Significant fixed effects in TCOMP included cohort-mating group and current lactation status for all traits. Sire group was significant for all traits except lactation cyclicity rate. Origin was significant for all traits except days to cycling and lactation cyclicity rate. Age of dam was significant for conception rate, pregnancy rate, calving rate and weaning rate. Sire group, dam group and calf birth month were significant for days to calving. Calf sex was significant for calving rate and weaning rate. Interactions between main effects were commonly present in final models, particularly interactions with lactation status. For analyses with the reduced set of fixed effects for traits at mating 2 any effects involving lactation status and effects of the calf were dropped from the previous full models for both BRAH and TCOMP for all traits.

Fixed effects for all lifetime reproductive traits in BRAH included lifetime management group and cow birth month. Origin was also significant for lifetime calving and weaning rates. For lifetime traits in TCOMP, lifetime management group was significant for all traits. Cow birth month was significant for lifetime annual calving and weaning rates, and sire breed group was significant when lifetime traits were restricted to cows present in all six matings.

Variance component estimation

Heritabilities. Trait heritabilities were estimated from univariate analyses for BRAH and TCOMP separately, using restricted maximum likelihood procedures in ASRemL (Gilmour *et al*. 2009) and the sets of fixed effects identified using SAS. All binary traits were analysed using a sire model with a logit-link function. Heritability (h_L^2) estimates on the underlying logit scale were computed as:

$$h_L^2 = \frac{4(\sigma_S^2)}{\frac{\pi^2}{3} + \sigma_S^2}$$

where $\pi^2/3$ is the assumed residual variance and σ_S^2 the estimated sire variance from the logit model. Heritabilities on the observed binomial scale (h^2) were approximated by multiplying the underlying-scale heritability (h_L^2) by $p(1 - p)$, where p is the mean trait incidence. As all other traits were analysed by fitting an additive genetic effect for the animal, assuming a linear model, heritabilities and variances for binary traits were also derived with a linear model for completeness. The heritabilities of traits from mating 2 were also estimated for a subset of the data involving lactating cows only.

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. Genetic correlations between pairs of traits were estimated from bivariate analyses, for each genotype separately, using ASReml. Linear models were assumed for all traits, and models were as described above. Analyses of correlations between mating 1 and 2 traits were performed with and without the inclusion of the fixed effects associated with previous lactation status and calf effects at mating 2.

Genotype differences. Model predicted genotype means were computed in ASReml as linear functions of the terms included in the model from a combined genotype dataset using procedures described by Gilmour *et al*. (2004). The computing of means were restricted to data from the Belmont Research Station location where direct comparison of the genotypes was possible because the two genotypes were born, raised, mated and managed together throughout the experiment. Additionally in these data, cows were also in mixed genotype groups throughout the mating period from the 2005 to 2006 mating onwards. To avoid averaging over unequal or poorly represented subclasses for cow and calf birth months, data for 18 BRAH cows were excluded from all predictions and a further 12 cows for predictions for mating 2 traits.

For all analyses the initial model included the significant fixed effects previously described and additional terms for genotype and first-order interactions with genotype. These models were then stepped down to yield final models for each trait. Predictions of genotype means for binary traits derived from logit models were back-transformed to the observed (binary) scale. For traits in the mating 2, genotype-predicted means were obtained separately for lactating and non-lactating cows.

Results

In all tables, binary traits are presented as rates (e.g. outcome per cow) however for clarity of discussion they are hereafter referred to as percentages (i.e. outcome per 100 cows). Unadjusted trait means presented in Tables 3 and 4 show BRAH had low reproductive trait levels (e.g. 77% conception rate, 72% calving rate and a 62% weaning rate) and rates further reduced at mating 2 (e.g. weaning rate 50%), reflecting a lactation cyclicity rate of only 53%. Average lifetime annual

Table 3.   Unadjusted trait means, standard deviations (s.d.) and ranges for Brahman female reproduction traits
See Table 2 for a description of traits

Trait	n	Mean	s.d.	Min.	Max.
Mating 1					
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
Weaning rate	1020	0.62	0.49	0	1
Days to calving (day)	1019	345.6	49.6	269	423
Mating 2					
Days to cycling (day)	1002	88.0	106.1	0	411
Lactation anoestrous interval (day)	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
Weaning rate	1009	0.50	0.50	0	1
Days to calving (day)	1005	363.1	51.8	260	423
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
Lifetime (mating 1–6)					
Lifetime annual calving rate	1020	0.70	0.24	0	1
Lifetime annual weaning rate	1020	0.60	0.28	0	1
Average calving rate retained cows	717	0.77	0.16	0	1
Average weaning rate retained cows	717	0.72	0.16	0	1

Table 4.   Unadjusted trait means, standard deviations (s.d.) and ranges for Tropical Composite female reproduction traits
See Table 2 for a description of traits

Trait	n	Mean	s.d.	Min.	Max.
Mating 1					
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
Weaning rate	1111	0.78	0.42	0	1
Days to calving (day)	1110	318.0	38.1	255	425
Mating 2					
Days to cycling (day)	1095	68.7	103.7	0	401
Lactation anoestrous interval (day)	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
Weaning rate	1094	0.65	0.48	0	1
Days to calving (day)	1094	344.6	49.7	265	425
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
Lifetime (mating 1–6)					
Lifetime annual calving rate	1117	0.83	0.22	0	1
Lifetime annual weaning rate	1117	0.73	0.26	0	1
Average calving rate retained cows	898	0.88	0.10	0	1
Average weaning rate retained cows	898	0.83	0.14	0	1

weaning rate in the full dataset was 60% overall, and 72% in the subset of cows present at mating 6.

For TCOMP mean unadjusted reproduction rates were generally higher, but showed a similar decrease from mating 1 to mating 2. In lactating cows at mating 2, 82% were cycling before weaning. Lifetime annual weaning rate was 73% overall, and 83% in cows present at mating 6.

Genotype differences

Genotype comparisons are presented in Table 5 for the subset of the cows managed together at Belmont Research Station. Mating 1 conception and pregnancy rates were not significantly different between BRAH and TCOMP. However, BRAH had lower calving (–9%; $P < 0.05$) and weaning rates (–10%; $P < 0.05$), and longer days to calving (+20.2 days; $P < 0.05$) compared with TCOMP cows. First-lactation BRAH cows had a longer lactation anoestrous interval (+56.9 days; $P < 0.05$) and a lower lactation cyclicity rate (–22%; $P < 0.05$) than TCOMP, and this translated into lower reproduction rates for BRAH in all traits of lactating cows. Differences between the genotypes were less for mating 2 traits of non-lactating cows, although BRAH had a lower weaning rate (–18%; $P < 0.05$) and longer days to calving (+16.4 days; $P < 0.05$) than TCOMP.

Table 5.   Model predicted means for female reproduction traits of similarly treated Brahman and Tropical Composite cows
See Table 2 for description of traits. Within a trait, means followed by different letters are significantly different ($P < 0.05$). Binary traits were analysed on underlying scale and means were back-transformed to the observed scale

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

TCOMP had higher lifetime annual calving (+10%; $P < 0.05$) and annual weaning (+14%; $P < 0.05$) rates compared with BRAH. TCOMP cows still present at mating 6 also had higher average calving and weaning rates. There was a lesser difference between the genotypes in cows still present at mating 6, reflecting that there were a greater percentage of BRAH cows that were culled or died before mating 6 compared with TCOMP.

Heritabilities

Heritability estimates (Table 6) for binary traits on the logit scale at mating 1 were higher than on the observed scale, and linear model estimates were intermediate. For example, the heritability for pregnancy rate in BRAH on the logit scale was 0.62 and 0.15 for weaning rate, and on the observed scale the estimates were 0.11 and 0.04, respectively. Estimates in TCOMP were considerably lower compared with BRAH, and not significantly different from zero, reflecting the high mean level (>90%) of these traits at mating 1. Days to calving heritabilities were 0.22 and 0.13 for BRAH and TCOMP, respectively.

Mating 2 heritability estimates (Table 7) for binary traits were generally similar to the equivalent mating 1 traits on the underlying scale, but higher on the observed scale. Estimates of heritabilities for all traits were higher in lactating cows than in all cows. For traits associated with lactation anoestrus in first-calf cows the heritabilities were moderate to high. For lactation anoestrous interval, lactation cyclicity rate and days to calving these were 0.51, 0.23, 0.49 in BRAH and 0.26, 0.08, 0.35 in TCOMP, respectively. In mating 2 analyses where lactation and calf fixed effects were not fitted (Table 8), heritability estimates for binary traits of BRAH were reduced. In TCOMP, the change in heritabilities was not as pronounced, and most likely reflects a lower impact of the changed fixed effects given the higher percentage of lactating cows at mating 2.

Total numbers of calves born and calves weaned from the first two matings were heritable traits in both BRAH (0.15 and 0.21) and TCOMP (0.14 and 0.16), respectively. The trait pregnant-and-weaned, had heritabilities that were moderate to high on the underlying scale (0.80 and 0.19) and 0.16 and 0.05 on the transformed observed scale for BRAH and TCOMP, respectively. Measures of lifetime annual calving and weaning rates (Table 9) had low heritabilities, while those for calving and weaning rates in cows still present at the sixth mating had low to moderate heritabilities, in both genotypes.

Genetic and phenotypic correlations

Relationships among early traits

Genetic correlations among mating 1 traits (Table 10) and among mating 2 traits (Table 11) were all very high and not different from unity in both genotypes, although standard errors were high for traits with low heritabilities, particularly for TCOMP for traits at mating 1. Phenotypic correlations between mating 1 traits were also moderate to high in both genotypes, and the magnitude of the correlations decreased as pairs of traits were more separated in time; for example, correlations between conception and pregnancy rates were higher than between conception and weaning rates. Similar magnitude correlations were also observed among the mating 2 traits, including the additional traits related to lactation anoestrus.

Estimates of the genetic correlations between pairs of traits in common across mating 1 and mating 2 are presented in Table 12 for models where either the full or reduced set of fixed effects was fitted. Given the low trait heritabilities, all genetic correlations had large standard errors, particularly for TCOMP. In the models fitting full fixed effects analyses often had difficulty converging, especially those for days to calving and weaning rate. Additive genetic variances were also observed to change from univariate estimates for several traits. These model instabilities arose from fitting fixed effects for mating 2 traits (e.g. lactation status) that were themselves part of the outcome for the mating 1 trait (i.e. weaning rate = 1). This applied particularly in BRAH, where the number of non-lactating cows was much

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

See Table 2 for a description of traits. Approximate standard errors in brackets

Trait	Logit model[A]				Linear model[B]	
	p	σ_A^2	h_L^2	h^2	σ_A^2	h^2
Brahman						
Conception rate	0.77	2.38	0.61 (0.22)	0.11	0.050	0.38 (0.13)
Pregnancy rate	0.76	2.42	0.62 (0.22)	0.11	0.059	0.42 (0.14)
Calving rate	0.72	1.18	0.33 (0.15)	0.07	0.035	0.22 (0.10)
Weaning rate	0.62	0.53	0.15 (0.10)	0.04	0.019	0.09 (0.07)
Days to calving	–	–	–	–	434	0.22 (0.09)
Tropical Composite						
Conception rate	0.95	0.98	0.28 (0.27)	0.01	0.002	0.05 (0.05)
Pregnancy rate	0.92	1.24	0.34 (0.21)	0.03	0.007	0.10 (0.06)
Calving rate	0.90	1.03	0.29 (0.16)	0.03	0.009	0.11 (0.06)
Weaning rate	0.78	0.52	0.15 (0.10)	0.03	0.011	0.07 (0.05)
Days to calving	–	–	–	–	183	0.13 (0.06)

[A]Estimates from subset of data with sire known; p = trait level or incidence; $\sigma_A^2 = 4 \times \sigma_s^2$; residual variance = $\pi^2/3$; h_L^2 = heritability on the logit scale; h^2 on observed scale approximated by $h_L^2 \times p(1-p)$.
[B]Estimates for binary traits from linear, sire model; $\sigma_A^2 = 4 \times \sigma_s^2$.

Table 7.   Heritabilities (h^2) and additive variances (σ_A^2) for reproductive traits recorded at mating 2 in Brahman and Tropical Composite cows using full fixed effect models

See Table 2 for a description of traits. Approximate standard errors in brackets

Trait	Logit model[A]				Linear model[B]	
	p	σ_A^2	h_L^2	h^2	σ_A^2	h^2
Brahman – all cows						
Days to cycling	–	–	–	–	2689	0.41 (0.12)
Conception rate	0.61	2.74	0.69 (0.21)	0.16	0.061	0.36 (0.12)
Pregnancy rate	0.59	2.42	0.62 (0.19)	0.15	0.063	0.35 (0.12)
Calving rate	0.56	1.98	0.52 (0.18)	0.13	0.060	0.32 (0.11)
Weaning rate	0.49	1.43	0.39 (0.15)	0.10	0.049	0.24 (0.10)
Days to calving	–	–	–	–	374	0.20 (0.08)
Pregnant-and-weaned	0.27	3.32	0.80 (0.22)	0.16	0.082	0.46 (0.14)
Total calves born 1 + 2	–	–	–	–	0.039	0.15 (0.07)
Total calves weaned 1 + 2	–	–	–	–	0.062	0.21 (0.08)
Brahman – lactating cows only						
Lactation anoestrous interval	–	–	–	–	5238	0.51 (0.18)
Lactation cyclicity rate	0.53	4.01	0.93 (0.25)	0.23	0.139	0.68 (0.20)
Conception rate	0.45	4.12	0.96 (0.26)	0.24	0.124	0.59 (0.18)
Pregnancy rate	0.43	4.46	1.01 (0.27)	0.25	0.133	0.63 (0.19)
Calving rate	0.41	3.70	0.88 (0.26)	0.21	0.125	0.59 (0.19)
Weaning rate	0.36	3.83	0.90 (0.25)	0.21	0.121	0.56 (0.18)
Days to calving	–	–	–	–	915	0.49 (0.14)
Tropical Composite – all cows						
Days to cycling	–	–	–	–	1088	0.18 (0.08)
Conception rate	0.80	1.24	0.34 (0.18)	0.05	0.015	0.12 (0.07)
Pregnancy rate	0.76	0.51	0.15 (0.12)	0.03	0.010	0.06 (0.06)
Calving rate	0.74	0.90	0.26 (0.14)	0.05	0.017	0.11 (0.07)
Weaning rate	0.66	0.55	0.16 (0.10)	0.04	0.020	0.10 (0.07)
Days to calving	–	–	–	–	320	0.17 (0.08)
Pregnant-and-weaned	0.58	0.67	0.19 (0.09)	0.05	0.031	0.14 (0.07)
Total calves born 1 + 2	–	–	–	–	0.038	0.14 (0.07)
Total calves weaned 1 + 2	–	–	–	–	0.055	0.16 (0.07)
Tropical Composite – lactating cows only						
Lactation anoestrous interval	–	–	–	–	1965	0.26 (0.11)
Lactation cyclicity rate	0.82	2.16	0.56 (0.25)	0.08	0.024	0.23 (0.10)
Conception rate	0.77	1.92	0.50 (0.19)	0.09	0.033	0.24 (0.10)
Pregnancy rate	0.73	0.82	0.23 (0.14)	0.05	0.019	0.12 (0.08)
Calving rate	0.71	1.35	0.37 (0.16)	0.08	0.037	0.22 (0.09)
Weaning rate	0.64	0.73	0.21 (0.13)	0.05	0.029	0.14 (0.09)
Days to calving	–	–	–	–	679	0.35 (0.13)

[A]Estimates from subset of data with sire known; p = trait level or incidence; $\sigma_A^2 = 4 \times \sigma_s^2$; residual variance = $\pi^2/3$; h_L^2 = heritability on the logit scale; h^2 on observed scale approximated by $h_L^2 \times p(1 - p)$.
[B]Estimates for binary traits from linear, sire model; $\sigma_A^2 = 4 \times \sigma_s^2$.

greater than for TCOMP. Effectively these models estimate correlations between trait 1 and a trait 2 that has been phenotypically adjusted for trait 1. The general observation for these models was that nevertheless the genetic and phenotypic correlations between traits across the two matings were low or positive for both genotypes.

In contrast, when lactation status and calf effects were ignored, genetic and phenotypic correlations between pairs of traits across matings 1 and 2 in BRAH were negative, clearly showing mating 1 performance was generally negatively related to mating 2 performance. In TCOMP, genetic correlations between pairs of traits tended to be positive but of lower magnitude, albeit with large standard errors.

Early reproduction with lifetime reproduction

Genetic correlation estimates for mating 1 and 2 traits with lifetime reproductive performance traits (Tables 13 and 14) had large standard errors, reflecting the low heritabilities for the lifetime traits, especially in TCOMP. Mating 1 traits in both BRAH and TCOMP were moderately genetically correlated with both lifetime annual calving and weaning rates, but lowly correlated with average calving and weaning rates of those cows remaining in the herd at mating 6. Weaning rate at mating 1 tended to have the highest magnitude correlations with lifetime reproduction traits.

Mating 2 traits (from full fixed effect models) were highly correlated with lifetime reproduction traits in both genotypes. The

correlations tended to be higher with lifetime calving rate traits than with weaning rate, particularly for the lactation anoestrus-associated traits. Lactation anoestrous interval had genetic correlations of –0.62 and –0.87 with lifetime annual weaning rate for BRAH and TCOMP, respectively. In BRAH, when mating 2 traits were modelled without full fixed effects the genetic correlations with lifetime traits reduced substantially. This was particularly the case where both lactating and non-lactating cows were included, and was more pronounced for lifetime annual calving and weaning rates compared with the average calving and weaning rates of cows still in the herd at six matings. In TCOMP, the genetic correlations were similar across models for mating 2 traits and approached unity in many instances.

Total numbers of calves born and weaned from matings 1 and 2 were both moderately to highly correlated (range 0.58–1.0) with all lifetime reproduction traits in both BRAH and TCOMP. Correlations with lifetime traits were also estimated for pregnant-and-weaned, and tended to be of greater magnitude for the lifetime traits for cows still in the herd at mating 6. Genetic correlations of the cumulative mating 1 and 2 traits (from reduced fixed effect models) with lifetime traits were of similar magnitude to the genetic correlations of mating 2 traits (from full fixed effect models) with lifetime traits.

Discussion

Reproduction rates in this experiment were similar to those from other reports in tropical production systems (Entwistle 1983; O'Rourke *et al.* 1995), and especially for the lower rates in lactating cows (Frisch *et al.* 1987; Holroyd *et al.* 1990; O'Rourke *et al.* 1991; Fordyce *et al.* 1996; Schatz and Hearnden 2008; Williams and Amstalden 2010). The genotype differences seen were of similar order to the 13.4% mean calving rate difference reported by Mackinnon *et al.* (1989, 1990) using

Table 8. Heritabilities (h^2) and additive variances (σ_A^2) for reproductive traits recorded at mating 2 in Brahman and Tropical Composite cows using reduced[A] fixed effect models

See Table 2 for a description of traits. Approximate standard errors in brackets. $\sigma_A^2 = 4 \times \sigma_s^2$; residual variance $= \pi^2/3$; h^2 approximated by $h_L^2 \times p(1 - p)$

Trait	σ_A^2	h_L^{2B}	h^2
Brahman			
Days to cycling	3809	–	0.36 (0.11)
Lactation cyclicity rate	3.61	0.86 (0.23)	0.21
Lactation anoestrous interval	5915	–	0.54 (0.14)
Conception rate	1.30	0.36 (0.13)	0.09
Pregnancy rate	1.25	0.35 (0.13)	0.08
Calving rate	1.18	0.33 (0.13)	0.08
Weaning rate	0.96	0.27 (0.12)	0.07
Days to calving	399	–	0.16 (0.08)
Tropical Composite			
Days to cycling	696	–	0.09 (0.06)
Lactation cyclicity rate	2.21	0.57 (0.25)	0.08
Lactation anoestrous interval	1987	–	0.26 (0.11)
Conception rate	0.88	0.25 (0.14)	0.04
Pregnancy rate	0.42	0.12 (0.10)	0.02
Calving rate	0.58	0.17 (0.11)	0.03
Weaning rate	0.46	0.14 (0.09)	0.03
Days to calving	304	–	0.14 (0.08)

[A]Models without lactation and calf effects.
[B]Heritability on the logit scale; estimates from subset of data with sire known.

Table 9. Heritabilities (h^2) and additive variances (σ_A^2) for lifetime reproduction traits for Brahman and Tropical Composite

See Table 2 for a description of traits. Approximate standard errors in brackets

Trait	Brahman		Tropical Composite	
	σ_A^2	h^2	σ_A^2	h^2
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)
Average calving rate retained cows	0.0061	0.30 (0.11)	0.0021	0.15 (0.09)
Average weaning rate retained cows	0.0069	0.31 (0.12)	0.0045	0.24 (0.11)

Table 10. Genetic and phenotypic correlations[A] among traits measured at mating 1 in Brahman and Tropical Composite

See Table 2 for description of traits. Approximate standard errors in brackets

Trait	Conception rate	Pregnancy rate	Calving rate	Weaning rate	Days to calving
Brahman					
Conception rate	–	1.0 (0.01)	0.99 (0.03)	0.93 (0.11)	–0.94 (0.05)
Pregnancy rate	0.95	–	1.0[B] (0.02)	0.93 (0.10)	–0.96 (0.04)
Calving rate	0.84	0.87	–	0.87 (0.11)	–0.96 (0.03)
Weaning rate	0.67	0.70	0.78	–	–0.93 (0.10)
Days to calving	–0.76	–0.80	–0.92	–0.73	–
Tropical Composite					
Conception rate	–	0.72 (0.23)	0.93 (0.21)	0.69 (0.42)	–0.64 (0.32)
Pregnancy rate	0.77	–	1.0[B] (0.06)	0.96 (0.22)	–0.99 (0.09)
Calving rate	0.66	0.77	–	1.0[B] (0.14)	–1.0[B] (0.03)
Weaning rate	0.41	0.48	0.63	–	–0.95 (0.17)
Days to calving	–0.58	–0.72	–0.89	–0.56	–

[A]Genetic above, phenotypic below; s.e. on phenotypic correlations ranged 0.01 to 0.03.
[B]Estimate exceeded bounds.

Table 11. Genetic correlations and phenotypic[A] among traits measured at mating 2 (model included full fixed effects for lactation status and calf effects)
See Table 2 for trait descriptions. Approximate standard errors in brackets

Trait	Conception rate	Pregnancy rate	Calving rate	Weaning rate	Days to calving	Days to cycling	Lactation anoestrous interval	Lactation cyclicity rate
				Brahman				
Conception rate	–	1.00 (0.01)	0.98 (0.03)	0.98 (0.05)	–0.98 (0.04)	–0.95 (0.05)	–1.00 (0.05)	0.96 (0.05)
Pregnancy rate	0.94	–	0.97 (0.02)	0.95 (0.05)	–0.96 (0.04)	–1.00 (0.05)	–1.0[B] (0.04)	1.00 (0.04)
Calving rate	0.87	0.91	–	1.00 (0.03)	–0.99 (0.02)	–0.95 (0.07)	–1.00 (0.06)	1.0[B] (0.05)
Weaning rate	0.76	0.79	0.87	–	–0.97 (0.06)	–0.95 (0.09)	–0.96 (0.09)	0.97 (0.08)
Days to calving	–0.80	–0.85	–0.93	–0.79	–	0.95 (0.08)	1.0[B] (0.07)	–0.99 (0.07)
Days to cycling	–0.71	–0.67	–0.62	–0.55	0.58	–	n.e.	–1.0[B] (0.02)
Lactation anoestrous interval	–0.75	–0.72	–0.69	–0.65	0.70	n.e.		n.e.
Lactation cyclicity rate	0.80	0.77	0.73	0.69	–0.71	–0.87	n.e.	–
				Tropical Composite				
Conception rate	–	1.0[B] (0.12)	0.93 (0.10)	1.0[B] (0.22)	–0.84 (0.14)	–0.88 (0.18)	–0.90 (0.12)	0.95 (0.10)
Pregnancy rate	0.87	–	0.98 (0.08)	1.0[B] (0.24)	–0.93 (0.10)	–0.90 (0.25)	–0.92 (0.26)	0.99 (0.24)
Calving rate	0.81	0.88	–	n.e.	–0.98 (0.03)	–0.88 (0.18)	–0.83 (0.20)	0.86 (0.18)
Weaning rate	0.66	0.71	n.e.	–	1.0* (0.11)	–0.99 (0.24)	–0.92 (0.26)	0.96 (0.25)
Days to calving	–0.74	–0.82	–0.92	–0.77	–	0.86 (0.15)	0.75 (0.20)	–0.87 (0.15)
Days to cycling	–0.76	–0.67	–0.62	–0.53	0.60	–	n.e.	–0.96 (0.05)
Lactation anoestrous interval	–0.78	–0.69	–0.66	–0.58	0.67	n.e.	–	–0.96 (0.04)
Lactation cyclicity rate	0.81	0.72	0.69	0.59	–0.64	–0.91	–0.93	–

[A]Genetic above, phenotypic below; s.e. on phenotypic range 0.01 to 0.02.
[B]Estimates exceeded bounds; n.e. not estimable or failed to converge.

Table 12. Genetic and phenotypic correlations for each trait across mating 1 and mating 2 from two models in Brahman and Tropical Composite
See Table 2 for trait descriptions. Approximate standard errors in brackets

MODEL[A]	Variance	Conception rate	Pregnancy rate	Calving rate	Weaning rate	Days to calving
			Brahman			
FULL	Genetic	0.03 (0.24)	–0.02 (0.24)	0.18 (0.29)	0.48[B] (0.34)	0.55[B] (0.21)
	Phenotypic	0.06 (0.04)	0.07 (0.04)	0.35 (0.04)	0.10[B] (0.05)	0.61[B] (0.03)
REDUCED	Genetic	–0.56 (0.18)	–0.60 (0.17)	–0.65 (0.20)	–0.05 (0.41)	–0.71 (0.20)
	Phenotypic	–0.33 (0.03)	–0.33 (0.03)	–0.34 (0.03)	–0.33 (0.03)	–0.33 (0.03)
			Tropical Composite			
FULL	Genetic	0.17 (0.52)	0.45 (0.47)	0.63 (0.39)	0.82[B] (0.64)	0.40[B] (0.31)
	Phenotypic	0.09 (0.04)	0.11 (0.04)	0.02 (0.04)	–0.09[B] (0.04)	0.46[B] (0.03)
REDUCED	Genetic	0.07 (0.55)	0.26 (0.51)	0.53 (0.40)	0.73 (0.53)	–0.04 (0.40)
	Phenotypic	0.04 (0.03)	0.06 (0.03)	0.04 (0.03)	–0.04 (0.03)	–0.05 (0.03)

[A]FULL = all significant fixed effects included; REDUCED = lactation status and calf fixed effects ignored.
[B]log converged but parameters not converged.

the Belmont herd that comprised female ancestors of the BRAH and TCOMP cows used in this study. However, the results are in contrast to those of Prayaga (2004), using other generations from the same herd, who reported no difference between Belmont Red and BRAH in calving rate for lactating or non-lactating cows.

Genotype differences were not apparent for conception or calving rates at the maiden mating, and reflect earlier results that showed no difference in age at puberty and percent cycling into first mating of these females (Johnston *et al.* 2009). However, the significantly lower weaning rate from the maiden mating suggests greater calf losses in BRAH. A difference in weaning rate was also observed for mating 2 in both lactating and non-lactating cows, as well as in lifetime weaning rates. These differences suggest further study is warranted, targeted at calf losses. The biggest differences between the genotypes were in the reproductive performance of lactating first-calf cows. The differences derived from the longer lactation anoestrous interval in BRAH and fewer cows that were cycling before weaning. The differences were much lower in non-lactating cows.

Heritability estimates of reproduction rates at mating 1 on the underlying scale were considerably larger than the mean of 0.05 for heifer conception rate reported in the review of Koots *et al.* (1995). In Angus heifers, Minick Bormann *et al.* (2006) reported a heritability for heifer pregnancy rate of 0.13 on the underlying scale, and Morris *et al.* (2000) an estimate of 0.12 on a linear scale. Our estimates of heritabilities for binary traits on the underlying

Table 13. Brahman estimates of the genetic and phenotypic correlations between early and lifetime reproduction traits: lifetime annual calving rate (LACR) and weaning rate (LAWR) and average calving (ACR) and weaning rate (AWR) for retained cows

See Table 2 for trait descriptions. Approximate standard errors in brackets

Trait	Genetic				Phenotypic[A]			
	LACR	LAWR	ACR	AWR	LACR	LAWR	ACR	AWR
Mating 1								
Conception rate	0.61 (0.20)	0.47 (0.26)	0.36 (0.22)	0.21 (0.24)	0.40	0.30	0.37	0.31
Pregnancy rate	0.60 (0.20)	0.51 (0.25)	0.32 (0.22)	0.20 (0.24)	0.42	0.31	0.35	0.32
Calving rate	0.50 (0.25)	0.44 (0.29)	0.28 (0.25)	0.21 (0.27)	0.43	0.30	0.36	0.32
Weaning rate	0.98 (0.21)	0.99 (0.18)	0.69 (0.26)	0.74 (0.25)	0.31	0.47	0.26	0.31
Days to calving	−0.46 (0.26)	−0.54 (0.27)	−0.21 (0.27)	−0.10 (0.29)	−0.43	−0.32	−0.35	−0.31
Mating 2 full model[B]								
Days to cycling	−0.55 (0.25)	−0.60 (0.25)	−1.0[C] (0.11)	−0.99 (0.13)	−0.28	−0.27	−0.42	−0.37
L. anoestrous interval	−0.71 (0.21)	−0.62 (0.24)	−1.0[C] (0.09)	−1.0[C] (0.11)	−0.46	−0.38	−0.51	−0.45
L. cyclicity rate	0.59 (0.23)	0.53 (0.26)	1.0[C] (0.09)	0.93 (0.14)	0.49	0.37	0.51	0.45
Conception rate	0.90 (0.13)	0.76 (0.20)	n.e.	1.00 (0.14)	0.56	0.45	n.e.	0.42
Pregnancy rate	0.75 (0.17)	0.69 (0.22)	n.e.	1.0[C] (0.15)	0.61	0.49	n.e.	0.43
Calving rate	0.89 (0.14)	0.81 (0.19)	1.0[C] (0.14)	0.85 (0.20)	0.69	0.56	0.56	0.47
Weaning rate	0.86 (0.19)	0.81 (0.18)	1.0[C] (0.21)	0.78 (0.23)	0.59	0.65	0.47	0.48
Days to calving	−1.0[C] (0.11)	−0.96 (0.17)	n.e.	−1.0[C] (0.20)	−0.68	−0.55	n.e.	−0.42
Mating 2 reduced model[B]								
Days to cycling	0.06 (0.29)	−0.05 (0.31)	−0.67 (0.23)	−0.63 (0.23)	0.00	0.06	−0.18	−0.09
L. anoestrous interval	−0.84 (0.18)	−0.71 (0.22)	n.e.	−1.0[C] (0.10)	−0.46	−0.39	n.e.	−0.44
L. cyclicity rate	0.74 (0.19)	0.58 (0.24)	1.0[C] (0.08)	0.99 (0.12)	0.49	0.36	0.51	0.44
Conception rate	0.34 (0.29)	0.27 (0.32)	1.0[C] (0.20)	0.71 (0.24)	0.26	0.15	0.26	0.14
Pregnancy rate	0.20 (0.30)	0.22 (0.32)	1.00 (0.23)	0.76 (0.26)	0.31	0.19	0.26	0.14
Calving rate	0.13 (0.32)	0.31 (0.33)	0.78 (0.28)	0.55 (0.31)	0.39	0.26	0.28	0.16
Weaning rate	0.11 (0.34)	0.20 (0.34)	0.66 (0.33)	0.47 (0.33)	0.34	0.37	0.24	0.20
Days to calving	−0.14 (0.34)	−0.36 (0.37)	−0.80 (0.34)	−0.60 (0.35)	−0.34	−0.21	−0.22	−0.10
Total calves born 1 + 2	0.82 (0.16)	0.79 (0.24)	0.75 (0.20)	0.58 (0.26)	0.71	0.50	0.62	0.46
Total calves weaned 1 + 2	0.93 (0.15)	0.84 (0.14)	0.97 (0.18)	0.71 (0.21)	0.58	0.71	0.52	0.60
Pregnant-and-weaned	0.55 (0.21)	0.59 (0.23)	0.98 (0.13)	0.84 (0.16)	0.43	0.42	0.49	0.47

[A]All approximate standard errors ranged 0.02 to 0.04.
[B]FULL = all significant fixed effects included; REDUCED = lactation status and calf fixed effects ignored.
[C]Estimates exceeded bounds; n.e. = not estimable or failed to converge.

scale were higher than the observed or linear scales, and this is common. Estimates on the observed scale were often considerably lower in TCOMP as a result of their generally higher mean levels of the reproductive traits. Also as a consequence of this, estimates of genetic correlations for TCOMP yielded some very large standard errors. These results were included for completeness and to allow possible trends to be observed. The heritabilities at mating 1, particularly for BRAH, suggest there is considerable potential to genetically change maiden heifer reproductive rates under the production systems in this study. This is supported by BRAH selection line results 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 present study.

Lactation anoestrus was clearly evident in this study and had a large influence on the reproductive outcomes from the second mating (i.e. at first re-breed). For BRAH, anoestrus up to the time of weaning was observed in almost half the first-lactation cows. Many experiments have reported extended postpartum anoestrous intervals (e.g. Baker 1968; Davis *et al*. 1993; Fordyce *et al*. 1997; Prayaga 2004) and McSweeney *et al*. (1993) reported weaning was required to break the anoestrus in Droughtmaster cows. Mating 2 heritability estimates, and particularly those associated with anoestrus in first-lactation cows, were moderate to large and are a key finding from this study. It shows a significant contribution of genetics to this commonly observed phenomenon in tropical cattle, and is further supported by the large between genotype differences in these traits that were also observed. The underlying physiological mechanisms of anoestrus in cattle have been well documented (Randel 1990; Short *et al*. 1990; Abeygunawardena and Demarawewa 2004; Montiel and Ahuja 2005; Williams and Amstalden 2010). Most studies have identified key factors influencing the anoestrous interval, but few, if any, have considered the role of genetics outside of noting that breed differences may exist. There are very few literature estimates of the heritability of anoestrous interval in beef cattle. Morris *et al*. (2000) reported a heritability of 0.11 for calving to conception interval in mixed age Angus cows. Mialon *et al*. (2000) estimated

Table 14.   Tropical Composite estimates of the genetic and phenotypic correlations between early and lifetime reproduction traits: lifetime annual calving rate (LACR) and weaning rate (LAWR) and average calving (ACR) and weaning rate (AWR) for retained cows
See Table 2 for trait descriptions. Approximate standard errors in brackets

Trait	Genetic				Phenotypic[A]			
	LACR	LAWR	ACR	AWR	LACR	LAWR	ACR	AWR
Mating 1								
Conception rate	0.56 (0.53)	0.54 (0.45)	–0.01 (0.56)	0.07 (0.48)	0.42	0.33	0.16	0.10
Pregnancy rate	1.0[C] (0.26)	0.65 (0.30)	0.24 (0.39)	0.16 (0.36)	0.43	0.35	0.23	0.16
Calving rate	0.78 (0.33)	0.56 (0.32)	0.32 (0.37)	0.27 (0.35)	0.54	0.43	0.29	0.24
Weaning rate	0.89 (0.48)	0.86 (0.28)	0.65 (0.38)	0.66 (0.28)	0.32	0.52	0.08	0.36
Days to calving	–0.75(0.30)	–0.57 (0.30)	–0.30 (0.36)	–0.19 (0.34)	–0.53	–0.43	–0.30	–0.26
Mating 2 full model[B]								
Days to cycling	–0.91 (0.46)	–0.99 (0.34)	–1.0[C] (0.22)	–0.63 (0.24)	–0.32	–0.30	–0.39	–0.34
L. anoestrous interval	–1.0[C] (0.46)	–0.87 (0.32)	–0.93 (0.22)	–0.55 (0.24)	–0.51	–0.43	–0.42	–0.36
L. cyclicity rate	1.0[C] (0.56)	0.66 (0.36)	0.66 (0.29)	0.18 (0.31)	0.51	0.42	0.41	0.35
Conception rate	1.0[C] (0.45)	1.0[C] (0.34)	1.0[C] (0.30)	0.76 (0.25)	0.53	0.43	0.47	0.39
Pregnancy rate	1.0[C] (0.32)	1.0[C] (0.34)	0.77 (0.39)	0.49 (0.40)	0.60	0.48	0.51	0.39
Calving rate	0.96 (0.25)	0.91 (0.29)	0.76 (0.29)	0.64 (0.28)	0.68	0.52	0.53	0.41
Weaning rate	1.0[C] (0.35)	0.85 (0.28)	1.00 (0.28)	0.84 (0.22)	0.56	0.65	0.40	0.50
Days to calving	–0.97 (0.20)	–0.76 (0.25)	–0.79 (0.25)	–0.62 (0.26)	–0.68	–0.55	–0.51	–0.41
Mating 2 reduced model[B]								
Days to cycling	–0.95 (0.57)	–0.89 (0.49)	–1.0[C] (0.29)	–0.63 (0.31)	–0.18	–0.08	–0.36	–0.23
L. anoestrous interval	–1.0[C] (0.45)	–0.83 (0.32)	–0.92 (0.22)	–0.54 (0.24)	–0.52	–0.44	–0.42	–0.47
L. cyclicity rate	1.0[C] (0.55)	0.64 (0.36)	0.66 (0.29)	0.17 (0.31)	0.51	0.42	0.41	0.36
Conception rate	1.0[C] (0.49)	1.0[C] (0.39)	1.0[C] (0.37)	0.71 (0.29)	0.40	0.30	0.46	0.31
Pregnancy rate	0.86 (0.47)	0.95 (0.47)	0.77 (0.43)	0.35 (0.45)	0.48	0.36	0.49	0.33
Calving rate	0.89 (0.33)	0.83 (0.37)	0.78 (0.31)	0.61 (0.31)	0.55	0.41	0.52	0.35
Weaning rate	1.0[C] (0.42)	0.83 (0.39)	0.98 (0.28)	0.81 (0.26)	0.45	0.52	0.40	0.43
Days to calving	–0.79 (0.30)	–0.63 (0.33)	–0.78 (0.27)	–0.62 (0.27)	–0.52	–0.38	–0.48	–0.31
Total calves born 1 + 2	1.0[C] (0.16)	0.89 (0.19)	0.81 (0.20)	0.60 (0.26)	0.74	0.59	0.65	0.47
Total calves weaned 1 + 2	1.0[C] (0.34)	0.92 (0.19)	0.75 (0.22)	0.71 (0.18)	0.57	0.72	0.42	0.64
Pregnant-and-weaned	1.0[C] (0.49)	1.0[C] (0.24)	0.86 (0.23)	0.64 (0.24)	0.49	0.53	0.45	0.52

[A]All approximate standard errors ranged 0.02 to 0.04.
[B]FULL = all significant fixed effects included; REDUCED = lactation status and calf fixed effects ignored.
[C]Estimates exceeded bounds.

a heritability of 0.35 for postpartum interval to first positive progesterone test in mixed age Charolais cows. Anovulation has been observed in dairy cattle studies; Bamber *et al.* (2009) reported a heritability of 0.17 on the underlying scale, and suggested selection against abnormally long intervals could be used to improve dairy cattle reproduction.

Heritabilities of lifetime reproduction traits were low, but were similar or larger than other published estimates (see reviews of Davis 1993; Koots *et al.* 1995; Cammack *et al.* 2009). Morris and Cullen (1994) reported a heritability of 0.04 for lifetime pregnancy rate to five matings in mixed *Bos taurus* breeds using a similar trait definition as in this study. Balieiro *et al.* (2008) also reported a heritability of 0.04 in Nellore cows for lifetime productivity defined simply as the total number of calves up to 6 years of age. The heritability estimates for lifetime calving rate were generally in agreement with previous estimates from the Belmont herd where Mackinnon *et al.* (1990) reported calving rate heritabilities on the linear scale very similar for BRAH (0.13) but higher for Belmont Reds (0.15) compared with our estimate for TCOMP. Similarly, Meyer *et al.* (1990) estimated a heritability of 0.17 for lifetime calving rate and 0.36 for total calves born for Belmont Reds from the same population. These higher estimates most likely reflect the lower average calving rate (64%) seen in the data of Meyer *et al.* (1990) to that for TCOMP (83%) in the present study.

The heritability estimate for days to calving from Meyer *et al.* (1990) of 0.09 was similar to the 0.07 reported by Burrow (2001) from records for the first three matings, but both were lower than our estimates in TCOMP for the first two matings. The significant divergence in cow pregnancy rates generated in selection lines of Droughtmaster cattle in a Northern Australia production environment (Hetzel *et al.* 1989; Davis *et al.* 1993) supports the present estimates. The considerable phenotypic variance observed for many of the reproductive traits means response to selection could be considerable, and as suggested by Davis *et al.* (1993), the gains from such selection are expected to be far greater those from simply culling non-pregnant cows.

Several of the traits recorded at the first two matings were moderately to highly genetically correlated with lifetime reproduction rates, and although their estimates had large standard errors consistently the correlations suggest rates of genetic progress in lifetime reproduction can be increased by selecting on these moderate to high heritability traits measured earlier-in-life. 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. 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 the trait days to calving is highly correlated with the other measures and those breeds currently using this BREEDPLAN trait (Graser *et al.* 2005) in selection will also be improving early and lifetime performance.

In BRAH, mating 2 trait genetic correlations were generally more predictive of lifetime reproductive performance, than were traits at mating 1, provided the estimates were from models that adjusted for lactation status and calf fixed effects. Correlations were low from models that did not fit the full fixed effects, suggesting reproductive performance at mating 2 is only predictive of lifetime performance when there is knowledge of the outcome of mating 1. This trend was less obvious for traits defined for lactating cows and for combinations of mating 1 and 2 outcomes, where, high to very high correlations with lifetime reproduction were already observed. In TCOMP, mating 2 trait genetic correlations with lifetime performance approached unity for many traits, and suggests the majority of the genetic variance in lifetime reproduction is associated with differences in reproductive performance at the first two matings. This conclusion is also supported by the results of Burrow (2001) and Martinez *et al.* (2004) in US Herefords.

This study has shown there is considerable genetic variation for lifetime female reproduction in tropical beef cattle, and several traits recorded early at the first two matings are highly correlated with lifetime performance. Potentially other traits recorded in the total experiment may also be useful in assisting with increasing rates of gain in lifetime reproduction rates such as age at puberty (Johnston *et al.* 2009), heifer and female body composition (Barwick *et al.* 2009b; Wolcott *et al.* 2014) and male reproduction traits (Corbet *et al.* 2013).

Conclusions

Lifetime female reproductive rates had low heritabilities in both BRAH and TCOMP cattle but components of earlier-in-life reproductive performance, particularly those at first re-breed in lactating cows, had higher heritabilities. Importantly selection to improve these early-in-life reproduction traits will result in improved lifetime annual reproduction rates. Opportunities exist, particularly in BRAH, to improve lifetime weaning rates though selection. Recording systems of seedstock herds need to be able to capture the required data. Enhancements may be required for genetic evaluation systems to evaluate reproduction by incorporating these new female traits, applying appropriate variance component estimates in a full multiple trait framework.

Acknowledgements

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