Towards multi-breed genomic evaluations for female fertility of tropical beef cattle[1]

Ben J. Hayes,[†,2] Nicholas J. Corbet,[‡] Jack M. Allen,[‖] Alan R. Laing,[§] Geoffry Fordyce,[†] Russel Lyons,[¶,] Michael R. McGowan,[¶] and Brian M. Burns[††]**

[†]Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, St Lucia, QLD 4067, Australia; [‡]Central Queensland University, School of Health, Medical and Applied Sciences, Rockhampton, QLD, Australia; [‖]Agricultural Business Research Institute, University of New England, Armidale, NSW, Australia; [§]Formerly Department of Agriculture and Fisheries, Ayr, QLD 4807, Australia; [¶]The University of Queensland, School of Veterinary Science, St Lucia, QLD 4607, Australia; **Neogen, The University of Queensland, Gatton, QLD 4343, Australia; and [††]Department of Agriculture and Fisheries, Rockhampton, QLD 4702, Australia

ABSTRACT: Developing accurate genomic evaluations of fertility for tropical beef cattle must deal with at least two major challenges (i) recording cow fertility traits in extensive production systems on large numbers of cows and (ii) the genomic evaluations should work across the breeds, crossbreds, and composites used in tropical beef production. Here, we assess accuracy of genomic evaluations for a trait which can be collected on a large scale in extensive conditions, *corpus luteum* score (**CLscore**), which is 1 if ovarian scanning indicates a heifer has cycled by 600 d and 0 if not, in a multi-breed population. A total of 3,696 heifers, including 979 Brahmans, 914 Droughtmasters, and 1,803 Santa Gertrudis in seven herds across 3-yr cohorts with CLscores, were genotyped for 24,211 SNPs. Genotypes were imputed to 728,785 SNPs. GBLUP and BayesR were used to predict GEBV. Accuracy of GEBV was evaluated with two validation strategies. In the first strategy, the last year cohort of heifers from each herd was used for validation, such that every herd had heifers in both reference and validation populations. In the second validation strategy, each herd in turn was removed in its entirety from the reference population, and was used for validation. For both validation strategies, accuracy of GEBV for single breed and multi-breed reference populations was assessed. For the first validation strategy, accuracy of GEBV ranged from 0.2 for Brahmans to 0.4 for Droughtmasters. Increasing marker density from 24K SNPs to 728K SNPs resulted in a small increase in accuracy, and including multiple-breeds in the reference did not help improve accuracy. These results suggest that provided a herd has animals in the reference population, the accuracy of the GEBV is largely determined by within herd (linkage) information. The situation was very different when entire herds were predicted in the second validation. In this case accuracy of GEBV using only 24K SNPs and only a within breed reference was close to zero for all breeds. Accuracy increased substantially when 728K SNPs, BayesR, and a multi-breed reference were used, from 0.15 for Brahmans to 0.35 for Santa Gertrudis. Given the second validation strategy is more likely to reflect the situation for many herds in tropical beef production (no animals in the reference), genomic evaluations for fertility in tropical beef cattle should be based on high-density markers (728K SNPs) and should be multi-breed.

Key words: fertility, genomic selection, tropical beef cattle

J. Anim. Sci. 2019.97:55–62
doi: 10.1093/jas/sky417

INTRODUCTION

Cow fertility is a major driver of profitability of beef production in northern Australia (Taylor and Rudder, 1986; Fordyce, 2012). There

[1]The research was funded by the Queensland Government Smart Futures Research Partnerships Program.

[2]Corresponding author: b.hayes@uq.edu.au

Received May 30, 2018.
Accepted October 25, 2018.

is considerable genetic variation for this trait, for example Johnston et al (2013) reported differences between sires of up to 15 d in the average days to calving for their daughters (where days to calving is the days from bull in to calving). However, cow fertility has been a difficult trait to select and make genetic gains for, as it is measured on females only and late in life. Accurate genomic evaluations for female fertility would allow selection of young bulls with superior genetic merit for these traits, accelerating genetic gain.

Accurate genomic evaluations for low heritability traits such as fertility require large reference populations (e.g., Goddard and Hayes, 2009), with thousands of cows measured for the trait and genotyped for genome-wide markers. Assembling such large reference populations within a single cattle breed is likely to be challenging, particularly where the cattle population consists of many breeds, crossbreds and composites. This is a feature of tropical beef production, including in Australia, where cattle include high proportion *Bos indicus* breeds (e.g., Brahman), stabilized composites with 50% to 30% *Bos indicus* (e.g., Droughtmaster and Santa Gertrudis), as well as adapted *Bos taurus* breeds.

Another challenge is to identify a female fertility phenotype that is feasible to measure on large numbers of cattle, in the extensive conditions that characterize tropical beef production. While lifetime productivity (number and weight of calves weaned over a cow's lifetime) is perhaps the ultimate fertility trait, this trait is difficult and very time-consuming to measure. Alternatives have been proposed which can be measured earlier in the cow's life, are correlated to lifetime productivity, and have moderate-to-high heritability. These include age at puberty and *postpartum anoestrus* interval (Barwick et al., 2009; Johnston et al., 2009). For example, age at puberty, as measured by the first appearance of a corpus luteum (**CL**), has a heritability of ~0.5 for tropically adapted breeds (Johnston et al., 2009), which is much higher than the heritability reported for most other fertility traits (e.g., Berry et al., 2014). Another trait proposed is age at first calving (Forni and Albuquerque, 2005); however, this trait has a low heritability of ~0.1. Although age at puberty is an attractive indicator trait for cow fertility, it also has challenges with recording as heifers must be scanned approximately every 3 wk to determine when the first CL appears. This approach was successfully used to record age at puberty for ~2,000 Brahman and Tropical composite cattle (Johnston et al., 2009). However, collecting data for this trait on the many thousand heifers that are likely to be required for accurate genomic evaluations may not be feasible. Corbet et al. (2017) proposed a proxy trait, the presence or absence of CL at 600 d assessed using ovarian scanning (corpus luteum score, **CLscore**), which is more feasible to collect on a large scale. This trait does, however, have a somewhat lower heritability than age at puberty, of 0.21 to 0.33, depending on breed (Corbet et al. 2017).

The accuracy of genomic predictions for age at first CL in tropical beef cattle was evaluated by Zhang et al. (2014) and Farah et al. (2016). Both studies used the same population, of Brahman (996) and Tropical Composite (1,097), with genotypes (real or imputed) for 729K markers. These studies used different genomic prediction methods, but both concluded the accuracy of genomic prediction was ~0.35 for Brahmans and lower at 0.23 in the tropical composite cattle.

Clearly what is needed to improve these accuracies is larger reference populations of genotyped cows with fertility phenotypes. Here, we investigate the accuracies of genomic prediction that can be achieved with a population of 3,969 heifers recorded for CLscore as recommended by Corbet et al. (2017). The population included three tropical beef breeds widely used in northern Australia. The potential to combine reference populations across breeds and the use of imputed high-density SNP genotypes to improve accuracies of genomic prediction were evaluated.

MATERIALS AND METHODS

Phenotypes and Genotypes

Fertility records were from heifers in seven herds in central, north, or south-eastern Queensland, Australia. Across the herds, there were 979 Brahman, 914 Droughtmaster, and 1,803 Santa Gertrudis heifers, in cohorts across 3 yr (2012–2014) (Table 1). The heifers were the offspring of 180 Brahman, 69 Droughtmaster, and 116 Santa Gertrudis sires, with on average 9, 15, and 16 daughters, with a range of 2 to 68 daughters per sire (Corbet et al., 2017). Ovarian activity was assessed in the heifers at ~600 d of age by real-time ultrasound scanning. This was a proxy trait for age at puberty, a moderately heritable trait correlated to lifetime fertility of cows. Heifers were given a CLscore based on the presence or absence of a CL (indicating cycled, or not). For more details on the trait and cattle, see Corbet et al. (2017).

All heifers were genotyped with 24,121 genome-wide SNP using the Geneseek GGP-LD array.

Table 1. Number of heifers with corpus luteum score (**CLscore**) phenotypes by breed, herd and year

Breed	Herd	Birth year	Number	Average CLscore	Average age day
Brahman	BRA1	2012	110	0.42	489
	BRA1	2013	159	0.71	613
	BRA1	2014	130	0.63	633
	BRA2	2011	82	0.73	723
	BRA2	2012	126	0.30	718
	BRA2	2014	165	0.39	607
	BRA3	2013	115	0.86	615
	BRA3	2014	92	0.70	623
Droughtmaster	DM1	2012	65	0.35	605
	DM1	2013	85	0.22	653
	DM1	2014	74	0.38	552
	DM2	2012	188	0.53	575
	DM2	2013	253	0.54	595
	DM2	2014	249	0.29	601
Santa Gertrudis	SG1	2012	298	0.94	525
	SG1	2013	363	0.52	499
	SG1	2014	365	0.70	526
	SG2	2012	279	0.70	535
	SG2	2013	243	0.79	524
	SG2	2014	255	0.75	517

SNPs were evaluated for average genotype call (GC) score (measure of genotyping quality), and SNPs with >10% of animals with GC score <0.6 were excluded from further analysis. Monomorphic SNPs were also excluded (where the SNPs were monomorphic across the entire population) and 20,414 SNPs remained. Of the remaining SNP, if individual genotype calls had GC score <0.6, they were set to missing, and genotypes were recovered with imputation.

The heifer genotypes were imputed up to 728,785 SNPs (Bovine HD array), using 3,456 Brahman, Droughtmaster, Santa Gertrudis, Tropical Composites, and other relevant breeds genotyped for the Bovine HD array. The 728,785 SNPs remained from 777K after a similar QC process as described above, with the addition that miss mapped SNPs were also excluded as described in Erbe et al. (2012). The Fimpute software was used for imputation (Sargelozei, 2014).

Model for Genomic Predictions and Validation

Two genomic prediction methods were evaluated, GBLUP and BayesR. The model for GBLUP was

$$\mathbf{CLscore} = 1_n\mu + \mathbf{age} + \mathbf{herdyear} + \mathbf{pc1} + \mathbf{pc2} + \mathbf{animal} + \boldsymbol{e}$$

where **CLscore** is a n (number of phenotypes) × 1 vector of CLscores, μ was the overall mean, $\mathbf{1}_n$ is a vector of 1s, **age** was a vector of ages fitted as covariate, **heardyear** is vector of contemporary groups (fitted as a fixed effect), **pc1** and **pc2** were the individual animal loadings for principal components 1 and 2, respectively (where the **pc**s were derived from the genomic relationship matrix among animals), and **animal** was a vector of random effects distributed $N(0,\boldsymbol{G}\sigma_g^2)$, where $\boldsymbol{G}$ is the genomic relationship matrix among the heifers constructed from the SNP genotypes (either 24K or 728K) as described by VanRaden (2008), σ_g^2 is the genetic variation captured by the SNP, and $\boldsymbol{e}$ is vector of random error terms, distributed $N(0,\boldsymbol{I}\sigma_e^2)$, where σ_e^2 is the error variance. Genomic heritability of CLscore was estimated with ASREML (Gilmour et al., 2009).

BayesR (Erbe et al., 2012) predicts SNP effects directly and assumes that SNP effects are drawn from the mixture of four normal distributions. The BayesR model was:

$$\mathbf{CLscore} = 1_n\mu + \mathbf{age} + \mathbf{heardyear} + \mathbf{pc1} + \mathbf{pc2} + \mathbf{Zg} + \boldsymbol{e}$$

where models terms are as described above, and $\boldsymbol{g}$ = vector of m SNP effects (m = 20,414 or 728,785), and $\boldsymbol{g} \sim N\left(0,\sigma_i^2\right)$ with four possibilities for $\sigma_i^2 = \left\{0, 0.0001\sigma_g^2 * 0.001\sigma_g^2 * 0.01\sigma_g^2\right\}$, where σ_g^2 is the genetic variance of the trait. So each SNPs is from one of four possible normal distributions: $N(0,0\sigma_g^2)$,) $N(0,0.0001\sigma_g^2)$, $N(0,0.001\sigma_g^2)$, and $N(0,0.01\sigma_g^2)$. $\boldsymbol{Z}$ is the standardized $n \times m$

genotype matrix. As described by Erbe et al. (2012), there are two latent parameters in the BayesR model, $b(i,k)$ and Pr.

$b(i,k)$ defines whether or not SNP i follows normal distribution k ($k = 1,2,3,4$), with

$$p(g_i|b(i,k)) = \begin{cases} 0, & b(i,1) = 1 \\ \frac{1}{\sqrt{2\pi\sigma_i^2[k]}} \exp\left(-\frac{g_i^2}{2\sigma_i^2[k]}\right), & b(i,k) = 1(k = 2,3,4) \end{cases}.$$

Parameter **Pr** defines the proportion of all the SNPs in each of four normal distributions. The prior of **Pr** is a Dirichlet distribution $\mathbf{Pr} \sim \text{Dirichlet}(\alpha)$, with $\boldsymbol{\alpha} = [1,1,1,1]$. The conditional distribution of SNP effect on the proportion parameter **Pr** is: $p(g_i \mid \mathbf{Pr}) = \text{Pr}_1 \times N(0,0\sigma_g^2 + \text{Pr}_2 \times N(0,0.0001\sigma_g^2 + \text{Pr}_3 \times N(0,0.001\sigma_g^2 + \text{Pr}_4 \times N(0,0.01\sigma_g^2)$

BayesR was implemented with Gibbs sampling to construct posterior distributions for the parameters including SNP effects as described by Moser et al. (2015). There were 50,000 iterations of the Gibbs chain with the first 20,000 iterations discarded as burn in. GEBV for validation animals were calculated as $\text{GEBV} = \boldsymbol{Z}\hat{g}$

Validation

To investigate the accuracy of genomic evaluations, two validation strategies were used. Either the entire last year of data (2014) were predicted, using all the other data as a reference (with phenotypes from 2014 born heifers excluded). That is, genomic breeding values for heifers in 2014 were predicted with 2011, 2012, and 2013 data. The genomic breeding values for these heifers were then correlated with their actual CLscores, corrected for fixed effects described above. The correlation was calculated within herds then averaged across herds within a breed.

In the second validation approach, each herd's data was entirely omitted in turn, genomic breeding values were estimated for the omitted herd using all the other herds, then the genomic breeding values were correlated with CLscore (corrected for fixed effects) for the omitted herd.

For each type of validation, reference populations were either of a single breed (the same as the validation set being predicted), or included all three breeds. For example, for within breed prediction, for a 2014 heifer validation cohort from a Brahman herd, only Brahman data were used as reference data. For multi-breed predictions, all other data regardless of breed were used. Note that for BayesR with 24K SNPs, results were almost identical to those from GBLUP with 24K SNPs, so are not presented here.

RESULTS

Based on the SNP genotypes, Droughtmasters were the most diverse breed, followed by Brahmans and Santa Gertrudis—in a principal component plot, Droughtmasters were clearly the most dispersed (Figure 1a). This is reflected in effective population size estimates derived from linkage disequilibrium (using the methods of Hayes et al. (2003) among SNP markers). The estimates of effective population size were 484, 576, and 373 for Brahman, Droughtmaster, and Santa Gertrudis, respectively. For comparison, the estimate of effective population size in Angus cattle using the same method was 101 (Bovine HapMap Consortium, 2009).

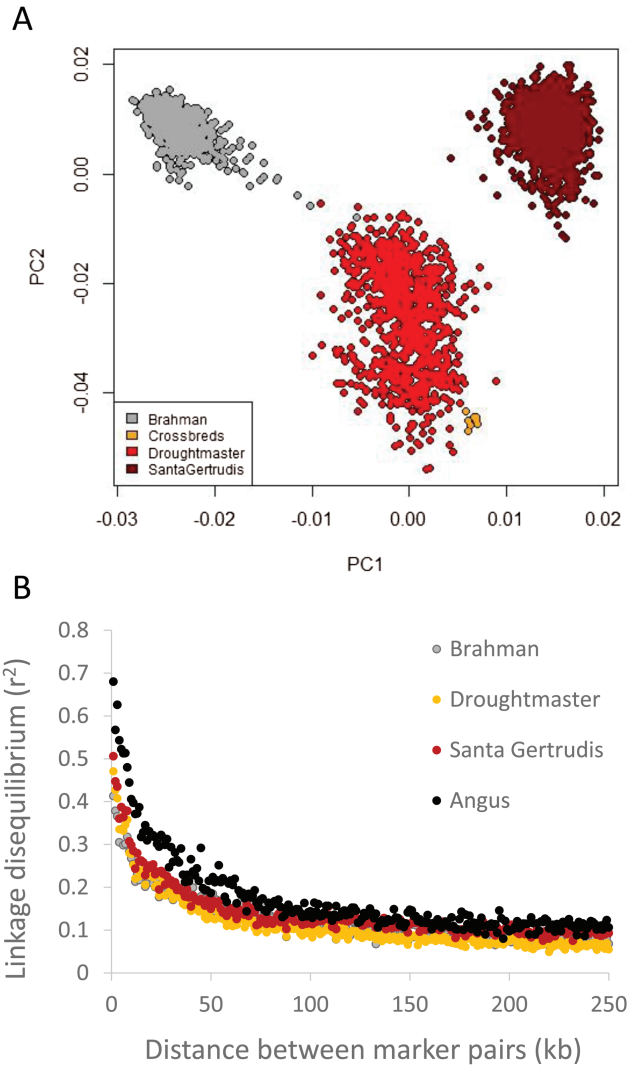

Figure 1. (a) Principal component analysis of SNP genotypes for Brahman, Droughtmaster, and Santa Gertrudis heifers. The first axis (PC1) separates animals on *Bos indicus* content. The second axis (PC2) separates animals on *Bos taurus* breed that contributed to the composite, for Santa Gertrudis and Droughtmasters. (b) Extent of linkage disequilibrium for each breed. The 728K SNPs array has a density of approximately an SNP every 7 kb, while the 24K array has a density of an SNP every ~125 kb. The 24K array genotypes were used to generate these plots.

The extent of linkage disequilibrium for each breed shows that linkage disequilibrium for the three tropical breeds was considerably lower, particularly at short distances between markers, than for Angus cattle, a representative *Bos taurus* breed. Droughtmasters had the lowest level of linkage disequilibrium at most distances (Figure 1b).

The genomic heritability of CLscore estimated with GBLUP was 0.22 ± 0.03 with 24K SNP, and 0.24 ± 0.03 with 728K SNPs, indicating that the higher density SNP captured slightly more of the genetic variance for the trait, although the difference was not significant. With BayesR, the estimate of heritability was 0.26 ± 0.03, indicating that BayesR with the high-density SNP may capture slightly more of the genetic variance, though again the difference was not significant between GBLUP and BayesR.

The accuracy of genomic breeding values, from the validation studies, was higher when predicting the last year of data (all herds included), than when entire herds were left out of the reference set and predicted, Figure 2a. When predicting the last year of data (2014), accuracy for Santa Gertrudis was higher than the other breeds for the within breed genomic evaluations for a number of the comparisons, likely reflecting the larger number of animals in the reference set for this breed (Table 1). We tested this by reducing the number of animals with phenotypes in the Santa Gertrudis reference by half, such that the number in the reference was similar to that for Droughtmasters. The accuracy of genomic breeding values was then reduced to a similar level to that achieved for Droughtmasters, suggesting the greater accuracy achieved for Santa Gertrudis when all data are used does indeed reflect the fact that there are more Santa Gertrudis heifers in the reference set.

The accuracy of across herd prediction was substantially higher when these predictions were based on 728K SNPs rather than 24K SNPs, Figure 2b, provided predictions were multi-breed. These results likely reflect the low levels of linkage disequilibrium (LD) in the three breeds—large numbers of SNP are required before the effects of all mutations affecting CLscore across the genome are captured. That is, large numbers of SNP are required to ensure all mutations are in high linkage disequilibrium with at least one SNP. Consistent with this hypothesis, the breed that gained the most (in accuracy of prediction) from the high-density markers was Droughtmaster, the breed with the highest effective population size and lowest levels of LD. In addition, Droughtmaster is a graded up composite "breed" of Brahman and initially shorthorn, but other *Bos taurus* breeds have been used in more recent times. Santa Gertrudis is a stabilized cross of Beef shorthorn and Brahman. Hence Droughtmaster could be expected to get some benefit from including Santa Gertrudis and Brahman data in the genomic analysis. Within breeds, shifting from 24K to 728K SNPs did not improve accuracies, this is likely a reflection of the relatively small numbers of animals available within each breed that were used to estimate SNP effects.

DISCUSSION

This study demonstrates that multi-breed genomic evaluations for fertility are possible in northern beef cattle, and genomic breeding values with moderate accuracies for a trait such as CLscore for heifers, an indicator trait for age at puberty, can be produced. CLscore is a one-off assessment of whether females have reached puberty or not based on the presence or absence of a CL or CA (corpus albicans). The CL experiences luteolysis at about day 17 of the cycle and regresses as a CA to usually become invisible beyond about 10 mm in diameter at ovulation. One limitation of this trait that should be pointed out is that in cycling females, a corpus hemorrhagica (CH) may not be visible, so that possibly 14% of cycling animals may be mis-diagnosed as acyclic using this method (Bicalho et al., 2008). The effect of this will be to lower the heritability of the trait, as it will be the same for all herds if assessed in a similar way. Despite this potential source of error, we observed moderate heritability for this trait (0.26), and it is feasible to measure this trait for large numbers of herds in extensive tropical environments. Heritability will be highest for CLscore when heifer cohorts are assessed as close as possible to the time when ~50% reach puberty (as was achieved for the herds in this study). This will be between one and 2 yr of age in most situations in Northern Australia, and for most tropical environments, but later for cohorts that have experienced the most difficult nutritional circumstances.

The accuracies of genomic predictions for CLscore were highest when all herds had some information in the reference population (e.g., from previous heifer cohorts), that is when 2014 heifers were used as a validation. In this case, using either higher density markers or BayesR only gave modest improvements in genomic prediction accuracy. Additionally, the advantage of multi-breed vs. single-breed evaluations for this validation strategy was small. These results suggest that if a herd is in the reference population, most of the information to predict future cohorts of the herd come from within herd information, i.e., linkage (particularly there is limited use of sires across herds,

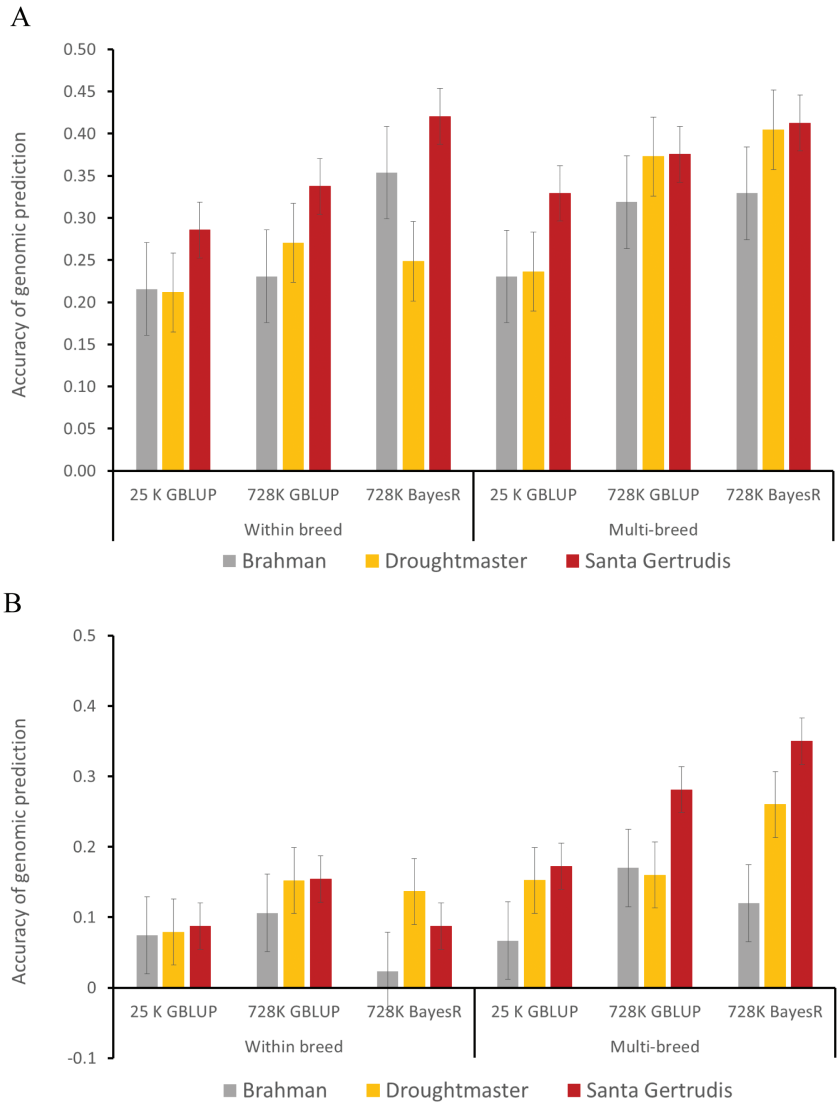

Figure 2. Accuracy of GEBV for corpus luteum score (**CLscore**) in heifers. (a) When the last year cohort (2014) of heifers with CLscores for each herd was dropped from the reference population and used for validation, such that every herd had heifers both in the reference population and the validation population. The accuracy of GEBV was then calculated as the correlation between the GEBV for the last year cohort of heifers and actual CLscore, divided by the square root of the heritability of CLscore (our estimate of h^2 was 0.24 using 728,785 SNPs). (b) When each herd in turn was removed in its entirety from the reference population, GEBV for all heifers in the omitted herd were predicted. The accuracy of GEBV was then calculated as the correlation between CLscore and GEBV in the omitted herd, and this was averaged across herds. For both validation strategies, accuracy of GEBV for single breed and multi-breed evaluations were assessed.

as was the case here), and 24K SNPs are sufficient to capture this.

The results were quite different when the validation involved predicting entire herds that were omitted from the reference population. In this situation, accuracies of predicting CLscore were very low with 24K SNPs or single breed evaluations. The accuracy of prediction increased considerably when predictions were made using a multi-breed reference, BayesR and 728K SNPs. Taken together, these results indicate that the accuracy of genomic predictions for herds not represented in the reference population depends on LD between the SNP and causal mutations affecting the trait (such that 728K SNPs are required for accurate predictions), and this LD persists across breed (at least for the three breeds considered here).

In most *Bos taurus* breeds of cattle, the advantage of moving from low-density (e.g. 50K) to high-density (e.g. 777K) SNP in terms of accuracy of genomic predictions is zero to small within breed (VanRaden et al., 2013, Gunia et al., 2014). This likely reflects the small effective population size of these breeds. Macleod et al. (2016) demonstrated that the increase in accuracy of prediction from higher density of markers, up to full genome sequence, was dependent on effective population size (N_e), with no advantage expected when N_e was 100, a reasonable advantage when N_e was 1,000, and a large advantage when N_e was 10,000. Our results demonstrate that in Brahman, Droughtmaster, and Santa Gertrudis, which all have an $N_e > 300$, high-density SNP (728K) results in higher accuracy of genomic

prediction, and additionally results in multi-breed evaluations contribute additional accuracy.

We did not observe any individual SNP with large effects on CLscore. As a result of running BayesR, the posterior probability that each SNP explains 1% of the variance or more is derived Figure 3a. The highest posterior probability of an SNP explaining 1% of the variance or greater was 0.24 for an SNP on chromosome 17 (36,395,706 bp). The fact that there were no SNP with higher posterior probabilities of explaining 1% of the variance suggests a highly polygenic genetic architecture for CLscore. A mutation in *Plag1*, a gene on chromosome 14, has been reported to affect age at puberty in Brahman cattle (Fortes et al., 2013). We do find a group of SNP with elevated posterior probabilities in this region (Figure 3a). In addition, we ran a traditional SNP by SNP genome-wide association study with the CLscore data and in this GWAS, the *Plag1* SNP (chromosome 14, 25,015,640 bp) was the fourth most significant SNP ($P = 0.00011$). The minor allele frequency for the SNP was 38% in Brahman, 20% in Droughtmasters, and 7% in Santa Gertrudis. However, even the effect of this mutation was modest for CLscore. There were a series of significant SNPs at the start of chromosome 21, and the same SNP had reasonably high posterior probabilities with BayesR (Figure 3b).

The second validation scenario considered here is probably more likely to reflect the application of genomic prediction in tropical beef cattle in the future. That is, a small proportion of herds will make up the reference population, and the majority of herds will not have animals in the reference. Our results suggest in this situation, genomic evaluations should be multi-breed and based on high density (e.g. 728K) SNP.

We have not actually demonstrated here that including information from a large number of animals on CLscore can increase accuracy of genomic predictions for age at puberty, where age at puberty is defined more precisely (e.g., in days, Johnston et al., 2009). An accompanying paper (Engle et al., 2018) uses a multi-trait approach, with data both on age at puberty as defined by Johnston et al. (2009) and CLscore to show that the accuracy of genomic predictions for age at puberty does benefit from inclusion of genotyped animals measured for CLscore.

It should also be pointed out that although we made use of multiple breed information here, the analysis produces genomic breeding values on a different and arbitrary base for each breed. To

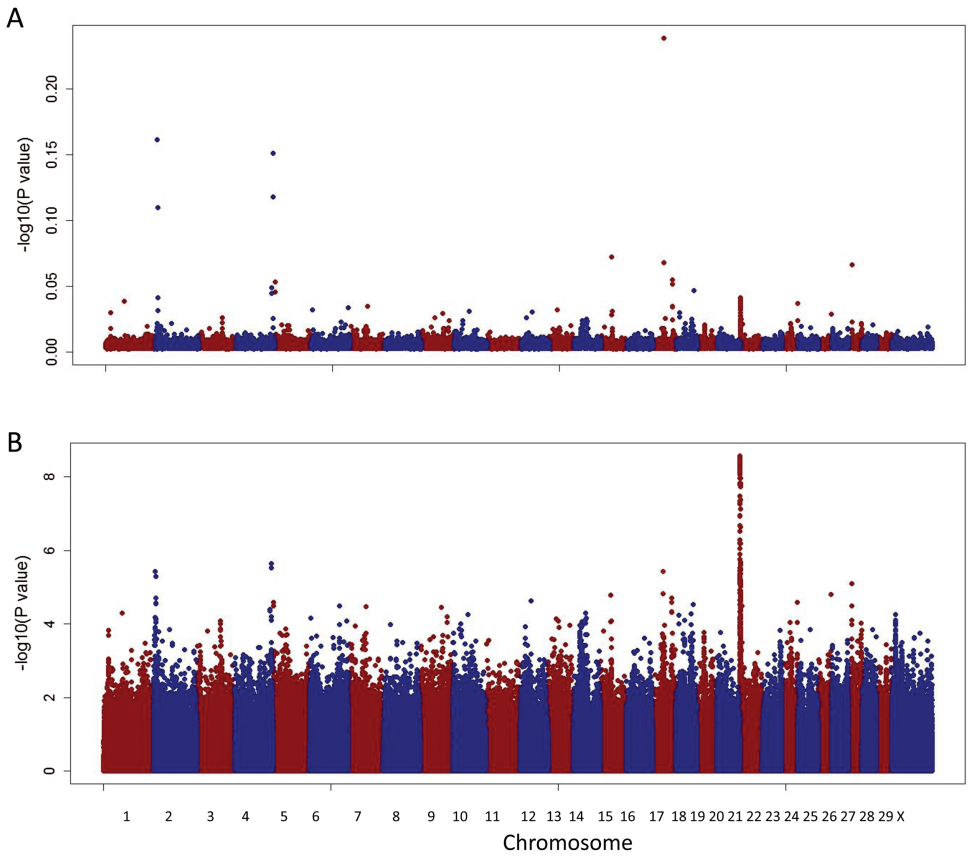

Figure 3. (A) Posterior probability of inclusion of an SNP in the BayesR model, for 728K genome-wide SNPs. The reference population was all 3,696 heifers with corpus luteum score (**CLscore**) phenotypes. Red denotes odd numbered chromosomes, blue denotes even numbered chromosomes. (B) Genome-wide association study, fitting each SNP in turn, using the same data.

produce genomic breeding values on the same base for the breeds, contemporary groups consisting of animals of multiple breeds are required.

ACKNOWLEDGMENTS

The authors would sincerely like to thank the seven participating herds. The research was funded by the Queensland Government Smart Futures Research Partnerships Program.

LITERATURE CITED

Barwick, S. A., D. J. Johnston, H. M. Burrow, R. G. Holroyd, G. Fordyce, M. L. Wolcott, D. Sim, and M. T. Sullivan. 2009. Genetics of heifer performance in 'wet' and 'dry' seasons and their relationships with steer performance in two tropical beef genotypes. Anim. Prod. Sci. 49:367–382. doi.org/10.1071/EA08273

Berry, D. P., E. Wall, and J. E. Pryce. 2014. Genetics and genomics of reproductive performance in dairy and beef cattle. Animal. 8 (Suppl. 1):105–121. doi:10.1017/S1751731114000743

Bicalho, R. C., K. N. Galvão, C. L. Guard, and J. E. Santos. 2008. Optimizing the accuracy of detecting a functional corpus luteum in dairy cows. Theriogenology 70:199–207. doi:10.1016/j.theriogenology.2008.03.015

Corbet, N. J., J. M. Allen, A. R. Laing, G. Fordyce, M. R. McGowan, and B. M. Burns. 2017. Using ultrasound to derive new reproductive traits in tropical beef breeds: implications for genetic evaluation. Anim. Prod. Sci. doi.org/10.1071/AN16616

Engle, B.N., N. J. Corbet, J. M. Allen, A. R. Laing, G. Fordyce, M. R. McGowan, B. M. Burns, R. E. Lyons, and B. J. Hayes. 2018. Multivariate genomic predictions for age at puberty in tropically adapted beef heifers. J. Anim. Sci. 97:90–100.

Erbe, M., B. J. Hayes, L. K. Matukumalli, S. Goswami, P. J. Bowman, C. M. Reich, B. A. Mason, and M. E. Goddard. 2012. Improving accuracy of genomic predictions within and between dairy cattle breeds with imputed high-density single nucleotide polymorphism panels. J. Dairy Sci. 95:4114–4129. doi:10.3168/jds.2011-5019

Farah, M. M., A. A. Swan, M. R. Fortes, R. Fonseca, S. S. Moore, and M. J. Kelly. 2016. Accuracy of genomic selection for age at puberty in a multi-breed population of tropically adapted beef cattle. Anim. Genet. 47:3–11. doi:10.1111/age.12362

Fordyce, G., S. Barwick, N. J. Corbet, B. M. Burns, and B. Holmes. 2012. Appendix 13 – Impact of improved reproduction in northern Australian cow herds. In Beef CRC Exit Report, Ed. Burrow, H. Cooperative Research Centres, Canberra, Australia.

Forni, S., and L. G. Albuquerque. 2005. Estimates of genetic correlations between days to calving and reproductive and weight traits in Nelore cattle. J. Anim. Sci. 83:1511–1515. doi:10.2527/2005.8371511x

Fortes, M. R., K. Kemper, S. Sasazaki, A. Reverter, J. E. Pryce, W. Barendse, R. Bunch, R. McCulloch, B. Harrison, S. Bolormaa, et al. 2013. Evidence for pleiotropism and recent selection in the PLAG1 region in Australian beef cattle. Anim. Genet. 44:636–647. doi:10.1111/age.12075

Gibbs, R. A., J. F. Taylor, C. P. Van Tassell, W. Barendse, K. A. Eversole, C. A. Gill, R. D. Green, D. L. Hamernik, S. M. Kappes, S. Lien, et al. 2009. Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds. Science. 324:528–532. doi: 10.1126/science.1167936

Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009. ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK. www.vsni.co.uk

Goddard, M. E., and B. J. Hayes. 2009. Mapping genes for complex traits in domestic animals and their use in breeding programmes. Nat. Rev. Genet. 10:381–391. doi:10.1038/nrg2575

Gunia, M., R. Saintilan, E. Venot, C. Hozé, M. N. Fouilloux, and F. Phocas. 2014. Genomic prediction in French charolais beef cattle using high-density single nucleotide polymorphism markers. J. Anim. Sci. 92:3258–3269. doi:10.2527/jas.2013-7478

Hayes, B. J., P. M. Visscher, H. C. McPartlan, and M. E. Goddard. 2003. Novel multilocus measure of linkage disequilibrium to estimate past effective population size. Genome Res. 13:635–643. doi:10.1101/gr.387103

Johnston, D. J., S. A. Barwick, N. J. Corbet, G. Fordyce, R. G. Holroyd, P. J. Williams, and H. M. Burrow. 2009. Genetics of heifer puberty in two tropical beef genotypes in northern Australia and associations with heifer- and steer-production traits. Anim. Prod. Sci. 49:399–412. doi.org/10.1071/EA08276

Johnston, D. J., S. A. Barwick, G. Fordyce, R. G. Holroyd, P. J. Williams, N. J. Corbet, and T. Grant. 2013. Genetics of early and lifetime annual reproductive performance in cows of two tropical beef genotypes in northern Australia. Anim. Prod. Sci. 54:1–15. doi.org/10.1071/AN13043

MacLeod, I. M., P. J. Bowman, C. J. Vander Jagt, M. Haile-Mariam, K. E. Kemper, A. J. Chamberlain, C. Schrooten, B. J. Hayes, and M. E. Goddard. 2016. Exploiting biological priors and sequence variants enhances QTL discovery and genomic prediction of complex traits. BMC Genomics 17:144. doi:10.1186/s12864-016-2443-6

Moser, G., S. H. Lee, B. J. Hayes, M. E. Goddard, N. R. Wray, and P. M. Visscher. 2015. Simultaneous discovery, estimation and prediction analysis of complex traits using a Bayesian mixture model. PLoS Genet. 11:e1004969. doi:10.1371/journal.pgen.1004969

Sargolzaei, M., J. P. Chesnais, and F. S. Schenkel. 2014. A new approach for efficient genotype imputation using information from relatives. BMC Genomics 15:478. doi:10.1186/1471-2164-15-478

Taylor, W. J., and T. H. Rudder. 1986. Reduction of sale age for export carcases: will it affect beef producers in tropical regions? Proc. Aust. Soc. Anim. Prod.. 16:379–382.

VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91:4414–4423. doi:10.3168/jds.2007-0980

VanRaden, P. M., D. J. Null, M. Sargolzaei, G. R. Wiggans, M. E. Tooker, J. B. Cole, T. S. Sonstegard, E. E. Connor, M. Winters, J. B. van Kaam, et al. 2013. Genomic imputation and evaluation using high-density Holstein genotypes. J. Dairy Sci. 96:668–678. doi: 10.3168/jds.2012–5702

Zhang, Y. D., D. J. Johnston, S. Bolormaa, R. J. Hawken, and B. Tier. 2014. Genomic selection for female reproduction in Australian tropically adapted beef cattle. Anim. Prod. Sci. 54:16–24. doi.org/10.1071/AN13016