# Multi-trait assessment of early-in-life female, male and genomic measures for use in genetic selection to improve female reproductive performance of Brahman cattle

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**Abstract.** Early-in-life female and male measures with potential to be practical genetic indicators were chosen from earlier analyses and examined together with genomic measures for multi-trait use to improve female reproduction of Brahman cattle. Combinations of measures were evaluated on the genetic gains expected from selection of sires and dams for each of age at puberty (*AGECL*, i.e. first observation of a *corpus luteum*), lactation anoestrous interval in 3-year-old cows (*LAI*), and lifetime annual weaning rate (*LAWR*, i.e. the weaning rate of cows based on the number of annual matings they experienced over six possible matings). Selection was on an index of comparable records for each combination. Selection intensities were less than theoretically possible but assumed a concerted selection effort was able to be made across the Brahman breed. The results suggested that substantial genetic gains could be possible but need to be confirmed in other data. The estimated increase in *LAWR* in 10 years, for combinations without or with genomic measures, ranged from 8 to 12 calves weaned per 100 cows from selection of sires, and from 12 to 15 calves weaned per 100 cows from selection of sires and dams. Corresponding reductions in *LAI* were 60–103 days or 94–136 days, and those for *AGECL* were 95–125 or 141–176 days, respectively. Coat score (a measure of the sleekness or woolliness of the coat) and hip height in females, and preputial eversion and liveweight in males, were measures that may warrant wider recording for Brahman female reproduction genetic evaluation. Pregnancy-test outcomes from Matings 1 and 2 also should be recorded. Percentage normal sperm may be important to record for reducing *LAI* and scrotal size and serum insulin-like growth factor-I concentration in heifers at 18 months for reducing *AGECL*. Use of a genomic estimated breeding value (EBV) in combination with other measures added to genetic gains, especially at genomic EBV accuracies of 40%. Accuracies of genomic EBVs needed to approach 60% for the genomic EBV to be the most important contributor to gains in the combinations of measures studied.

**Additional keywords:** accuracy, tropical, anoestrus, genetic evaluation, genetic gain, lifetime, puberty, weaning rate.

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## Introduction

Low reproductive performance limits the profitability of beef production in tropical and subtropical northern Australia (McCosker *et al.* 2010), especially in the Brahman, a major breed of these environments (Entwistle 1983; Chenoweth 1994; Burrow *et al.* 2003). Weaning rates of 62%, 50% and 60% were recently reported for Brahmans per female exposed at their first, second, and average of their first six annual matings, respectively (Johnston *et al.* 2014*a*). Recording selection criteria in the harsh, very extensive environments of northern Australia is difficult, so the criteria to be recorded must be very practical.

Genomic measures are among those with potential to be used, because DNA samples are quite readily obtained and processing can occur remotely.

The genetics of female reproduction were examined, along with other traits, in an experiment in northern Australia with tropical genotypes. Bivariate estimates of genetic relationships from that experiment have been reported for female puberty (Johnston *et al.* 2009, 2014*b*; Hawken *et al.* 2012), early and lifetime female reproduction (Johnston *et al.* 2014*a*, 2014*b*), cow growth and body composition (Wolcott *et al.* 2014*a*, 2014*b*), adaptation (Prayaga *et al.* 2009; Wolcott *et al.* 2014*b*), and early

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heifer performance (Barwick *et al.* 2009; Wolcott *et al.* 2014*c*). There are related reports on male measures (Burns *et al.* 2013; Corbet *et al.* 2013; Johnston *et al.* 2014*b*) and genomic measures (Zhang *et al.* 2014) as predictors of female performance.

The present study aimed to take the potentially most practical and genetically useful measures identified in the earlier bivariate analyses and consider their multi-trait use as selection criteria to improve female reproduction in the Brahman. The female reproductive traits (italicised all throughout) analysed were the age at which a *corpus luteum* was first observed (*AGECL*), referred to as age at puberty, lactation anoestrous interval (*LAI*) and lifetime annual weaning rate (*LAWR*), these being important reproductive traits of tropical cattle (Frisch *et al.* 1987; Johnston *et al.* 2014*a*) and other livestock (Purvis *et al.* 1987). Combinations of female, male and genomic measures were evaluated for their potential to be used in selection to improve each of the traits, based on estimates of the expected genetic gain. Resulting accuracies for selecting sires and dams are also presented.

## Materials and methods
### Animals and environments

All traits and measures were examined in Brahmans in environments typical for the breed in northern Australia (Barwick *et al.* 2009; Johnston *et al.* 2014*a*). Brahman females in the experiment were the progeny of 54 sires. Management was according to regional practice. Females were joined to calve first at 3 years and were culled for reproductive failure if they failed to wean a calf in any two consecutive years. Male measures were recorded on young bull progeny of the same cows and these animals were the progeny of a further 60 Brahman sires. Environment and management details for these progeny were given by Burns *et al.* (2013) and Corbet *et al.* (2013).

### Traits and measures
#### Reproduction traits

The traits and measures studied are shown in Table 1. Further details of the *AGECL*, *LAI* and *LAWR* traits were given by Johnston *et al.* (2009, 2014*a*). Briefly, *LAI* was the anoestrous interval of lactating cows at their first opportunity to re-breed, assessed in 3-year olds. *LAWR* was the average weaning rate of cows based on the number of annual mating opportunities they experienced over their first six annual matings. *LAWR* aligns (over six age groups) with the weaning rate of a mixed-aged herd, which is commonly the reproduction trait of breeding objectives (Barwick and Henzell 2005). Others in cattle (Meyer *et al.* 1990) and sheep (Turner 1969; Purvis *et al.* 1987) have also defined reproductive success in relation to the number of mating exposures of females. *AGECL* affects the number of times a female can be bred, and thus, potentially, generation interval; while an extended anoestrus in re-breeding heifers has been considered a key limiter of tropical cattle reproduction (Frisch *et al.* 1987; Chenoweth 1994; Johnston *et al.* 2014*a*). In the same Brahman females as considered here, Johnston *et al.* (2014*a*, 2014*b*) found genetic correlations for *AGECL* with *LAI* and *LAWR* of 0.31 and –0.36, respectively, and a genetic correlation between *LAI* and *LAWR* of –0.62.

### Female and male measures

The measures studied were chosen from the original experiment by considering their heritability, consistency of genetic correlation with female reproduction, standard errors of estimates, and especially their practicality for industry recording. Some additional measures were included because of their perceived interest to industry. Measures studied generally had standard errors of genetic correlation estimates with female reproduction traits in the range 0.10–0.30. Female adaptive measures were from Prayaga *et al.* (2009) and Wolcott *et al.* (2014*b*), 18- and 24-month heifer measures from Barwick *et al.* (2009) and Wolcott *et al.* (2014*c*), and early mating measures from Johnston *et al.* (2014*a*, 2014*b*). Male non-semen and semen measures were from Corbet *et al.* (2013) and Johnston *et al.* (2014*b*). To aid the distinction between female and male measures, female measures are shown in italics throughout the paper. In total, 33 female or male measures were included for study, and these are described in Table 1.

### Genomic measures

Genomic estimated breeding values (EBVs) of 30%, 40% or 60% accuracy, based on genotyping of males, were assumed to be additional measures available for each of the female reproduction traits (Table 1). Zhang *et al.* (2014) reported genomic EBV accuracies of 30–40% for some related traits of cattle from the same experiment, and accuracies of the order of 60% have been reported in dairy cattle (VanRaden *et al.* 2009). Genomic EBVs were evaluated singly and in combination with other measures for use as selection criteria for each reproduction trait. Genomic EBVs of 40% accuracy for some other measures that were correlated with the reproduction traits were also considered, and were evaluated singly.

### Evaluation of measures

The basis for comparing measures was their ability to contribute to the genetic gain expected from selection individually for each of *AGECL*, *LAI* and *LAWR*. Combinations of measures were considered systematically. Direct selection for the traits was also considered. Expected genetic gain ($\Delta G / year$) was estimated from the four pathways of selection (sires to breed sires, dams to breed sires, sires to breed dams, dams to breed dams), following Rendel and Robertson (1950), i.e.

$$\Delta G/\text{year} = \frac{\sum i_j r_j \sigma_A}{\sum L_j},$$

where $i_j$, $r_j$ and $L_j$ are selection intensity, accuracy of selection and generation interval in the $j^{th}$ pathway, and $\sigma_A$ is the additive genetic standard deviation of the reproduction trait. The analyses systematically eliminated measures that contributed least to the estimated gain, while retaining all measures that were contributing at least 5% of the gain. Analyses of measures were conducted in blocks, approximately corresponding to the categories shown in Table 1, with retained measures being carried forward to be considered with other measures. This resulted, for example, in derivation of the best combinations (for genetic gain) of female measures, of male measures, of these in combination, and ultimately of these in combination with genomic measures.

**Table 1. Description of traits and measures**

Full descriptions of female reproductive traits are given by Johnston *et al*. (2009, 2014a), adaptive measures by Prayaga *et al*. (2009), 18 and 24 m measures by Barwick *et al*. (2009), Mating 1 and 2 measures by Johnston *et al*. (2014a) and male measures by Corbet *et al*. (2013)

| Trait and measure | Abbreviation[A] | Measurement age |
|---|---|---|
| *Female reproductive traits* | | |
| Age at puberty (first *corpus luteum*) (m) | *AGECL* | 25 months |
| Lactation anoestrous interval of 3-year-old cows (days) | *LAI* | 3.6 years |
| Lifetime annual weaning rate (calves weaned/cow)[B] | *LAWR* | 8.5 years |
| *Female adaptive measures* | | |
| Coat colour (lower score = lighter colour) | *COLOUR* | 9 months |
| Navel score (lower score = more pendulous) | *NAVEL* | 9 months |
| Rectal temperature (°C) | *TEMP13* | 13 months |
| Coat score (lower score = sleeker coat) | *COAT* | 12 months |
| *Female 18- and 24-month measures* | | |
| Liveweight (kg) at 18, 24 m | *LWT18, LWT24* | 18, 24 months |
| Hip height (cm) at 18, 24 m | *HH18, HH24* | 18, 24 months |
| Scan P8 fat depth (mm) at 18 m | *SFAT18* | 18 months |
| Scan eye muscle area (cm$^2$) at 18 m | *SEMA18* | 18 months |
| Serum IGF-I (ng/mL) at 18, 24 m | *IGF18, IGF24* | 18, 24 months |
| *Female Mating 1 and 2 measures* | | |
| Pregnant at Mating 1, 2 pregnancy test (yes/no) | *PREG1, PREG2* | 28, 40 months |
| Days to calving 1 (bull-in to 1st calving) (days) | *DC1* | 37 months |
| Weaned calf and pregnant at 2nd pregnancy test (yes/no) | *W1P2* | 40 months |
| *Male non-semen measures* | | |
| Serum inhibin (ng/mL) | IN | 4 months |
| Serum luteinising hormone (ng/mL) | LH | 4 months |
| Serum IGF-I (ng/mL) | IGF6 | 6 months |
| Flight time (s) | FT | 6 months |
| Rectal temperature (°C) | TEMP12 | 12 months |
| Scrotal circumference (cm) at 12, 18 m | SC12, SC18 | 12, 18 months |
| Liveweight (kg) at 15 m | LWT15 | 15 months |
| Hip height (cm) at 15 m | HH15 | 15 months |
| Scan P8 fat depth (mm) at 15 m | SFAT15 | 15 months |
| Scan eye muscle area (cm$^2$) | SEMA15 | 15 months |
| Body condition score | CS | 15 months |
| Sheath score | SHEATH | 18 months |
| Preputial eversion (mm) | EV | 18 months |
| *Male semen measures* | | |
| Sperm mass activity score | MASS | 18 months |
| Sperm progressive motility (%) | MOT | 18 months |
| Percent normal sperm (%) | PNS | 18 months |
| *Genomic measures* | | |
| Genomic EBV of 30, 40, or 60% accuracy from genotyping of males | GEN30, GEN40, GEN60 | 9 months |

[A]Female traits and measures are italicised, male measures are not.
[B]Based on the number of mating opportunities of the cow up to six possible matings.

Estimates of selection intensities and generation intervals were derived to be applicable to a Brahman breeding program as described below. This included simplifying assumptions, so care is needed in using the calculated estimates of genetic gains outside of their main purpose here of comparing the relativity of measures. Selection was assumed to be only for the individual female reproduction trait and no account was taken of rates of inbreeding (Bijma *et al*. 2001) or other possible contributors to long-term response (Bulmer 1971; Goddard 2009). A further difference was that selection on BLUP evaluations in practice would optimise selection across

ages (James 1987). The derived estimates of gains were adjusted to gains per 10 years for presentation and are best viewed as approximations of the selection gains in Brahmans that may be possible.

### Accuracies of selection

The MTIndex software of J. van der Werf was used to facilitate estimation of selection accuracies. Accuracies were estimated for individual selection pathways and summarised for each of sires and dams. For each combination of measures, the best linear

index $\mathbf{I} = \mathbf{bX}$ of the measures ($\mathbf{X}$) was evaluated. From selection index theory, $\mathbf{b} = \mathbf{P}^{-1}\,\mathbf{G}$, accuracy of $\mathbf{I}$ is $\sigma_I/\sigma_A$, $\mathbf{P}$ is the phenotypic variance–covariance matrix among the measures, $\mathbf{G}$ is the genetic covariance matrix relating the measures to the reproduction trait, and $\sigma_A$ is the additive genetic standard deviation of the reproduction trait.

### Records modelled

The same record types and numbers of records were assumed to be available for all measures. For female measures, records for selecting sires were a record on the dam and records on 20 female half-sibs. The same was assumed for selecting dams, but with the addition of their own record. For male measures (including for genomic measures, where genotyping was of males), records for selecting sires were their own record, a record on the sire (of the candidate) and records on 20 male half-sibs. The same male records were assumed for selecting dams, except for the absence of their own record.

### Genetic and phenotypic parameters

The $\mathbf{P}$ and $\mathbf{G}$ matrices used were based on estimates from Barwick *et al.* (2009), Johnston *et al.* (2009, 2014a, 2014b), Prayaga *et al.* (2009), Corbet *et al.* (2013) and Wolcott *et al.* (2014b, 2014c), and a small number of unreported estimates from the same analyses (M. L. Wolcott, pers. comm.). To help ensure positive definite matrices and minimise deviations from original bivariate estimates, smaller matrices were first constructed for blocks of measures. Measures and parameter values were then carried forward in subsequent analyses. For positive definiteness of matrices in analyses of *LAWR*, it was necessary to reduce genetic correlations of measures with *LAWR* to ~70% of their bivariate values. This reduction was not applied to genomic measures (i.e. accuracies of genomic EBVs were retained at their assumed levels), but was applied to genetic correlations with *LAWR* for all other measures. Final parameter estimates used for evaluating combinations of female, male and genomic measures for *LAWR* are shown in Appendix 1.

Phenotypic correlations between female and male measures were derived as $\sqrt{h_1^2} \cdot r_{A_{1,2}} \cdot \sqrt{h_2^2}$, assuming zero environmental correlations, where $h_1^2$ and $h_2^2$ are the heritabilities of the female and male measures and $r_{A_{1,2}}$ is the genetic correlation between them. Genomic EBVs for *AGECL*, *LAI* and *LAWR* had assumed heritabilities of 0.999 and genetic variances of $r^2 \cdot \sigma_{A_t}^2$, where $r$ is the genomic EBV accuracy and $\sigma_{A_t}^2$ is the additive genetic variance for the $t^{th}$ trait. Genetic correlations of genomic EBVs with other measures were derived as $r \cdot r_{A_k}$, from path coefficient theory, where $r_{A_k}$ is the genetic correlation of measure $k$ with the reproduction trait. Corresponding phenotypic correlations were derived as $r \cdot r_{A_k} \cdot \sqrt{h_k^2}$, assuming zero environmental correlations and genomic EBV heritabilities of unity. Where the genomic EBV examined was for a correlated measure $k$, its genetic variance was $r^2 \cdot \sigma_{A_k}^2$, genetic correlation with the reproductive trait was $r \cdot r_{A_k}$, and phenotypic correlation with the reproductive trait was $r \cdot r_{A_k} \cdot \sqrt{h_t^2}$, where $h_t^2$ is the heritability of the reproduction trait. For estimating genetic gains in *AGECL*, *LAI* and *LAWR*, genetic standard deviations used were 85.88 days, 72.37 days and 0.0877, respectively, from

Johnston *et al.* (2009, 2014a). Binary measures in the study of Johnston *et al.* (2014a) were analysed on both transformed and linear scales. The genetic standard deviations used for including *PREG1* and *PREG2* in indexes were from the linear model estimates of Johnston *et al.* (2014a), following Dempster and Lerner (1950).

### Selection intensities

Selection intensities were derived for a Brahman seedstock herd of 13 000 cows, assuming the use of artificial insemination (AI) in 12% of matings, each AI sire being used in 40 matings per year for 2 years, and each natural-service sire being used in 25 matings per year for 4 years. In this circumstance, the annual requirement for bulls was 40 AI sires and 460 natural-service sires, or 20 new AI sires and 115 new natural-service sires per year. AI sires were assumed to be used to breed sires and dams, and natural-service sires to breed dams. Assuming that ~4000 young bulls and ~4000 heifers survive to first mating and new sires come from 50% of those surviving, AI sires to breed sires were the top 20 of 2000 (1%; $i = 2.665$), and sires to breed dams were the top 135 of 2000 (6.75%; $i = 1.9345$). Dams to breed sires were the top 800 of 8000 (10%, assuming some selection across ages; $i = 1.755$). There was limited other opportunity for selection of dams with the calf-weaning rate modelled (i.e. 65%; Johnston *et al.* 2014a); dams to breed dams were the top 3800 of 4000 (95%; $i = 0.1086$). These selection intensities were used in estimating the expected genetic gains for comparing all combinations of measures. For the identified best combinations, expected gains were also calculated assuming no selection of dams.

### Generation intervals

Generation intervals were assessed as the average age of selected parents at the birth of progeny (Table 2). The age structure used was derived from Brahman seedstock industry data and included cow calving age groups that ranged from 3 to 13 years. For direct selection on *LAWR* (requiring outcomes from six matings), selected cows at the birth of progeny had a minimum age of 10 years if they calved first at 3 years. The corresponding minimum cow age was 6 years for selection on the total calves weaned from Matings 1 and 2 (Johnston *et al.* 2014a), 5 years for selection on *LAI*, *PREG2* or *W1P2*, 4 years for selection on *PREG1* or *DC1*, and 3 years for selection on any of the other measures of Table 1. For selection on combinations of measures, the minimum cow age was that applying for the last available measure of the combination. Generation interval results were re-derived assuming cows calved first at 2 years, to provide an upper limit to the genetic gain estimates. Where cows calved first at 2 years, minimum cow ages were reduced by 1 year (Table 2).

The average age of selected cows at the birth of progeny was determined from the age distributions applying for different minimum cow ages. The average age of selected bulls was determined from their minimum age at the birth of progeny and their assumed usage. AI sires were assumed to have been progeny tested for 2 years before being used with equal probability over 2 years. Natural-service sires were assumed used with equal probability over 4 years. For selection to

breed dams, both AI (12%) and natural-service (88%) sires were assumed to be used.

## Results

The accuracies of selection of sires and dams and estimated genetic gains in *AGECL*, *LAI* and *LAWR* are presented in Tables 3–8. For each trait, the results for selection on combinations of measures are presented first (Tables 3, 5, 7), followed by the results for selection on individual measures (Tables 4, 6, 8).

### Age at puberty

The best combination of female measures for selecting to reduce *AGECL*, when Mating 1 and 2 measures were unavailable, was *COAT* and *IGF18*, *COAT* being more important to the resulting genetic gain than *IGF18* (Table 3). When male measures other than semen measures were those available, IGF6, EV and SC12, in order of importance, were the best combination. Using these male measures did not reduce *AGECL* as much as using the female measures (116.2 cf. 140.1 days in 10 years), but had the larger effect (93.4 cf. 89.3 days) where only sire selection was practiced. Where both female and male measures were available, the best combination was *COAT*, SC12 and *IGF18*, irrespective of whether semen measures were available, and the estimated reduction was 151.2 days. If hormone measures were unavailable, the best combination was *COAT* and SC12 and the estimated reduction was 141.0 days. Adding either *PREG1* or PNS added only a small amount (less than 5%) to the expected genetic gain, but accuracies increased, particularly with the addition of *PREG1*. Where a genomic EBV for *AGECL* of accuracy 30%, 40% or 60% (i.e. GEN30, GEN40 or GEN60) was available, the best combination was unchanged if GEN30 was available, GEN40 replaced SC12 as the second-most important measure when it was available, and GEN60 was the most important measure, in combination with *COAT* and *IGF18*, when it was available. If hormone measures were unavailable, GEN30 replaced *IGF18*, SC12 replaced *IGF18* when GEN40 was available, and GEN60 and *COAT* were the best combination when GEN60 was available. In summary, the estimated 10-year reduction in

*AGECL* was 141.0 days for selection of both sires and dams on the basis of *COAT* and SC12 measures. There was a further 10.2-day reduction if *IGF18* was available, or corresponding reductions of 8.4, 14.9 and 25.6 days if GEN30, GEN40 or GEN60 for *AGECL* were available. Where both *IGF18* and genomic measures were available, the further reductions (compared against 141.0) were 16.1 and 35.3 days for GEN40 and GEN60 (Table 3).

Table 4 shows the direction and size of the estimated genetic change in *AGECL* from selection on individual measures. The directions of association were the same when measures were in combinations. The reduction in *AGECL* from direct selection, and from selection on genomic measures by themselves, was less than for selection on most combinations of measures (Tables 3, 4). The reduction from selection on a genomic measure was less when the genomic EBV was for a trait only correlated with *AGECL* (e.g. GEN40 for SC12). Table 4 also shows that there was an advantage to selection using SC12 over SC18, a consistent benefit from using *IGF18* or IGF6, and a similar benefit between using PNS or MASS. Selection to increase any of *SFAT18*, *SEMA18* or *LWT18* also reduced *AGECL*, but the gains from this were lower.

### First-lactation anoestrous interval

The best combination of female measures for selecting to reduce *LAI*, when Mating 1 and 2 measures were unavailable, was *COAT*, *NAVEL*, *HH18* and *LWT18* (a reduction of 93.7 days in 10 years), and was superior to the best male-measure combination of TEMP12 and SC12 (71.3 days; Table 5). The same female measures remained the best except when semen measures were available (113.9 days), in which case PNS was the most important. Mating 1 measures were not meaningful to include for *LAI* since by definition *LAI* was in lactating cows. Mating 2 measures were not included with other measures as their genetic correlations with *LAI* were essentially unity (Johnston *et al*. 2014*a*). In the absence of Mating 2 measures, having GEN30 for *LAI* available increased accuracies of selection and led to a greater reduction in *LAI* (121.7 days in 10 years). When GEN40 was available, these further increased (127.4 days) and GEN40

Table 2.    **Generation intervals and average ages of selected Brahman bulls and cows at the birth of progeny, according to the minimum age of selected animals at the birth of progeny**

Minimum age of selected animals at the birth of progeny is decided by the earliest age at which all measures required for selection are available. Cows are assumed to calve first at 3 years. Corresponding results when cows calve first at 2 years are in parentheses

| Parameter | Minimum age of selected animals at the birth of progeny (years) | | | | |
|---|---|---|---|---|---|
| | 3 | 4 | 5 | 6 | 10 |
| *Selection to breed sires (sires to breed sires and dams to breed sires)* | | | | | |
| Average age bulls (years) | 5.50 (4.50) | 5.50 (5.50) | 5.50 (5.50) | 6.50 (5.50) | 10.50 (9.50) |
| Average age cows (years) | 5.89 (5.23) | 6.63 (5.89) | 7.47 (6.63) | 8.22 (7.47) | 11.25 (10.62) |
| Generation interval[A] | 5.70 (4.87) | 6.07 (5.70) | 6.49 (6.07) | 7.36 (6.49) | 10.88 (10.06) |
| *Selection to breed dams (sires to breed dams and dams to breed dams)* | | | | | |
| Average age bulls (years) | 4.62 (3.62) | 5.50 (4.62) | 6.38 (5.50) | 7.26 (6.38) | 11.38 (10.38) |
| Average age cows (years) | 5.89 (5.23) | 6.63 (5.89) | 7.47 (6.63) | 8.22 (7.47) | 11.25 (10.62) |
| Generation interval[A] | 5.26 (4.43) | 6.07 (5.26) | 6.93 (6.07) | 7.74 (6.93) | 11.32 (10.50) |

[A]Average age of selected parents at the birth of progeny.

**Table 3.  Combinations of measures giving the greatest genetic gain in Brahman heifer age at puberty (*AGECL*, days), assuming differing categories of measures are available**

Measures in combinations are listed in their order of greatest importance to genetic gain. Also shown are the accuracies of selection of sires and dams. See Table 1 for details of the measures considered in each category. Female measures are italicised, male measures are not

| Best combination of measures[A] | Accuracy of selection | | Estimated 10-year decrease |
| | Sires | Dams | in *AGECL* (probable range[B]) |
| --- | --- | --- | --- |
| *Female (without Matings 1 and 2)* | | | |
| (a) *COAT, IGF18* | 0.50 | 0.70 | 140.1 (89.3–165.2) |
| *Male non-semen* | | | |
| (a) IGF6, EV, SC12 | 0.52 | 0.31 | 116.2 (93.4–137.0) |
| *Female (without Matings 1 and 2) and male non-semen* | | | |
| (a) *COAT*, SC12, *IGF18* | 0.56 | 0.70 | 151.2 (100.2–178.2) |
| *Female and male non-semen* | | | |
| (a) *COAT*, SC12, *IGF18* | 0.56 | 0.70 | 151.2 (100.2–178.2) |
| *Female and male* | | | |
| (a) *COAT*, SC12, *IGF18* | 0.56 | 0.70 | 151.2 (100.2–178.2) |
| (b) *COAT*, SC12 | 0.53 | 0.62 | 141.0 (95.4–166.2) |
| (c) *COAT*, SC12, (*PREG1*) | 0.58 | 0.72 | 142.4 (94.8–157.7) |
| (d) *COAT*, SC12, (PNS) | 0.55 | 0.63 | 144.4 (98.6–170.2) |
| *Female, male and genomic* (GEN30, GEN40 *or* GEN60 for *AGECL*) | | | |
| (a)[C] *COAT*, SC12, *IGF18* | 0.56 | 0.70 | 151.2 (100.2–178.2) |
| (b) *COAT*, SC12, GEN30 | 0.57 | 0.63 | 149.4 (103.5–176.0) |
| (a) *COAT*, GEN40, *IGF18* | 0.59 | 0.70 | 157.1 (105.9–185.2) |
| (b) *COAT*, GEN40, SC12 | 0.61 | 0.63 | 155.9 (109.8–183.7) |
| (a) GEN60, *COAT, IGF18* | 0.69 | 0.71 | 176.3 (124.6–207.8) |
| (b) GEN60, *COAT* | 0.67 | 0.63 | 166.6 (120.5–196.3) |

[A]Combination (a) is the end result of step-down analyses of the estimated genetic gain. Combination (b) further assumes hormone measures are unavailable. Combinations (c) and (d) are combination (b), with addition of Matings 1 and 2 or semen measures, respectively. Measures in parentheses increased genetic gain by less than 5%.
[B]The lower value applies to selection only of sires, the upper value to when cows calve first at 2 years.
[C]Including Gen30 increased genetic gain by less than 5%.

was the second-most important measure. When GEN60 was available, it was the most important measure of the combination with *COAT*, PNS and *NAVEL*, and the reduction in *LAI* was 135.6 days. In summary, Mating 2 measures were closely related to *LAI* (Johnston *et al.* 2014*a*). In the absence of Mating 2 measures, selection of both sires and dams using *COAT*, *NAVEL*, HH18 and LWT18 was estimated to yield a 10-year reduction in *LAI* of 93.7 days. Where PNS was available, there was a further 20.2-day reduction. Where both PNS and genomic measures were available, the further reductions (compared against 93.7) were 28.0, 33.7 and 41.9 days for GEN30, GEN40 and GEN60 for *LAI* (Table 5).

Table 6 shows the direction and size of the genetic change in *LAI* from selection on individual measures. The directions of association were the same when measures were in combinations. Rankings of measures often differed when they were in combinations versus individually, the rankings involving HH18 and LWT18 being an example. Directions of associations for rectal temperature and liveweight were inconsistent between female and male measures. The decrease in *LAI* from selecting on *COAT*, *NAVEL*, HH18 and LWT18 in combination (Table 5) was of similar order (~93 days) to that from direct selection on *LAI*, and greater than from selection on any of

the individual measures except GEN60 for *LAI* (Tables 5, 6). Where PNS was also available, selection on the combination was as effective as or more effective than selection on GEN60 individually (113.9 vs 109.5 days).

*Lifetime annual weaning rate*

Considering all of the results of Table 7, the 10-year increase in *LAWR* from selection on combinations of measures was estimated to range from 0.070 to 0.154 calves weaned per cow (i.e. 7.0–15.4 calves weaned per 100 cows) when selection was of both sires and dams, and from 5.6 to 11.7 calves weaned per 100 cows when selection was only of sires. Accuracies of selection ranged from 0.30 to 0.64 and from 0.20 to 0.60 for sires and dams, respectively, for selection of both sires and dams. If hormone measures were available, the best combination of female and male measures was HH24, LWT15, EV, *COAT* and LH. The estimated 10-year increase in *LAWR* from selection on this combination was 0.132, and it was only marginally increased (0.135) when MOT was available. Where LH was unavailable, the estimated increase was 0.123 using HH24, EV, LWT15 and *COAT*, and 0.132 where MOT was available. Other measures contributing to a lesser extent to within-sex combinations were *NAVEL*, IN and SC12. Adding *PREG1* and *PREG2* increased selection accuracies

**Table 4. Consequences for Brahman heifer age at puberty (*AGECL*, days) of selecting on individual measures**

Results are for an increase in the measure unless indicated. See Table 1 for details of measures. Female traits and measures are italicised, male measures are not

| Individual measure | Accuracy of selection | | Estimated 10-year decrease in *AGECL* (probable range[A]) |
|---|---|---|---|
| | Sires | Dams | |
| *Direct selection* | | | |
| *AGECL*[B] | 0.45 | 0.78 | 125.4 (73.8–138.9) |
| *Components of combinations*[C] | | | |
| *COAT*[B] | 0.43 | 0.61 | 122.7 (78.3–144.6) |
| SC12 | 0.34 | 0.19 | 74.7 (60.9–88.1) |
| *IGF18* | 0.37 | 0.51 | 103.9 (66.8–122.4) |
| IGF6 | 0.40 | 0.24 | 89.6 (71.7–105.6) |
| PNS | 0.28 | 0.19 | 64.4 (50.5–75.9) |
| *PREG1* | 0.38 | 0.52 | 95.1 (61.2–105.4) |
| EV[B] | 0.21 | 0.14 | 46.9 (37.0–55.2) |
| *Genomic for AGECL*[D] | | | |
| GEN30[B] | 0.30 | 0.15 | 65.0 (54.0–76.6) |
| GEN40[B] | 0.40 | 0.20 | 86.6 (72.0–102.1) |
| GEN60[B] | 0.60 | 0.30 | 130.0 (108.1–153.2) |
| *Other measures and genomic* | | | |
| SC18 | 0.24 | 0.13 | 51.9 (42.6–61.1) |
| *SFAT18* | 0.19 | 0.25 | 51.9 (33.4–61.2) |
| *SEMA18* | 0.17 | 0.22 | 46.0 (29.8–54.2) |
| *LWT18* | 0.17 | 0.23 | 47.5 (30.6–56.0) |
| MASS18 | 0.29 | 0.20 | 67.6 (53.0–79.6) |
| GEN40 for SC12 | 0.16 | 0.08 | 34.7 (28.8–40.8) |
| GEN40 for *PREG1* | 0.28 | 0.14 | 60.6 (50.4–71.5) |

[A]The lower value applies to selection only of sires, the upper value to when cows calve first at 2 years.
[B]Results are for a decrease in the measure.
[C]Components of the combinations identified in Table 3.
[D]Assumes genotyping of males.

but did not increase the estimated gain. Where GEN30 for *LAWR* was available, there was an increase in the estimated gain (0.143 calves weaned per cow in 10 years) when LH was available, but otherwise only a marginal increase (0.136). Where GEN40 was available, it was the second-most important of the combination with *HH24*, EV, MOT and LWT15. The estimated gain in *LAWR* from selecting on that combination was also 0.143, showing that having GEN40 available was equivalent to the combined availabilities of GEN30 and LH. Where GEN60 was available, it was the most important measure of the combination with *HH24* and *COAT*. The estimated gain from selecting on this combination (0.154) was unchanged by availability of either LH or MOT. In summary, the 10-year increase in *LAWR* from selection of both sires and dams was 0.123 calves weaned per cow (12.3 calves weaned per 100 cows) for selection on *HH24*, EV, LWT15 and *COAT* measures. Where either LH or MOT was available, there was a further 0.009 increase, and where both were available, the increase was 0.012. Where genomic measures were available as well as MOT, the estimated increases (compared against 0.123) were 0.013, 0.020 and 0.031, respectively, for GEN30, GEN40 and GEN60 for *LAWR* (Table 7).

Table 8 shows the direction and size of the genetic change in *LAWR* from selection on individual measures, including from selection on the total calves weaned from Matings 1 and 2 (*TWEAN1+2*), a further measure from Johnston *et al.* (2014*a*). The same directions of association occurred when measures were in combinations. There was little genetic association of *SFAT18* with *LAWR*. The 10-year increase in *LAWR* from selecting on *HH24*, EV, LWT15 and *COAT* (0.123) was only slightly less than from selecting on GEN60 for *LAWR* as an individual measure (0.133), and it was virtually the same as this when the measures were further combined with LH or MOT (0.132) (Tables 7, 8). Greater increases in *LAWR* occurred when genomic measures were used in combination with other measures.

**Table 5. Combinations of measures giving the greatest genetic gain in Brahman first lactation anoestrous interval (*LAI*, days), assuming differing categories of measures are available**

Measures in combinations are listed in their order of greatest importance to genetic gain. Also shown are the accuracies of selection of sires and dams. See Table 1 for details of the measures considered in each category. Female measures are italicised, male measures are not

| Best combination of measures[A] | Accuracy of selection | | Estimated 10-year decrease in *LAI* (probable range[B]) |
|---|---|---|---|
| | Sires | Dams | |
| *Female (without Matings 1 and 2)* | | | |
| *COAT*, *NAVEL*, *HH18*, *LWT18* | 0.39 | 0.55 | 93.7 (60.0–110.4) |
| *Male non-semen* | | | |
| TEMP12, SC18 | 0.38 | 0.23 | 71.3 (57.4–84.1) |
| *Female (without Matings 1 and 2) and male non-semen* | | | |
| *COAT*, *NAVEL*, *HH18*, *LWT18* | 0.39 | 0.55 | 93.7 (60.0–110.4) |
| *Female (without Matings 1 and 2) and male* | | | |
| PNS, *COAT*, *HH18*, *NAVEL*, *LWT18* | 0.51 | 0.59 | 113.9 (77.5–134.2) |
| *Female (without Matings 1 and 2), male and genomic* (GEN30, GEN40 or GEN60 for *LAI*) | | | |
| PNS, *COAT*, *HH18*, *NAVEL*, GEN30, *LWT18* | 0.56 | 0.59 | 121.7 (85.1–143.4) |
| *COAT*, GEN40, PNS, *HH18*, *NAVEL*, *LWT18* | 0.60 | 0.60 | 127.4 (90.7–150.2) |
| GEN60, *COAT*, PNS, *NAVEL* | 0.68 | 0.53 | 135.6 (102.8–159.8) |

[A]Combinations in each category are the end result of step-down analyses of the estimated genetic gain.
[B]The lower value applies to selection only of sires, the upper value to when cows calve first at 2 years.

**Table 6.    Consequences for Brahman first lactation anoestrous interval (*LAI*, days) of selecting on individual measures**

Results are for an increase in the measure unless indicated. See Table 1 for details of measures. Female traits and measures are italicised, male measures are not

| Individual measure | Accuracy of selection | | Estimated 10-year decrease in *LAI* (probable range[A]) |
|---|---|---|---|
| | Sires | Dams | |
| *Direct selection* | | | |
| *LAI*[B] | 0.45 | 0.75 | 93.1 (55.4–103.0) |
| *Components of combinations*[C] | | | |
| PNS | 0.30 | 0.21 | 58.8 (46.1–69.3) |
| *COAT*[B] | 0.26 | 0.37 | 62.3 (39.8–73.5) |
| *HH18* | 0.13 | 0.18 | 30.5 (19.5–36.0) |
| *NAVEL*[B] | 0.20 | 0.27 | 47.3 (30.5–55.7) |
| *LWT18*[B] | 0.03 | 0.04 | 6.1 (3.9–7.1) |
| TEMP12[B] | 0.33 | 0.22 | 62.8 (49.5–74.0) |
| SC18 | 0.24 | 0.13 | 43.7 (35.9–51.5) |
| *Genomic for LAI*[D] | | | |
| GEN30[B] | 0.30 | 0.15 | 54.8 (45.5–64.5) |
| GEN40[B] | 0.40 | 0.20 | 73.0 (60.7–86.0) |
| GEN60[B] | 0.60 | 0.30 | 109.5 (91.1–129.1) |
| *Other measures and genomic* | | | |
| MOT | 0.18 | 0.13 | 35.5 (27.5–41.8) |
| HH15 | 0.12 | 0.07 | 21.9 (17.6–25.8) |
| LWT15 | 0.07 | 0.05 | 14.3 (11.4–16.8) |
| *TEMP13* | 0.11 | 0.15 | 26.5 (17.2–31.3) |
| SC12 | 0.16 | 0.09 | 29.2 (23.8–34.4) |
| *IGF18* | 0.15 | 0.20 | 35.0 (22.5–41.3) |
| *SFAT18*[B] | 0.11 | 0.15 | 26.3 (16.9–31.0) |
| *SEMA18*[B] | 0.08 | 0.11 | 18.3 (11.8–21.6) |
| *PREG2*[E] | 0.40 | 0.62 | 81.0 (49.7–89.5) |
| GEN40 for *PREG2*[E] | 0.38 | 0.19 | 69.4 (57.7–81.7) |
| GEN40 for PNS | 0.21 | 0.10 | 38.3 (31.9–45.2) |

[A]The lower value applies to selection only of sires, the upper value to when cows calve first at 2 years.
[B]Results are for a decrease in the measure.
[C]Components of the combinations identified in Table 5.
[D]Assumes genotyping of males.
[E]Assumes that genetic correlation of *PREG2* with *LAI* is –0.95.

## Discussion

### Effectiveness of genetic selection

Reproductive traits are among the most problematic for genetic improvement as they are complex and usually have low heritabilities. The present results showed multi-trait selection using combinations of early-in-life measures could be effective in reducing *AGECL* and *LAI* and in increasing *LAWR* in Brahman cattle. The low reproduction level of the Brahman (Johnston *et al.* 2014*a*) is an important contributor to the significant gains estimated, because it leads to higher variances for the reproductive traits, which are commonly binomial in nature. For selection on a best combination of any female and male, or female, male and genomic measures, accuracies of selection for *AGECL*, *LAI* and *LAWR* were in the range 0.39–0.69 and 0.46–0.72 for sires and dams, respectively, 10-year reductions in *AGECL* and *LAI* ranged from 141 to 176 days and from 94 to

136 days, respectively, and the corresponding increase in *LAWR* ranged from 0.12 to 0.15. The corresponding gains from only sire selection ranged from 95 to 125 days for *AGECL*, from 60 to 103 days for *LAI*, and from 0.08 to 0.12 (i.e. 8–12 calves weaned per 100 cows) for *LAWR* (Tables 3, 5, 7). Gains would be greater where first calving is at 2 years. The gains that may occur in industry will depend on the actual selection intensities achieved by Brahman breeders. The present estimates are for selection intensities lower than theoretically possible but where a concerted selection effort is made across the Brahman breed. Under these assumptions, the genetic gains that may occur were substantial.

### Selection on combinations of measures

The results for combinations of measures together suggested that female *COAT* and *HH24* and male EV and LWT15 are measures that could assist Brahman selection for female reproduction (Tables 3, 5, 7). Coat characters have been considerably studied (Turner and Schleger 1958, 1960; Olson *et al.* 2003), although not previously as genetic indicators of reproductive performance, while the genetics of preputial eversion in young bulls, i.e. the extent of protrusion of the prepuce, a structural fault of bulls (Anon 2005), was only recently considered by Corbet *et al.* (2013). A lower *COAT* score (i.e. a sleeker coat) was important especially for reducing *AGECL* and *LAI*, greater *HH24* (or *HH18*) for increasing *LAWR*, and lower EV (i.e. less preputial eversion) and WT15 for increasing *LAWR*. Where semen measures were available, PNS was important for reducing *LAI*, and MOT for increasing *LAWR*. Other measures that were also important were *IGF18*, *NAVEL* and *LWT18* in females and SC12 and LH in males. Use of a genomic EBV in combination with other measures was important for all traits, especially at genomic EBV accuracies of at least 40%. At accuracies of 60%, a level similar to that observed in dairy cattle (VanRaden *et al.* 2009), the genomic EBV was the most important measure of the combinations for each trait.

The results also suggested that hip height and liveweight should be considered jointly for their genetic impact on Brahman female reproduction. This was largely due to liveweights of males being more negatively associated with *LAWR* in Brahmans (Wolcott *et al.* 2014*c*) than were liveweights of females (Wolcott *et al.* 2014*b*), and to hip heights and liveweights being evaluated separately in each sex. In evolutionary biology, it is recognised that important differences in relationships with fitness can exist between the sexes (Kirkpatrick 2009), and the relationships mentioned here may be an example of that. The differences assumed, however, need validating in further Brahman data. Wolcott *et al.* (2014*b*, 2014*c*) showed that liveweights of Brahman females and steers were favourably or lowly genetically related to *LAWR*, which was similar to the lack of genetic antagonism generally observed between weights of young animals and female reproduction (Burrow *et al.* 1991; Meyer *et al.* 1991; Davis *et al.* 1993; Archer *et al.* 1998). Wolcott *et al.* (2014*c*), however, showed that liveweights of Brahman bulls were negatively genetically related to *LAWR*. Vargas *et al.* (1999) linked cows with greater reproductive performance to smaller-frame scores, but it was not clear that the association was due to genetic causes. Wolcott *et al.*

**Table 7. Combinations of measures giving the greatest genetic gain in Brahman lifetime annual weaning rate (*LAWR*, calves weaned/cow), assuming differing categories of measures are available**

*LAWR* is based on the number of mating opportunities of cows over up to six possible matings. Measures in combinations are listed in their order of greatest importance to genetic gain. Also shown are the accuracies of selection of sires and dams. See Table 1 for details of the measures considered in each category. Female measures are italicised, male measures are not

| Best combination of measures[A] | Accuracy of selection | | Estimated 10-year increase in *LAWR* (probable range[B]) |
|---|---|---|---|
| | Sires | Dams | |
| *Female (without Matings 1 and 2)* | | | |
| (a)   *HH24, COAT, NAVEL* | 0.36 | 0.49 | 0.103 (0.066–0.121) |
| *Male non-semen* | | | |
| (a)   EV, IN, LH, SC12 | 0.40 | 0.25 | 0.092 (0.074–0.109) |
| (b)   EV, LWT15 | 0.30 | 0.20 | 0.070 (0.056–0.083) |
| *Female and male non-semen* | | | |
| (a)   *HH24*, LWT15, EV, *COAT*, LH | 0.50 | 0.52 | 0.132 (0.093–0.155) |
| (b)   *HH24*, EV, LWT15, *COAT* | 0.46 | 0.50 | 0.123 (0.085–0.145) |
| (c)   *HH24*, EV, LWT15, (*COAT*), (*PREG1*), (*PREG2*) | 0.51 | 0.59 | 0.112 (0.076–0.124) |
| *Female and male* | | | |
| (a)   *HH24*, EV, LWT15, MOT, LH | 0.54 | 0.48 | 0.135 (0.099–0.159) |
| (b)   *HH24*, EV, MOT, LWT15, *COAT* | 0.51 | 0.51 | 0.132 (0.094–0.156) |
| (c)   *HH24*, EV, LWT15, (MOT), (*COAT*), (*PREG1*), (*PREG2*) | 0.54 | 0.60 | 0.117 (0.081–0.130) |
| *Female, male and genomic* (GEN30, GEN40, or GEN60 for *LAWR*) | | | |
| (a)   *HH24*, EV, LWT15, MOT, GEN30, LH | 0.58 | 0.48 | 0.143 (0.107–0.169) |
| (b)   *HH24*, EV, MOT, GEN30, LWT15 | 0.55 | 0.46 | 0.136 (0.101–0.160) |
| (c)   *HH24*, EV, GEN30, (LWT15), (MOT), (*PREG1*), (*PREG2*) | 0.58 | 0.57 | 0.122 (0.087–0.134) |
| (a, b)   *HH24*, GEN40, EV, MOT, LWT15 | 0.59 | 0.46 | 0.143 (0.109–0.169) |
| (c)   *HH24*, GEN40, EV, (LWT15), (MOT), (*PREG1*), (*PREG2*) | 0.61 | 0.57 | 0.127 (0.092–0.140) |
| (a, b)   GEN60, *HH24, COAT* | 0.64 | 0.49 | 0.154 (0.117–0.181) |
| (c)   GEN60, *HH24*, (*COAT*), (*PREG1*), (*PREG2*) | 0.66 | 0.59 | 0.135 (0.099–0.149) |

[A]Combination (a) is the end result of step-down analyses of the estimated genetic gain. Combination (b) further assumes that hormone measures are unavailable. Combination (c) is combination (b) with addition of Matings 1 and 2 or semen measures. Measures in parentheses increased genetic gain by less than 5%.

[B]The lower value applies to selection only of sires, the upper value to when cows calve first at 2 years.

(2014*b*) found no clear genetic association between hip height and female reproduction in a Tropical Composite genotype, whereas in the same experiment, the genetic association between female hip height (*HH24* and *HH18*) and female reproduction in Brahmans was consistently favourable.

Generation interval was an important factor affecting estimates of genetic gains. This was especially evident where *PREG1* and *PREG2* measures were added to combinations, such as, for example, for selecting to increase *LAWR* using female and male measures (Table 7). Adding *PREG1* and *PREG2* measures decreased the expected gain from selection, despite the accuracy of selecting sires increasing from 0.51 to 0.54 and that for dams increasing from 0.51 to 0.60. Generation intervals for selection to breed sires and dams were initially 5.70 and 5.26 years, respectively, but increased to 6.49 and 6.93 years with the addition of *PREG1* and *PREG2* (Table 2). Similar effects were seen when *PREG1* and *PREG2* (or *PREG1* alone) were added to combinations that included genomic measures (Table 7), and to combinations for improving *AGECL* and *LAI* (Tables 3, 5).

### Selection on individual measures

Estimated genetic gains from selecting on combinations of measures were about twice as large as those from selecting on individual measures, emphasising the likely benefit of multi-trait analyses for genetic evaluation of *AGECL*, *LAI* and *LAWR*. Genomic measures were also less effective individually than they were in combination with other measures. The results showed that there were numerous individual measures that might be selected on to achieve some amount of improvement in *AGECL*, *LAI* or *LAWR* (Tables 4, 6, 8), but that many fewer measures were important when they were considered together (Tables 3, 5, 7).

Selection on *SFAT18* yielded only small gains in the reproduction traits relative to the gains with other measures. It was estimated to reduce *AGECL*, increase rather than reduce *LAI*, and have little effect on *LAWR* (Tables 4, 6, 8). Most reports have shown increased fatness is genetically favourable for reproduction (e.g. Berry *et al*. 2003; Meyer and Johnston 2003), although this is commonly in temperate genotypes and between measures and reproduction assessed early in life. The possible antagonism here between *SFAT18* and *LAI* (Table 6; also Wolcott *et al*. 2014*b*) could potentially implicate deficiencies in heat adaptation in Brahman lactation anoestrus.

Indirect selection to improve *AGECL*, *LAI* and *LAWR* was almost always superior to direct selection, through the use of multiple measures and, for *LAWR*, through the shorter generation intervals involved. The indirect measures also would be more practical to record. Selecting on a genomic EBV for the

**Table 8. Consequences for Brahman lifetime annual weaning rate (*LAWR*, calves weaned/cow) of selecting on individual measures**

*LAWR* is based on the number of mating opportunities of cows over up to six possible matings. Results are for an increase in the measure unless indicated. See Table 1 for details of measures. Female traits and measures are italicised, male measures are not

| Individual measure | Accuracy of selection | | Estimated 10-year increase in *LAWR* (probable range[A]) |
|---|---|---|---|
| | Sires | Dams | |
| *Direct selection* | | | |
| *LAWR* | 0.34 | 0.45 | 0.048 (0.031–0.052) |
| *Components of combinations*[B] | | | |
| HH24 | 0.24 | 0.33 | 0.069 (0.044–0.082) |
| EV[C] | 0.27 | 0.18 | 0.064 (0.050–0.075) |
| MOT | 0.27 | 0.19 | 0.064 (0.050–0.075) |
| LWT15[C] | 0.14 | 0.09 | 0.033 (0.026–0.039) |
| *COAT*[C] | 0.20 | 0.27 | 0.057 (0.036–0.067) |
| *PREG1* | 0.20 | 0.27 | 0.051 (0.033–0.056) |
| *PREG2* | 0.25 | 0.34 | 0.059 (0.038–0.065) |
| IN | 0.16 | 0.08 | 0.035 (0.029–0.041) |
| LH | 0.18 | 0.12 | 0.043 (0.034–0.050) |
| SC12[C] | 0.12 | 0.07 | 0.028 (0.023–0.033) |
| *NAVEL* | 0.15 | 0.20 | 0.043 (0.028–0.051) |
| *Genomic for LAWR*[D] | | | |
| GEN30 | 0.30 | 0.15 | 0.066 (0.055–0.078) |
| GEN40 | 0.40 | 0.20 | 0.089 (0.074–0.104) |
| GEN60 | 0.60 | 0.30 | 0.133 (0.110–0.156) |
| *Other measures and genomic* | | | |
| *HH18* | 0.20 | 0.28 | 0.059 (0.038–0.069) |
| *LWT18* | 0.18 | 0.25 | 0.051 (0.033–0.061) |
| *SFAT18* | 0.05 | 0.07 | 0.014 (0.009–0.016) |
| MASS | 0.25 | 0.17 | 0.058 (0.046–0.069) |
| SC18 | 0.09 | 0.05 | 0.020 (0.016–0.023) |
| *DC1*[C] | 0.17 | 0.23 | 0.044 (0.028–0.048) |
| *W1P2* | 0.23 | 0.31 | 0.053 (0.034–0.058) |
| *TWEAN1+2*[E] | 0.26 | 0.35 | 0.054 (0.035–0.061) |
| GEN40 for *DC1*[C] | 0.16 | 0.08 | 0.035 (0.029–0.042) |
| GEN40 for *W1P2* | 0.17 | 0.09 | 0.038 (0.031–0.044) |
| GEN40 for *TWEAN1+2* | 0.24 | 0.12 | 0.053 (0.044–0.063) |

[A]The lower value applies to selection only of sires, the upper value to when cows calve first at 2 years.
[B]Components of the combinations identified in Table 7.
[C]Results are for a decrease in the measure.
[D]Assumes genotyping of males.
[E]Total calves weaned from Matings 1 and 2, from Johnston *et al.* (2014*a*).

reproduction trait was much more effective than selecting on a genomic EBV for a correlated measure (Tables 4, 6, 8). For best use of genomic measures, traits need to be clearly defined and consideration also given to what other measures may be available.

### Issues for Brahman genetic evaluation

Whether a measure is adopted for recording by industry is ultimately decided by its measurement cost as well as benefit. While the focus here was on practical measures that could be recorded, these measures would also differ in their cost, ease of recording and requirement for industry infrastructure. Hormone measures would likely require infrastructure for processing large

numbers of samples, and semen measures may have additional requirements if the measures are not the same as used for bull breeding soundness evaluations (Holroyd *et al.* 2002; Fordyce *et al.* 2006). Subjective scores could require training and standardisation of industry scorers. Genomic measures would require ongoing recording of phenotypes in industry and for genotyping to be cost-effective (Van Eenennaam *et al.* 2011; Johnston *et al.* 2012). In beef cattle, these are challenging requirements, for, as shown here (Tables 4, 6, 8), the benefits from genomic measures are less when the genomic EBV is for a measure only correlated with the trait of interest. Superficially, genomic measures seem to avoid the need for industry to record management-group details, a usual pre-requisite for separating genetic and environmental effects, as the genotype is not affected by the animal's prior environment. However, since management group details are needed for the animals in the training populations used for deriving genomic predictions, and for deriving phenotypes where genomic relationships are directly used (Misztal *et al.* 2009), the requirement for industry recording of management group is also not avoided.

The complexity of female reproduction adds to the difficulty in deciding the reproductive trait or traits to be focussed on in genetic evaluation. Currently, in BREEDPLAN, the female reproduction trait included is days to calving, assuming a repeatability model (Johnston and Bunter 1996; Graser *et al.* 2005). Because of their importance, the *LAWR*, *LAI* and *AGECL* traits might all be considered candidates for this focus, along with other aspects of cow productivity, such as cow longevity. Also, in genotypes where the genetic variation in lifetime reproduction is fully explained by early-in-life differences, genetic evaluation may be justified in focussing only on the early-in-life reproduction. This did not seem to be the case in the present Brahman population, where the total number of calves weaned from the first two matings (*TWEAN1 + 2*; Johnston *et al.* 2014*a*) was only a marginally more accurate predictor of *LAWR* than were other individual indirect measures (Table 8).

### General considerations

The results described are for Brahman cattle and may not apply to other breeds. The stepwise procedure used for evaluating combinations of measures may also have been prone to bias. The order in which blocks of measures were combined, for example, could have favoured the importance of genomic measures, as these were combined last. The genetic correlation estimates on which the results depended often had high standard errors, although in the experiment where these were obtained, standard errors were lower for Brahman (and trait heritabilities were higher) than they were for a Tropical Composite genotype. The procedure for choosing the measures to study excluded those with very high standard errors. It also placed considerable emphasis on the consistency of the genetic correlations across the range of female reproduction traits described by Johnston *et al.* (2014*a*).

*PREG1* and *PREG2* may contribute more to genetic gains in practice than was shown, as BLUP selection across age groups could allow some greater use to be made of these records. Supporting the case for industry to record *PREG1* and *PREG2* is that pregnancy testing is often a part of normal management, so

the marginal cost of this recording would be small. The female and male measures studied were also treated separately in each sex, which meant that there was little opportunity for the same type of measure to be important in both sexes. Where it is possible for this separation to be relaxed, the genetic gains expected may be greater.

The present study was concerned only with genetic selection for female reproduction, whereas in practice selection has to be for the whole breeding objective. Although female reproduction is a major component of the breeding objective in Brahman production systems, other traits such as cow longevity and the ability of young animals to grow to market weight before the onset of an additional annual dry season, are also important (Anon 2011). Male measures were considered here only for their ability to predict female performance. The value in industry recording male measures, especially semen measures, needs to also consider their potential use in bull breeding-soundness evaluations and in predicting bull performance (Holroyd *et al.* 2002; Fordyce *et al.* 2006). *LAWR* here was also concerned only with reproduction *per se* and did not include differences in the length of productive life of cows (O'Rourke *et al.* 1995). These other aspects are to be considered separately.

## Conclusions

Multi-trait analyses incorporating early-in-life measures could significantly benefit genetic evaluation of female reproduction in Brahman cattle. Results need confirming but showed that selection on combinations of practical early-in-life measures (without or with the availability of genomic measures) could be effective in reducing *AGECL* and *LAI* and in increasing *LAWR*. They suggested *HH24* and *COAT* in females and EV and LWT15 in males may warrant wider recording in the Brahman for this purpose. Recording of *PREG1* and *PREG2* measures also should be encouraged. Recording of PNS may be important for reducing *LAI* and SC12 and *IGF18* for reducing *AGECL*. The genetic gains estimated to be possible in each of *AGECL*, *LAI* and *LAWR* were substantial, assuming a concerted selection effort could be made across the Brahman breed. The suggested gains in *LAWR* in 10 years were of the order of 8–12 calves weaned per 100 cows from selection of sires and 12–15 calves weaned per 100 cows from selection of sires and dams.

There were many individual measures on which selection would yield some benefit in *LAWR*, *LAI* or *AGECL*, but many fewer measures were important when considered together. Use of a genomic EBV in combination with other measures added to genetic gains, especially at genomic EBV accuracies of 40%. Accuracies of genomic EBVs needed to approach 60% for the genomic EBV to be the most important contributor to gains in the combinations of measures studied.

## Acknowledgements

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**Appendix 1. Heritabilities ($h^2$), genetic variances and genetic and phenotypic correlations with lifetime annual weaning rate (*LAWR*) and among female, male and genomic measures**

Variances are from Barwick *et al.* (2009), Prayaga *et al.* (2009), Corbet *et al.* (2013) and Johnston *et al.* (2014*a*). Correlations are from bivariate estimates of Johnston *et al.* (2014*a*, 2014*b*) and Wolcott *et al.* (2014*b*, 2014*c*), adapted as required for positive definite matrices. Values are as utilised for analyses of Brahman *LAWR*, including a genomic estimated breeding value for *LAWR* of 40% accuracy. *LAWR* is based on the number of mating opportunities of cows over up to six possible matings. GEN40 for *LAWR* parameters are as described in the text. Genetic variances are shown on the diagonal. Genetic correlations are shown above and phenotypic correlations below the diagonal. See Table 1 for a description of measures and units of measurement. Female measures are italicised, male measures are not

| Trait and measure | $h^2$ | Trait | Female measure | | | | | Male measure | | | | Genomic measure |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *LAWR* | *HH24* | *COAT* | *PREG1* | *PREG2* | LH | EV | LWT15 | MOT | PNS | GEN40 for *LAWR* |
| *LAWR* | 0.11 | **0.0077** | 0.43 | –0.33 | 0.37 | 0.50 | 0.29 | –0.44 | –0.21 | 0.55 | 0.13 | 0.40 |
| *HH24* | 0.51 | 0.04 | **7.42** | 0.10 | 0.20 | 0.03 | –0.12 | 0.12 | 0.45 | 0.28 | –0.09 | 0.17 |
| *COAT* | 0.63 | –0.10 | –0.02 | **1.38** | –0.57 | –0.20 | –0.20 | 0.33 | 0.01 | –0.42 | –0.14 | –0.13 |
| *PREG1* | 0.42 | 0.31 | 0.01 | –0.14 | **0.059** | 0.00 | –0.10 | –0.13 | –0.18 | 0.35 | 0.25 | 0.15 |
| *PREG2* | 0.35 | 0.49 | 0.03 | –0.11 | 0.07 | **0.063** | 0.28 | –0.20 | –0.10 | 0.58 | 0.28 | 0.21 |
| LH | 0.31 | 0.13 | –0.05 | –0.09 | 0.00 | 0.09 | **4.15** | –0.10 | 0.14 | 0.08 | –0.01 | 0.12 |
| EV | 0.30 | –0.21 | 0.05 | 0.14 | –0.05 | –0.05 | –0.01 | **126.3** | 0.07 | 0.03 | 0.13 | –0.18 |
| LWT15 | 0.39 | –0.11 | 0.20 | 0.00 | –0.07 | –0.02 | 0.05 | 0.05 | **244.6** | –0.06 | –0.09 | –0.08 |
| MOT | 0.15 | 0.25 | –0.06 | –0.14 | 0.05 | 0.13 | 0.03 | 0.03 | 0.11 | **123.9** | 0.75 | 0.22 |
| PNS | 0.25 | –0.04 | –0.16 | 0.03 | 0.08 | 0.08 | 0.05 | 0.01 | 0.07 | 0.28 | **198.5** | 0.05 |
| GEN40 for *LAWR* | 0.999 | 0.13 | 0.12 | –0.10 | 0.10 | 0.12 | 0.07 | –0.10 | –0.05 | 0.09 | 0.03 | **0.0012** |