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Genetic parameter estimates for male and female fertility traits using genomic data to improve fertility in Australian beef cattle

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Abstract

Context. Studies have shown that favourable genetic correlations exist between female and male fertility traits. However, investigations regarding these correlations in Australian tropical beef cattle are limited to either pedigree or single-breed analysis.

Aim. The study aims to use genomic information to estimate genetic parameters of six female and seven male fertility traits measured during the first 2 years of life, in two tropical breeds.

Methods. Single-, bivariate and multi-trait models were used to analyse fertility data from Brahman (BB; 996 cows and 1022 bulls); and Tropical Composite (TC; 1091 cows and 998 bulls) cattle genotyped with high-density single-nucleotide polymorphism chip assay.

Key results. Heritability estimates in BB cows ranged from low (0.07 ± 0.04) for days to calving at the first calving opportunity (DC1, days) to high (0.57 ± 0.08) for age at first *corpus luteum* (AGECL, days). In BB bulls, estimates varied from low (0.09 ± 0.05) for sperm motility (score 1–5) to high (0.64 ± 0.06) for scrotal circumference (SC) measured at 24 months (SC24, cm). Similarly, heritability estimates in TC cows were low (0.04 ± 0.03) for DC1 and high (0.69 ± 0.02) for AGECL. In TC bulls, the heritability was low (0.09 ± 0.05) for sperm motility and high (0.69 ± 0.07) for SC24. Within-sex for both breeds, blood concentrations of insulin growth-factor 1 (IGF1) measured in cows at 18 months (IGF1c) were negatively correlated with female fertility phenotypes. In BB, across-sex, bulls' blood concentration of IGF1 measured at 6 months (IGF1b) was a good indicator trait for the following four female traits: AGECL, the first postpartum anoestrus interval, age at first calving and DC1. In TC, IGF1b and percentage normal sperm were good predictors of female fertility phenotypes.

Conclusions. The heritability estimates and genomic correlations from the present study generally support and confirmed the earlier estimates from pedigree analyses. The findings suggest that selection for female fertility traits will benefit male fertility, and *vice versa*.

Implications. Heritability estimates and genomic correlations suggest that we can select for fertility traits measured early in life, with benefits within and across sex. Using traits available through veterinary assessment of bull fertility as selection indicators will enhance bull and cow fertility, which can lead to better breeding rates in tropical herds.

Keywords: genetic correlation, fertility, heritability, beef cattle, genomics.

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Introduction

In cow-calf operations, the number of calves produced per cow in their lifetime is indicative of beef productivity and sustainability (Johnston *et al.* 2014*a*; Zhang *et al.* 2014). Increasing the number of calves to ensure enterprise profitability is a complex challenge that involves both

female and male fertility (Hansen 2006). Improving fertility in both sexes will create numerous benefits across the supply chain and contributes to the beef industry as a whole.

Female and male cattle may employ different reproductive strategies, resulting in the evolution of sex dimorphism (Fairbairn *et al.* 2007). Interestingly, since both sexes share almost identical genomes apart from the sex chromosome, there is a possibility that selection in one sex can result in indirect selection on the other sex, constraining the evolution of sexual dimorphism (Lande 1984; Poissant *et al.* 2010; Pennell and Morrow 2013). It is then expected that sex-specific genes would allow independent evolution within sexes and genes that are expressed in both males and females would foster similarities in both sexes (Lande 1984). Genetic correlations can be very high across sexes, when studying traits that are homologous in both male and female (Poissant *et al.* 2010). But there are obviously traits that are not homologous. Reproductive strategies, dimorphism and genetics form an interesting interdisciplinary field, where researchers investigate the intra-locus sexual conflict.

After the study of Land (1973), who first reported the interplay between male and female reproduction in mammals, several studies in beef cattle have shown the existence of favourable genetic correlations between bull and cow fertility (Johnston *et al.* 2014*b*; Raidan *et al.* 2019). The genetic correlation between scrotal circumference (SC) and female fertility traits justifies the commercial use of SC in selection programs across the world (Lunstra and Cundiff 2003; Gargantini *et al.* 2004). However, investigation about sex interplay in tropical beef cattle in Australia has been limited to either pedigree (Johnston *et al.* 2014*b*; Jeyaruban and Johnston 2017; Johnston and Moore 2019) or single-breed analysis (Raidan *et al.* 2019). Considering the diverse range of breeds, crossbreeds and composites that characterise the Australian beef industry, there is a need to study the relationships between female and male fertility in more than one breed. Therefore, the present study aims to estimate genetic parameters for a range of male and female fertility traits, in two tropical beef breeds of Australia. We also discuss the implication of these results for selective breeding.

Materials and methods

Animals and phenotypes

Institutional Animal Care and Use Committee approval was not needed for the present study because data used were retrieved from existing databases. Animals used in the study were bred by the Cooperative Research Centre for Beef Genetic Technologies (Beef CRC). These animals were reared under a range of extensive environments at four research stations in Queensland. The details on the routine management, feeding regimes and health treatments have been previously described in Johnston *et al*. (2009), Burns *et al*. (2013) and Wolcott *et al*. (2014). Cows were culled only for husbandry reasons (i.e. disease) or if they failed to wean a calf in two consecutive years. Otherwise, they were kept for six mating opportunities. Briefly, 2018 Brahman (BB) cattle (996 cows and 1022 bulls) and 2089 Tropical Composite (TC) cattle (1091 cows and 998 bulls) were used for the study. The same number of traits were studied in the two populations (six cow traits, and seven bull traits), but the exact number of animals recorded for each trait varied (Table 1). BB cattle are of *Bos indicus* origin, while TC originated from crossing *Bos indicus* and *Bos taurus* breeds. The breed composition of these two populations has been previously investigated. TC breed exhibits more genetic variation than BB (Porto-Neto *et al.* 2013*a*, 2013*b*). Since, breed composition can affect genetic parameter estimates, we model the first two principal components (PC1 and PC2) in addition to the genomic relationship matrix (GRM) to account for the, quite varied, breed composition in the TC breed, for all traits studied. The

Table 1. Trait description and summary statistics of cow and bull fertility traits

Trait	Description	Summary statistics			
		N	Mean ± s.d. Brahman	*N*	Mean ± s.d. Tropical Composite
	Cow phenotypes				
AGECL	Age at detection of first *corpus luteum* (days)	980	750.65 ± 141.80	996	651.25 ± 120.32
PPAI	Postpartum anoestrus interval (days)	618	180.37 ± 109.05	822	142.58 ± 109.88
IGF1c	Cows' blood concentration of IGF1 at 18 months of age	995	191.33 ± 89.30	1015	226.38 ± 75.69
DC1	Days-to-calving 1st breeding opportunity (days)	996	345.41 ± 48.49	1091	319 ± 37.86
DC5	Days-to-calving averaged for 5 breeding opportunities (days)	794	344.37 ± 19.23	922	329.21 ± 18.53
AFC	Age at first calving (years)	944	3.23 ± 0.49	1058	3.06 ± 0.38
	Bull phenotypes				
IGF1b	Bulls' blood concentration of IGF1 at 6 months of age (ng/mL)	964	556.14 ± 328.96	998	615.2 ± 332.86
MAS	Sperm mass activity at 24 months of age (%)	986	2.67 ± 1.01	970	2.98 ± 0.76
MOT	Sperm motility at 24 months of age (%)	990	71.55 ± 20.71	970	74.89 ± 19.49
PNS	Percentage normal sperm at 24 months of age (%)	938	73.71 ± 21.95	993	73.0 ± 0.21
SC12	Scrotal circumference at 12 months of age (cm)	1020	21.39 ± 2.70	998	26.5 ± 3.21
SC18	Scrotal circumference at 18 months of age (cm)	1022	26.73 ± 2.66	998	30.28 ± 2.82
SC24	Scrotal circumference at 24 months of age (cm)	1022	29.76 ± 2.82	998	31.78 ± 24.25

use of PC1 and PC2 was not necessary for the BB herd, which had a more uniform breed composition.

Genotypes and imputation

All animals used were either genotyped with the BovineSNP50 (Matukumalli *et al.* 2009) or the BovineHD (Illumina Inc., San Diego, CA, USA) chips. Animals genotyped with the medium-density single-nucleotide polymorphism (SNP) panel had their genotypes imputed up to 770 000 as described by Bolormaa *et al.* (2015). Before performing imputation, all the original SNP genotypes were remapped to the new assembly of the bovine reference genome (ARS_UCD1.2, GenBank assembly accession GCA_002263795.2; Rosen *et al.* 2020) and were phased using Eagle software (Loh *et al.* 2016). Subsequently, Minimac3 was used to impute the lower-density genotypes for all autosome (Das *et al.* 2016) and Minimac4 for the X-chromosome. The X-chromosome was imputed after separating the non-pseudoautosomal (nPAR) and pseudoautosomal regions (PAR) following the recent definition of these two regions by Johnson *et al.* (2019). After imputation, only SNPs with an imputation accuracy higher than 0.8 were retained for subsequent analyses, resulting in a dataset with 722 208 SNPs for both sexes in the two breeds.

Genomic relationship matrix (GRM)

First, we performed quality control by excluding all SNPs with a minor allele frequency smaller than 0.05 within breed for each sex, before constructing the GRM. As a result, 561 080 and 562 974 genotypes remained for BB cows and bulls respectively. In TC, 688 407 and 688 095 genotypes remained for cows and bulls respectively. GRMs were then constructed following Method 1 of VanRanden (VanRaden 2008) implemented in GIBBS2F90 (Misztal *et al.* 2002). For the across-sex study, we merged the unfiltered genotypes for both sexes in each breed and performed the quality control as described above, resulting in 554 712 and 688 603 SNPs for both BB and TC respectively. Before constructing the GRM, we separated the X-chromosome into nPAR and PAR regions following the boundary described by Johnson *et al.* (2019). The PAR region is small, consisting of 1977 SNPs, which were removed from the analyses. After removing PAR SNPs, we used the genotypes of 554 712 and 686 626 SNPs for BB and TC respectively, to build the GRM. First, we constructed a GRM using all the SNPs in autosomes, for each breed separately, using GCTA software (Yang *et al.* 2011). Second, for the X-chromosome nPAR region, we constructed another GRM using the specific function for the nPAR region as specified in GCTA software (Yang *et al.* 2011). The final GRM for both BB and TC breeds was created by merging both the autosome GRM and the X-chromosome nPAR region GRM. The merged GRM was imported into GIBBS2F90 for further analyses.

Statistical analyses

Within sex, heritability estimates were computed using single- and multi-trait models, while genomic correlations were estimated using bivariate and multi-trait models. Bivariate models were employed to estimate the genomic correlations between male and female traits. All analyses were performed using GIBBS2F90 (Misztal *et al.* 2002). The general mixed-model equation was as follows:

within-sex: single- and multi-trait models

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{e} \tag{1}$$

where $\boldsymbol{y}$ is a vector of observations for the analysed traits within sex for each breed, $\boldsymbol{b}$ is a vector of fixed effects, $\boldsymbol{a}$ is the vector of random additive animal effects, $\boldsymbol{e}$ is the vector of random residual effects, and $\boldsymbol{X}$ and $\mathbf{Z}$ are incidence matrices relating records to their respective effects for every individual in the GRM. The assumptions for this analysis were as follows:

$$\varepsilon \begin{bmatrix} \mathbf{y} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \tag{2}$$

$$\mathbf{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{K} & \mathbf{0} \\ \mathbf{0} & \mathbf{R} \otimes \mathbf{I} \end{bmatrix} \tag{3}$$

where $\boldsymbol{G}$ is the additive genetic covariance matrix of order $n \times n$, where n is the number of traits analysed, $\boldsymbol{K}$ is the genomic relationship matrix for all animals, $\boldsymbol{R}$ is the residual covariance matrix of order $n \times n$, $\boldsymbol{I}$ is an identity matrix, $\otimes$ is the Kronecker product operator.

Within-sex bivariate model was as follows:

$$\begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \emptyset \\ \emptyset & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta_1} \\ \boldsymbol{\beta_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_1} & \emptyset \\ \emptyset & \boldsymbol{Z_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix} \tag{4}$$

All parameters in Eqn 4 have been described in Eqn 1. Subscripts 1 and 2 here are parameters relative to Traits 1 and 2 within sex for each breed. The assumptions of the structure of (co)variances for bivariate model were as follows:

$$\mathbf{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{G} \otimes \boldsymbol{K} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{R} \otimes \boldsymbol{I} \end{bmatrix}; \boldsymbol{G} = \begin{bmatrix} \boldsymbol{\sigma^2_{a1}} & \boldsymbol{\sigma_{a12}} \\ \boldsymbol{\sigma_{a12}} & \boldsymbol{\sigma^2_{a2}} \end{bmatrix}; \boldsymbol{R} = \begin{bmatrix} \boldsymbol{\sigma^2_{e1}} & \boldsymbol{\sigma_{e12}} \\ \boldsymbol{\sigma_{e12}} & \boldsymbol{\sigma^2_{e2}} \end{bmatrix} \tag{5}$$

where $\boldsymbol{G}$ and $\boldsymbol{R}$ are the additive and residual covariance matrices of order 2 × 2, $\boldsymbol{\sigma^2_{a1}}$, $\boldsymbol{\sigma^2_{a2}}$ are the additive genetic variances for Trait 1 and Trait 2, $\boldsymbol{\sigma_{a12}}$ is the covariance for the two traits, $\boldsymbol{\sigma^2_{e1}}$, $\boldsymbol{\sigma^2_{e2}}$ are the residual variances for Trait 1 and Trait 2, and $\boldsymbol{\sigma_{e12}}$ is the residual (co)variance for the traits.

Across-sex bivariate model

$$\begin{bmatrix} \boldsymbol{y_B} \\ \boldsymbol{y_C} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_B} & \emptyset \\ \emptyset & \boldsymbol{X_C} \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta_B} \\ \boldsymbol{\beta_C} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_B} & \emptyset \\ \emptyset & \boldsymbol{Z_C} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_B} \\ \boldsymbol{a_C} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_B} \\ \boldsymbol{e_C} \end{bmatrix} \tag{6}$$

All parameters in Eqn 3 have been described in Eqn 1. Subscripts B and C here are parameters relative to traits measured either in bulls (B) or in cows (C) for each breed. The assumptions of the structure of (co)variance for bivariate model were as follows:

$$\boldsymbol{G} = \begin{bmatrix} \boldsymbol{\sigma^2_{aB}} & \boldsymbol{\sigma_{aBC}} \\ \boldsymbol{\sigma_{aBC}} & \boldsymbol{\sigma^2_{aC}} \end{bmatrix}; \boldsymbol{R} = \begin{bmatrix} \boldsymbol{\sigma^2_{eB}} & 0 \\ 0 & \boldsymbol{\sigma^2_{eC}} \end{bmatrix} \tag{7}$$

where $\boldsymbol{G}$ and $\boldsymbol{R}$ are the additive and residual covariance matrix of order 2 × 2 (bull and cow), $\boldsymbol{\sigma^2_{aB}}$, and $\boldsymbol{\sigma^2_{aC}}$ are respectively, the additive genetic variances for the bull and cow, $\boldsymbol{\sigma_{aBC}}$ is the

covariance between the two sexes, σ^2_{eB} and σ^2_{eC} are the residual (co)variances for the bull and cow traits respectively. It is assumed that there is no residual covariance between the two sexes.

The fixed effects included in the model were specific for each trait and were deemed significant for the phenotypic variations observed (Table 2). The contemporary group (CG) effect was relevant for most traits. The CG represents cohort of animals born in the same year and raised together under the same management conditions. Information about CG has been described in detail by Barwick *et al*. (2009), Burns *et al*. (2013) and Johnston *et al*. (2014*b*). In BB, there were 58 levels for males and 78 levels for females in terms of CG. In TC, there were 46 levels for males and 74 levels for females in terms of CG. The laboratory assay batch was an important aspect of the enzyme-linked immunosorbent assay (ELISA; Moore *et al.* 1995) used to measure IGF1 (in BB there were 51 batches; in TC, 38 batches). Age of dam and the age of the animal at the time of trait recording were considered and included in the model as linear covariates when significant.

Posterior means and standard deviations for (co)variance components, heritabilities and genetic correlations were obtained using the POSTGIBBSF90 (Misztal *et al.* 2002). The analysis consisted of a single chain of 100 000 cycles discarding the first 20 000 cycles, taking a sample at every 50 iterations to obtain the parameters. The standard error of heritability estimates and genomic correlations were obtained using the OPTION se_covar_function of the POSTGIBBSF90 program (Misztal *et al.* 2002).

Table 2. Fixed effects included in the models for the analyses
CG; contemporary group; Batch, the batch of the IGF1 assay; AOD, age of dam; Age, age of the animal when measured; PC1, principal component 1; PC2, principal component 2 (PC1 and 2 are based on overall genotypes subject to a principal-component analyses)

Trait	Fixed effects					
	CG	Batch	AOD	Age	PC1	PC2
			Brahman			
AGECL	X					
PPAI	X					
IGF1c	X			X		
DC1	X					
DC5	X					
AFC	X					
IGF1b		X	X			
MAS	X			X		
MOT	X			X		
PNS	X			X		
SC12	X			X		
SC18	X					
SC24	X			X		
			Tropical Composites			
AGECL	X				X	X
PPAI	X				X	X
IGF1c	X			X	X	X
DC1	X				X	X
DC5	X				X	X
AFC	X				X	X
IGF1b		X	X		X	X
MAS	X			X	X	X
MOT	X			X	X	X
PNS	X			X	X	X
SC12	X			X	X	X
SC18	X				X	X
SC24	X			X	X	X

Results

Heritability estimates

The estimates of heritability and their corresponding standard errors for both single- and multi-trait models are presented in Table 3. The estimates for BB cows ranged from low to moderate for both models. Days to calving at the first calving opportunity (DC1) had the lowest heritability for both single-trait (0.07 ± 0.04) and multi-trait (0.17 ± 0.05) models, while AGECL had the highest estimates for both models (single-trait: 0.56 ± 0.08; multi-trait: 0.57 ± 0.08). For TC cows, the estimates of heritability ranged from low to moderate for single-trait models and from low to high for multi-trait models. DC1 had the lowest heritability for both single-trait (0.04 ± 0.03) and multi-trait (0.12 ± 0.03) models, while AGECL had a moderate estimate for the single-trait (0.46 ± 0.08) and a high estimate for the multi-trait (0.69 ± 0.02) model. For BB and TC bulls, the heritability estimates in most cases followed a similar pattern, with the estimates ranging from low to high in both populations. For the single-trait models, sperm motility (MOT) had the lowest heritability estimate in BB (0.09 ± 0.05) and TC (0.09 ± 0.05), while SC24 had the highest estimates in both breeds (0.62 ± 0.07 in BB and 0.62 ± 0.08 in TC). For multi-trait analysis, again SC24 had the highest estimates of heritability in both breeds (0.64 ± 0.06 in BB and 0.69 ± 0.07 in TC), while MOT had the lowest estimate in BB (0.09 ± 0.02) and sperm mass activity (MAS) had the lowest estimate in TC

Table 3. Heritability estimates and standard error for cow and bull fertility traits in Brahman and Tropical Composite
BB, Brahman; TC, Tropical Composite; h^2, heritability estimate

Trait	BB				TC			
	Single-trait model		Multi-trait model		Single-trait model		Multi-trait model	
	h^2	s.e.	h^2	s.e.	h^2	s.e.	h^2	s.e.
				Female traits				
IGF1c	0.46	0.08	0.44	0.08	0.42	0.09	0.57	0.05
AGECL	0.56	0.08	0.57	0.08	0.46	0.08	0.69	0.02
PPAI	0.42	0.10	0.43	0.09	0.27	0.09	0.63	0.03
AFC	0.15	0.06	0.21	0.06	0.06	0.05	0.14	0.04
DC1	0.07	0.04	0.17	0.05	0.04	0.03	0.12	0.03
DC5	0.31	0.09	0.35	0.08	0.07	0.05	0.31	0.04
				Male traits				
IGF1b	0.43	0.07	0.51	0.08	0.48	0.07	0.53	0.01
MAS	0.15	0.06	0.14	0.04	0.06	0.04	0.18	0.06
MOT	0.09	0.05	0.09	0.02	0.09	0.05	0.22	0.06
PNS	0.35	0.07	0.40	0.07	0.31	0.08	0.34	0.07
SC12	0.60	0.07	0.62	0.07	0.59	0.08	0.61	0.07
SC18	0.61	0.06	0.63	0.06	0.62	0.07	0.64	0.07
SC24	0.62	0.07	0.64	0.06	0.62	0.08	0.69	0.07

(0.18 ± 0.06). Generally, heritability estimates from the multi-trait analysis were higher than the estimates from a single-trait models and were usually accompanied by lower standard errors.

Genomic correlations: cow-fertility traits

Genetic correlation (bivariate and multivariate) among cow-fertility phenotypes for both BB and TC are presented in Table 4. In general, a range of strong positive and negative genetic correlations was recorded between the studied traits for both breeds. Given the low heritabilities of age at first calving (AFC) and DC1 in both breeds, all genetic correlation estimates with these traits had large standard errors. The magnitude of the errors was reduced in the multi-trait model.

For BB cows, the strongest genetic correlation was observed between AGECL and DC1 for both bivariate (BB: 0.76 ± 0.20) and multivariate (BB: 0.59 ± 0.17) model. However, for TC cow, the strongest correlation was observed between PPAI and DC5 (TC: 0.89 ± 0.14) for bivariate and AGECL and PPAI (TC: 0.87 ± 0.05) for multi-trait model.

Genomic correlation: bull fertility

Genetic correlation (bivariate and multivariate) among bull fertility phenotypes for both BB and TC breeds are presented in Table 5. Generally, the estimates of genetic correlation were all positive in both genotypes for both models, indicating a lack of genetic antagonism among the studied traits. A notable

Table 4. Genetic correlations across cow fertility traits for the bivariate models (below diagonal) and the multi-trait models (above diagonal) in Brahman and Tropical Composites

Standard error (s.e.) in parentheses. BB, Brahman; TC, Tropical Composites; bold indicates an estimate with a s.e. less than 1/2 the size of the correlation

Trait	IGF1c	AGECL	PPAI	AFC	DC1	DC5
			BB cow			
IGF1c		–0.55 (0.11)	–0.30 (0.16)	–0.51(0.18)	0.03 (0.19)	–0.36 (0.17)
AGECL	–0.53 (0.12)		0.19 (0.16)	0.12 (0.18)	0.59 (0.17)	0.45 (0.15)
PPAI	–0.22 (0.17)	0.20 (0.16)		0.11 (0.21)	0.27 (0.20)	0.55 (0.19)
AFC	–0.60 (0.12)	0.17 (0.23)	0.23 (0.26)		0.11 (0.22)	–0.10 (0.20)
DC1	–0.26 (0.40)	0.76 (0.20)	0.37 (0.38)	0.25 (0.49)		0.54 (0.16)
DC5	–0.27 (0.19)	0.41 (0.17)	0.65 (0.25)	–0.30 (0.36)	0.78 (0.31)	
			TC cow			
IGF1c		–0.68 (0.06)	–0.54 (0.08)	–0.66 (0.18)	–0.63 (0.13)	–0.53 (0.10)
AGECL	–0.43 (0.15)		0.87 (0.05)	0.53 (0.14)	0.50 (0.13)	0.55 (0.10)
PPAI	–0.24 (0.23)	0.74 (0.13)		0.53 (0.10)	0.69 (0.08)	0.76 (0.08)
AFC	–0.42 (0.38)	0.57 (0.21)	0.53 (0.38)		0.41 (0.21)	0.24 (0.19)
DC1	–0.60 (0.33)	0.47 (0.26)	0.82 (0.20)	0.54 (0.38)		0.60 (0.12)
DC5	–0.55 (0.24)	0.30 (0.28)	0.89 (0.14)	–0.52 (0.45)	0.29 (0.49)	

Table 5. Genetic correlations across bull fertility traits for the bivariate models (below diagonal) and the multi-trait models (above diagonal) in Brahman and Tropical Composites

Standard error (s.e.) in parentheses. BB, Brahman; TC, Tropical Composites; bold indicates an estimate with a s.e. less than 1/2 the size of the correlation

Trait	IGF1b	MAS	MOT	PNS	SC12	SC18	SC24
				BB bull			
IGF1b		0.26 (0.17)	**0.51 (0.11)**	0.27 (0.14)	**0.55 (0.09)**	**0.38 (0.10)**	0.22 (0.11)
MAS	0.14 (0.26)		**0.70 (0.12)**	**0.67 (0.13)**	**0.27 (0.14)**	**0.57 (0.11)**	**0.54 (0.12)**
MOT	0.33 (0.27)	**0.77 (0.20)**		**0.79 (0.07)**	0.10 (0.13)	0.24 (0.12)	**0.27 (0.11)**
PNS	0.25 (0.17)	**0.81 (0.18)**	**0.79 (0.19)**		0.12 (0.13)	0.21 (0.11)	0.13 (0.12)
SC12	**0.54 (0.10)**	0.35 (0.23)	0.15 (0.27)	0.02 (0.15)		**0.86 (0.03)**	**0.75 (0.05)**
SC18	**0.37 (0.11)**	**0.55 (0.16)**	0.28 (0.25)	0.20 (0.13)	**0.89 (0.05)**		**0.93 (0.02)**
SC24	**0.23 (0.12)**	**0.59 (0.17)**	0.31 (0.26)	0.12 (0.14)	**0.83 (0.06)**	**0.97 (0.02)**	
				TC bull			
IGF1b		**0.69 (0.03)**	**0.88 (0.04)**	**0.57 (0.14)**	**0.38 (0.15)**	0.26 (0.16)	0.14 (0.16)
MAS	**0.51 (0.31)**		**0.92 (0.04)**	**0.59 (0.16)**	0.34 (0.17)	0.33 (0.17)	0.25 (0.16)
MOT	0.13 (0.28)	**0.91 (0.22)**		**0.57 (0.15)**	0.11 (0.17)	0.17 (0.17)	0.17 (0.17)
PNS	0.20 (0.17)	**0.82 (0.20)**	**0.71 (0.24)**		0.25 (0.15)	0.22 (0.14)	0.19 (0.14)
SC12	0.11 (0.13)	**0.73 (0.26)**	0.47 (0.36)	**0.33 (0.15)**		**0.87 (0.03)**	**0.75 (0.05)**
SC18	0.04 (0.12)	0.58 (0.32)	0.40 (0.31)	0.31 (0.16)	**0.89 (0.04)**		**0.95 (0.01)**
SC24	–0.03(0.13)	0.51 (0.34)	0.45 (0.28)	0.25 (0.15)	**0.77 (0.06)**	**0.97 (0.01)**	

exception was the correlation between IGF1b and SC24 (–0.03 ± 0.33) for the bivariate model. However, these estimates were positive for all traits when analysed using a multi-trait model. The strongest genetic correlation was observed between SC18 and SC24 for both bivariate (BB: 0.97 ± 0.02; TC: 0.97 ± 0.01) and multivariate (BB: 0.93 ± 0.02; TC: 0.95 ± 0.01) models.

Across-sex genomic correlations

Estimated genetic correlations (bivariate) between cow and bull traits for BB and TC are presented in Table 6. Some standard errors for these correlations are larger than the genomic correlation itself, implying that the correlations are not significant.

For BB, IGF1b was favourably correlated with all the female fertility phenotypes, with the strongest negative correlation recorded between IGF1b and AGECL (–0.65 ± 0.13) and the lowest observed between IGF1b and DC5 (–0.02 ± 0.20). Semen-quality traits (MAS, MOT and percentage normal sperm (PNS)) had a negative correlation with PPAI, with estimates of –0.81 ± 0.30, –0.75 ± 0.39 and –0.50 ± 0.19 respectively. SC12, SC18 and SC12 had a moderate negative genetic correlation with AGECL (–0.32 ± 0.15) and (–0.36 ± 0.12), (–0.25 ± 0.12) respectively. Moderate negative correlations were also observed between SC12 and DC1 (–0.32 ± 0.30) as well as SC12 and DC1 (–0.21 ± 0.31) respectively.

Similar to the result observed for IGF1b in BB, this trait was also favourably correlated with AGECL (–0.55 ± 0.14) and PPAI (–0.17 ± 0.22) in TC, with the strongest estimate being recorded for DC5 (–0.94 ± 0.13). PNS had a strong negative correlation with DC1 (–0.60 ± 0.28) and a moderate negative correlation with AFC (–0.24 ± 0.28). A moderate genetic correlation was also recorded between SC12 and AGECL (–0.26 ± 0.13). SC12 had a negative correlation with DC1 (–0.06 ± 0.58).

Discussion

The objective of most cattle breeding programs is to maximise genetic gain for traits that are of economic relevance to beef production. In part, the success of these breeding programs depends on the accuracies with which the genetic parameters are estimated (Wellmann and Bennewitz 2019). Nowadays, many traits are important to cattle breeders. Producers are often interested in a combined selection objective that uses information from many traits to form a total merit index (Cole and VanRaden 2018). Genetic parameters estimated from a multi-trait model are regarded as more accurate because their estimates utilise additional genomic information and use the complex covariance structure among traits (Analla *et al.* 1995; Zhang *et al.* 2018). Moreover, these multi-trait models are expected to produce higher estimates of heritability than single-trait models, due to the additional information. For most traits, we observed higher heritabilities in the multi-trait model. This difference between single- and multi-trait analyses was more evident in TC than in BB. Perhaps, this could be partly explained by the higher genetic variation that composite breeds exhibit than their founders (Rasali *et al.* 2006). The increase in the proportion of segregating alleles in composite breeds could be advantageous and this information could have been captured in the multi-trait model. In either case, the use of multi-trait models is likely to be advantageous.

Heritability estimates for all phenotypes reported herein, in both BB and TC breeds, are in line with previous estimates for similar traits from single-trait models with either pedigree (Corbet *et al.* 2009; Corbet *et al.* 2013; Johnston *et al.* 2014*b*; Johnston and Moore 2019) or genomic information (Raidan *et al.* 2019; Fortes *et al.* 2020). Estimated heritabilities imply that genetic improvement can be made through selection for these fertility traits. However, some of the studied traits will respond to selection faster than others. The lower heritability estimates for calving traits, such as AFC or DC1, or semen-quality traits, such as MAS and MOT, imply that these traits are not going to respond as fast as AGECL or IGF1 in selective breeding. Probably, the environmental effects are higher for these traits with lower heritabilities and it may be efficient to explore the correlated response via other fertility traits to achieve faster genetic progress (Raidan *et al.* 2019). Most importantly, MAS and MOT were measured here as visual scores and there is a degree of subjectiveness to these traits.

Table 6. Genomic correlations estimated between cow and bull fertility traits in Brahman and Tropical Composite cattle
Standard error (s.e. in parentheses). BB, Brahman; TC, Tropical Composite; bold indicates an estimate with a s.e. less than 1/2 the size of the correlation

Trait	IGF1b	MAS	MOT	PNS	SC12	SC18	SC24
			BB				
IGF1c	**0.86 (0.11)**	0.26 (0.27)	–0.41 (0.44)	0.10 (0.17)	**0.39 (0.13)**	**0.46 (0.13)**	**0.32 (0.13)**
AGECL	**–0.65 (0.13)**	–0.20 (0.27)	–0.37 (0.41)	0.00 (0.17)	**–0.32 (0.15)**	**–0.36 (0.12)**	–0.24 (0.12)
PPAI	–0.34 (0.18)	**–0.81 (0.30)**	–0.75 (0.39)	**–0.50 (0.19)**	–0.12 (0.15)	–0.12 (0.15)	–0.07 (0.15)
AFC	–0.22 (0.29)	0.65 (0.49)	0.66 (0.84)	0.07 (0.29)	0.20 (0.21)	0.14 (0.21)	0.15 (0.21)
DC1	–0.30 (0.21)	0.56 (0.44)	–0.31 (0.55)	–0.01 (0.56)	–0.32 (0.30)	–0.21 (0.31)	–0.04 (0.30)
DC5	–0.02 (0.20)	–0.23 (0.33)	0.01 (0.51)	–0.02 (0.22)	0.20 (0.16)	0.21 (0.15)	0.24 (0.16)
			TC				
IGF1c	**0.93 (0.11)**	0.14 (0.63)	0.20 (0.43)	–0.04 (0.22)	0.17 (0.14)	–0.01 (0.14)	–0.08 (0.13)
AGECL	**–0.55 (0.14)**	0.44 (0.66)	0.43 (0.44)	0.04 (0.21)	**–0.26 (0.12)**	–0.10 (0.13)	–0.01 (0.12)
PPAI	–0.17 (0.22)	0.13 (0.82)	0.74 (0.59)	0.20 (0.28)	0.10 (0.20)	0.26 (0.19)	0.29 (0.17)
AFC	0.44 (0.33)	–0.14 (0.60)	0.28 (0.56)	–0.24 (0.28)	–0.43 (0.35)	0.13 (0.46)	0.32 (0.30)
DC1	0.10 (0.50)	–0.31 (0.69)	–0.20 (0.72)	**–0.60 (0.28)**	–0.06 (0.58)	0.20 (0.50)	0.45 (0.37)
DC5	**–0.94 (0.13)**	0.11 (0.53)	–0.25 (0.46)	–0.46 (0.43)	–0.21 (0.48)	0.19 (0.36)	0.58 (0.30)

Assessment of semen motility by using computer-assisted semen analysis could remove some of the human error and perhaps provide a more heritable trait for selection.

Several studies have suggested measuring the concentration of IGF1 as an indicator for cow reproductive potential (Taylor *et al.* 2004; Velazquez *et al.* 2008). From our results, IGF1c is favourably correlated with most of the female fertility traits studied in both breeds, indicating its multiple roles in reproduction. Therefore, the increased level of IGF1 concentration in the blood could be an indication for cows with the potential to reach puberty early, conceive, calve, and also re-breed early for the next calving season. These favourable correlations between IGF1 and several other fertility traits such as age at first ovulation, conception rate to first service, age at first calving, calving rate, and postpartum anoestrus interval have been reported in several studies (Yilmaz *et al.* 2004, 2006; Falkenberg *et al.* 2008; Velazquez *et al.* 2008). Late onset of puberty is an important component of the reduced lifetime productivity observed in tropically adapted beef (Lesmeister *et al.* 1973; Johnston *et al.* 2014*a*). This explains the estimated positive genetic correlation between AGECL and other female fertility traits in the two breeds. Therefore, genetic selection for increased concentration of IGF1 measured in heifers at ~18 months of age might contribute to early puberty and improve lifetime reproductive rates in Brahman cattle. IGF1 is highly influenced by nutritional status, and so proper nutritional programming will be required to accelerate puberty in heifers (Zulu *et al.* 2002; Alves *et al.* 2017).

Similar to our study, Corbet *et al*. (2013) found no genetic antagonism between bull fertility phenotypes. Regardless, it might be difficult to recommend a single phenotype as a reliable indicator of bull fertility. For instance, if we select bulls on the basis of sperm morphology and other assessments are neglected (i.e. assessment such as physical health that is required for mating in extensive beef farms), then the required genetic progress might not be achieved. Thus, various measurements of bull fertility as obtainable using the bull breeding soundness evaluation (BBSE) are important for sensible breeding decisions (Fordyce *et al.* 2006). Selecting bulls by using multiple indicator traits provides a better chance of improving the overall fertility of the herd.

Genetic improvement programs for female fertility in beef cattle has been hindered by the difficulty of collecting accurate fertility-related phenotypes needed to improve the predictive ability of genomic selection models (Tiezzi and Maltecca 2011). Some nucleus herds (or research stations) are capable of collecting very detailed, accurate and sometimes expensive fertility phenotypes (Schatz *et al.* 2010). However, the size from these nucleus herds tends to be relatively small and sample size affects the predictive power of genomic selection. In contrast, commercial herds might be a source of large datasets, with the disadvantage that phenotypes may be less precise (Hayes *et al.* 2019*a*). Traits that are directly related to female fertility are not feasible to measure on a large number of cattle in extensively managed herds, which characterise the typical production system of tropically adapted beef cattle in Australia and other countries (Hayes *et al.* 2019*b*). This challenge, as well as the complexity of the production systems faced by animal breeders, point to a potential solution, namely, focussing on favourably correlated traits (i.e. traits that are easy to measure early in life) that together act as a fertility index (Brito Lopes *et al.* 2016). Since bull fertility phenotypes are heritable and less expensive to measure than lifetime female fertility data, identification of traits in male that have a high genetic correlation with female fertility could significantly aid the improvement of reproductive performance of tropically adapted cows (Jeyaruban and Johnston 2017). Moreover, high selection intensity is achievable in males, allowing few genetically superior bulls to contribute to a large percentage of the genetic make-up of the next generation (Martinez-Velazquez *et al.* 2003; Weigel 2017). From the present study, IGF1 measured in bull favourably correlated with early fertility phenotypes in the BB breed. These favourable across-sex correlations have been reported in previous studies investigating the correlation between male and female reproductive traits such as age at puberty, pregnancy rate, age at first calving, days to calving and calving rate (Yilmaz *et al.* 2006; Johnston *et al.* 2014*b*). This implies that selection for concentration of IGFI as early as at 6 months in bulls might improve reproductive performance in BB cattle. Notwithstanding, it will be important to investigate the cost of measuring IGF1 in bulls on herd profitability before recommending this practice. Even if selection decision is made at this early age, assessment of bulls through BBSE will still be required to ensure that the selected bulls are indeed capable of breeding, because (a) the correlation between IGF1 and BBSE success is far from perfect, and (b) several circumstances and environmental factors, including disease, might affect bull fertility in the timespan between 6 and 24 months of age (i.e. between IGF1 measurement and the first mating season of a bull).

However, in TC breed, IGF1b was favourably correlated only with AGECL, PPAI and DC5, but not with AFC and DC1. These traits (AFC and DC1) were correlated only with PNS in this breed. Nevertheless, the estimates are in tandem with the findings of Johnston *et al*. (2014*b*), who reported a favourable correlation between IGF1b and AGECL in TC breed. The authors also found PNS to be genetically correlated with most early female fertility phenotypes. Therefore, IGF1b and PNS could be useful as indirect selection criteria for improving female reproduction in TC breed.

Of note from our study is the difference in the period of measurement of IGF1 across the sexes. In cow, IGF1 was measured at 18 months, whereas the measurement was observed in bull as early as at 6 months of age. There is considerable evidence that IGF1 concentration varies with age (Abribat *et al.* 1990; Larnkjær *et al.* 2012; Michaelsen 2013). As we are not certain on the implication of measuring IGF1 early on female fertility, further research is required to firmly establish this trait as a biomarker for pubertal development that might be useful for a selection decision for cattle breeding. The big gain from genomic selection is the ability to estimate genomic breeding values at birth or even at embryo for both male and female calves quite accurately without the need for the animal's own performance record, as long as there is a sizable and relevant reference population (Hayes and Goddard

2010; Taylor 2014; Hayes *et al.* 2019*b*). These genomic estimated breeding values may allow breeders to make an accurate selection decision before the breeding season and assist with stoking decisions.

Findings from Johnston *et al*. (2014*b*) have shown that SC is a modest predictor of age at puberty in tropically adapted beef cattle. In the present study, SC18 better reflected puberty in BB, while the estimate could be as short as 12 months in TC. This is not surprising as Brahman are typically late pubertal when compared with Bos *taurus* breeds (Lunstra and Cundiff 2003; Lopez *et al.* 2006). Furthermore, SC measured at 12 and 18 months in Brahman was also found to be a moderate predictor for DC1. However, in TC, the estimate of genetic correlation between SC12 and DC1 was negative, although not very large, indicating that selection for SC12 had a favourable influence on DC1. The estimate becomes positive at 18 and 24 months, albeit with a large standard error. These results correspond with the findings of Jeyaruban and Johnston (2017), where moderate genetic correlations were observed between SC measured between 300 and 700 days of age and DC1 for BB breed. The authors also reported a negative estimate for Santa Gertrudis cattle, a stabilised composite with 50% to 30% *Bos indicus* content (Hayes *et al.* 2019*b*). This estimate is consistent with what we observed for TC. Differences in results for SC12, SC18 and SC24 are expected, especially when we consider the breed differences in pubertal development between BB and TC. BB cattle are late pubertal and so it is expected that we observe a lot of variation in SC in the early measurements (Lunstra *et al.* 1978; Lunstra and Cundiff 2003). As we progress to 24 months of age, most bulls have already passed puberty, which means there is less variation in the trait and SC24 might not be a good indicator of female fertility traits anymore. In TC, at 12 months, many bulls have reached pubertal and are also producing sperm, which is different from the BB (Corbet *et al.* 2013). Therefore, depending on breed, different ages for SC measurement are required to better capture these favourable correlations with female fertility traits.

Conclusions

The heritability estimates and genomic correlations from the present study generally support and confirmed the earlier estimates from pedigree analyses. Within sex, IGF1c might be used as a predictor of female fertility and BBSE traits might be combined to accurately predict bull fertility. Across sex, IGF1b might be a useful indicator for early-in-life female fertility traits in Brahmans, while both IGF1b and PNS could be indicator traits for female fertility in TC. The findings from this study suggest that selection for fertility traits will have a favourable correlated response to selection within and across sex.

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Conflicts of interests

Marina R. S. Fortes is an Associate Editor of Animal Production Science but was blinded from the peer-review process for this paper. All other authors declare no conflicts of interest.

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