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Comparison of Bayesian methods for genomic prediction for resistance to worm infection in meat sheep

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ABSTRACT. The objective of this study was to compare the performance of various Bayesian methods for genomic prediction of characteristics indicative of resistance to worms in Santa Inês sheep. Phenotypic records were collected from 271 animals belonging to six breeders in the states of Piauí and Maranhão, five from commercial herds and one from the conservation center of the research unit of Embrapa Central-North in Campo Maior, Piauí. Phenotypic records were collected from 271 animals of the Santa Inês sheep breed

belonging to six breeders located Sub-região Centro-Norte do Brasil in the states of Piauí and Maranhão, five coming from commercial herds and one from herds at the conservation center of the federal research unit Embrapa Central-North (Campo Maior, Piauí). Phenotypic records of *Strongyloides* sp. eggs in the feces (STE), log transformed fecal egg count (LFEC), FAMACHA score of the ocular conjunctiva (FAM), and body condition score (BCS) were used. All animals were genotyped using the OvineSNP50 BeadChip (Illumina Inc.). After quality control, 44,548 SNP markers and all the DNA samples remained for further analyses. The following models were tested to estimate the effects of markers: Bayesian ridge regression (BRR), Bayes A, Bayes B, Bayes C, and Bayesian least absolute shrinkage and selection operator (BLASSO). The correlations between Genomic Breeding Values (GEBVs) and observed breeding values were calculated and used as indicators of prediction accuracy of the genomic models. We also calculated the accuracy of the pedigree-based BLUP for comparison. Variance components, heritability, and GEBvs were calculated using the BRR model. The BRR model was considered best, due to its prediction accuracy and because this model used the lowest number of parameters. Accuracy gains higher than 60% were obtained using Bayesian models in comparison to the pedigree-based model. The heritability estimates were 0.560, 0.242, 0.253, and 0.244 for STE, LFEC, FAM, and BCS, respectively. The Bayesian models showed similar performance for prediction accuracy and significantly outperformed the pedigree-based model. The BRR model is the most recommended for genomic selection for the traits evaluated.

INTRODUCTION

Santa Inês is a hairless sheep breed originating from the Northeast of Brazil, which has stood out for decades in the Brazilian meat sheep industry, due to its desirable characteristics such as meat and skin qualities, prolificacy, maternal capacity and adaptability (de Simoni Gouveia et al., 2017). The incidence of worm infections has been frequently mentioned as a major factor that negatively affects sheep production worldwide (Snyman and Fisher, 2019). In addition to the high costs involved in the acquisition and application of anthelmintics, drug-resistant nematodes have become an international problem in sheep farming (Zvinorova et al., 2016). Due to the factors mentioned above, a search for new control strategies has been stimulated. Selection of animals genetically resistant to gastrointestinal nematode infections is considered one of the main strategies (Kemper et al., 2010).

Traditionally, the genetic improvement of animals for complex traits has been conducted through selection based on pedigree and phenotype records. Since the

implementation of genomic selection in the early years of the twenty-first century (Meuwissen et al., 2001), it has been possible to include information of single nucleotide polymorphism (SNP) markers in animal breeding schemes. Genomic selection provides more accurate estimated breeding values in comparison to the traditional pedigree-based selection, especially for low heritability traits (Dekkers, 2007). Furthermore, genomic selection enables the evaluation of the genetic merit for traits measured late in animal's life and for traits that are difficult or expensive to measure (Meuwissen et al., 2016).

The difference among genomic approaches used for prediction of genetic merit is basically the assumptions about marker effects (de los Campos et al., 2009; Habier et al., 2011; Meuwissen et al., 2016). Bayesian methods represent some of the main approaches used for estimation of marker effects (Habier et al., 2011; Meuwissen et al., 2016). The popularity of Bayesian methods for genomic predictions is especially due to the possibility to model marker effects using different prior distributions (Fernando et al., 2014). In general, genomic prediction methods may have different performance when different phenotypes are used (Usai et al., 2009; Habier et al., 2011). Furthermore, the results of predictions may be different due to differences in genetic architecture of different traits (Hayes et al., 2009) and this can influence the prediction accuracy. The accuracy of genomic breeding values is influenced by several factors, such as the trait heritability, the reference population size, the method used for estimation of SNP effects, linkage disequilibrium between markers and quantitative trait loci (QTL), and the distribution of QTL effects (Bastiaansen et al., 2012). Therefore, it is important to compare the performance of different methods using real data and identify the methods that provide the most accurate predictions. Thus, continuing the previous work of our research group (Vieira et al., 2021), the aim of our current study was to compare the performance of different Bayesian methods used for the genomic prediction of traits that indicate resistance to gastrointestinal parasitic infections in Santa Inês sheep.

MATERIAL AND METHODS

Experimental characterization

The present study is a continuation of our research project, in which genetic parameters and genetic values are estimated using single and multi-trait analyses for resistance to infection by gastrointestinal nematodes in Santa Inês ewes (Vieira et al., 2021). The present work used Bayesian methods to estimate the parameters. Phenotypic records were collected from 271 animals of the Santa Inês sheep breed belonging to six breeders located in the central-northern region of Brazil: being (1) Floriano/PI, (2) Campo Maior/PI, (2) José de Freitas/PI and (1) Santa Inês/MA which were selected by racial pattern and body size. All properties with an average of 50 animals, raised in a semi-confinement system, with access to pasture during the day and food supplementation in the trough. All properties had an average of 50 animals, raised in a semi-confinement system, with access to pasture during the day and food supplementation in the trough. All animals used in this study were registered with the Brazilian Sheep Farming Association (ARCO) or belonged to the sheep and goat conservation center of the federal research unit Embrapa Meio-Norte (Campo Maior, Piauí).

The resistance of the animals to gastrointestinal nematode infections was assessed based on the following traits: log transformed fecal egg count (LFEC); presence of Strongyloides sp. eggs (STE); FAMACHA score of the ocular conjunctiva (FAM); and body condition score (BCS). The phenotypic records were collected from December 2013 to May 2014 in animals with ages greater than eight months. Fecal samples were taken directly from the animals' rectum using plastic bags labeled with the animal identification (Vieira et al., 2021). A saturated solution of salt (NaCl) was used for quantification of eggs per gram of faeces (epg) by microscopic visualization in McMaster chamber, following the method described by Gordon and Whitlock (1939). The epg values were log transformed, so that $LFEC = \log_{10} (epg + 1)$.

The verification of the coloration of the ocular mucosa of animals was performed using a FAMACHA chart, attributing scores ranging from 1 (robust red) to 5 (white) (Van Wyk and Bath, 2002) that indicate the degree of anaemia of sheep and if the animals require deworming. BCS was measured using a 1-5 scale (Russel et al., 1969). The procedure consisted of the visual appraisal, palpation of the prominences of the spinous and transverse bones of the spine, fat coverage, and muscle development between the last rib and the ileum wing.

The presence or absence of eggs of the genus Strongyloides sp. is binary, i.e., 1 indicates the presence (success) and 0 indicates absence (fail) of this phenotype. For this reason, the normal distribution was assumed for this trait after the binary values were converted into probability of occurrence, dividing the exponential value by the exponential value summed up to one.

Genomic data set

Genomic data were obtained from DNA samples isolated from blood collected in the animal's jugular vein using vacuum tubes containing EDTA anticoagulant. A total of 271 DNA samples were genotyped using the OvineSNP50 BeadChip (Illumina Inc., CA, USA).The genotyping quality control was performed using the package HapEstXXR (Knueppel et al., 2015) of the statistical software R (R Core Team, 2013). Single nucleotide polymorphic markers with unknown positions, located on sex chromosomes or mitochondrial DNA, with minor allele frequency lower than 0.05, call rate lower than 0.95, GenCall score lower than 0.70, and in extreme departure from Hardy-Weinberg equilibrium ($P < 10^{-5}$) were removed. A total of 44,548 SNPs remained for further analyses.

Statistical analyses

Breeding values obtained using the pedigree-based BLUP were estimated using restricted maximum likelihood (REML), with the ASREML software (Gilmour et al., 2009). The genomic estimated breeding values (GEBVs) were obtained using the following Bayesian models: Bayesian ridge regression (BRR); BayesA; BayesB; BayesCπ; and Bayesian LASSO. For the Bayesian models, the data were analyzed using the R package BGLR (Pérez and de los Campos, 2014). The analyses consisted of a chain of 200,000 cycles, burn-in of 30,000 cycles, and thinning parameter of 5.

The fixed effects considered in the models were contemporary group (month and year of collection, farm, and month and year of birth), sex, birth type, and age of the animal

at the moment of collection as a covariate (linear effect). After the phenotypes were obtained, a genome-wide selection (GWS) analysis was considered for each trait using the Bayesian methods in study. All genomic analyses were based on the following model proposed by Meuwissen et al. (2001):

$$y = 1\mu + \sum_i x_i\, g_i + e \qquad \text{(Eq. 1)}$$

where: y is the vector of phenotypes; 1 is a vector with the same dimension of y, with all rows equal 1; μ is the mean of the trait; g_i is the random effect of each SNP marker (i=1,2,...,p); x_i is the incidence matrix of each marker i; and e is the vector of residuals of the model.

Validation and comparison of models

The predictive ability of the models was assessed through cross-validation. For this, the principal component analysis for the matrix of genotypes was carried out to identify subpopulations genetically more distant. Each subpopulation represented a group of individuals that was used in the cross-validation. This division was used to increase the statistical rigor of the predictive ability, as the groups formed by the clustering of the two first principal components are genetically distant. Therefore, the original set of genotypic data containing 271 animals was divided into the subsets G1, G2, and G3, which contained 151, 67, and 53 animals, respectively (Figure 1).
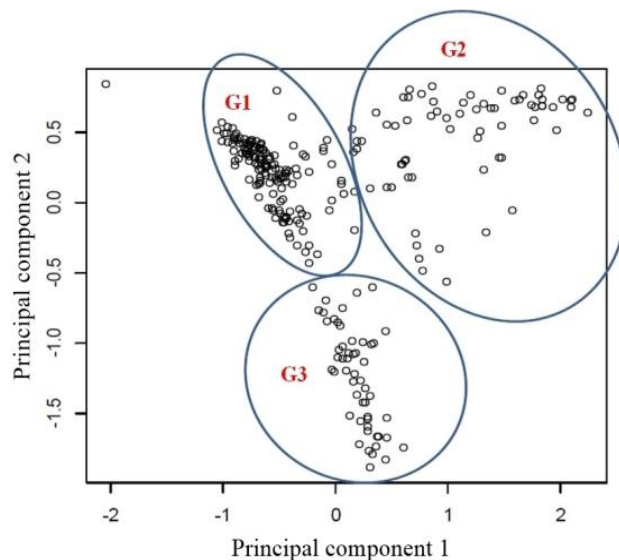
Figure 1. Subdivision of the original population in three groups (G1, G2, and G3) used in the cross-validation analysis to evaluate the predictive ability of the genomic models.

Three analyses were performed for each model so that a subset was removed in each analysis and the remaining data of each subset were subsequently used for validation. Therefore, the predictive ability was calculated as the correlation between the corrected phenotypic values and GEBVs. Considering that three subsets of validation were used, three

correlation estimates were obtained for each model. The means of the correlations were used as a criterion to determine the best model, i.e., the model with higher ability to predict the genetic merit of the individuals using only genomic and phenotypic information (Legarra et al., 2008; Verbyla et al., 2010).

RESULTS

The estimates of predictive accuracy obtained using the different Bayesian models evaluated were not significantly different and the values are within the interval of standard deviation of the models for all traits (Table 1). As the BRR method was considered the best in this study, it was used for estimation of variance components, heritability (Table 2), and prediction of genomic breeding values, considering the complete data set. The magnitude of heritability estimates ranged from moderate (0.24 ± 0.45 for BCS) to high (0.56 ± 0.59 for STE). This indicates that satisfactory gains can be achieved through direct selection for the studied traits.

Table 1. Accuracy estimates of different models for genetic evaluation of Santa Inês sheep for resistance to worm infection.

Trait	BLUP	Bayes A		Bayes B		Bayes C		BLASSO		BRR	
	R ± SD	R ± SD	GA	R ± SD	GA	R ± SD	GA	R ± SD	GA	R ± SD	GA
STE	0.104 ± 0.17	0.175 ± 0.08	0.071	0.170 ± 0.08	0.066	0.175 ± 0.08	0.071	0.180 ± 0.08	0.076	0.169 ± 0.08	0.065
LFEC	-0.022 ± 0.08	0.020 ± 0.05	0.042	0.021 ± 0.05	0.043	0.013 ± 0.05	0.035	0.013 ± 0.05	0.035	0.023 ± 0.04	0.045
FAM	-0.029 ± 0.07	0.005 ± 0.03	0.034	0.022 ± 0.03	0.051	0.009 ± 0.04	0.038	0.021 ± 0.04	0.050	0.009 ± 0.04	0.038
BCS	-0.001 ± 0.07	0.135 ± 0.09	0.136	0.144 ± 0.09	0.145	0.141 ± 0.08	0.142	0.156 ± 0.06	0.157	0.137 ± 0.09	0.138
Trait	BLUP	Bayes A		Bayes B		Bayes C		BLASSO		BRR	
	R ± SD	R ± SD	GA	R ± SD	GA	R ± SD	GA	R ± SD	GA	R ± SD	GA
STE	0.104 ± 0.17	0.175 ± 0.08	0.071	0.170 ± 0.08	0.066	0.175 ± 0.08	0.071	0.180 ± 0.08	0.076	0.169 ± 0.08	0.065
LFEC	-0.022 ± 0.08	0.020 ± 0.05	0.042	0.021 ± 0.05	0.043	0.013 ± 0.05	0.035	0.013 ± 0.05	0.035	0.023 ± 0.04	0.045
FAM	-0.029 ± 0.07	0.005 ± 0.03	0.034	0.022 ± 0.03	0.051	0.009 ± 0.04	0.038	0.021 ± 0.04	0.050	0.009 ± 0.04	0.038
BCS	-0.001 ± 0.07	0.135 ± 0.09	0.136	0.144 ± 0.09	0.145	0.141 ± 0.08	0.142	0.156 ± 0.06	0.157	0.137 ± 0.09	0.138

R= accuracy of the model; SD= standard deviation of the accuracy; GA= gain in accuracy in comparison to the traditional pedigree-based model (BLUP); STE= presence of *Strongyloides* sp. eggs; LFEC= log transformed fecal egg count ($\log_{10}$ (eggs per gram + 1)); FAM= Famacha score; BCS=body condition score.

Table 2. Estimates of variance components and heritability (h^2) for traits associated with resistance to worm infection in Santa Inês sheep obtained using the Bayesian ridge regression method.

	$\sigma_e^2 \pm$ SD	$\sigma_u^2 \pm$ SD	$h^2 \pm$ SD
STE	0.010 ± 0.002	0.014 ± 0.004	0.560 ± 0.590
LFEC	2.351 ± 0.276	0.749 ± 0.249	0.242 ± 0.470
FAM	0.180 ± 0.022	0.061 ± 0.020	0.253 ± 0.480
BCS	0.292 ± 0.033	0.094 ± 0.027	0.244 ± 0.450

σ_u^2 = additive genetic variance; σ_e^2 = residual variance; SD= standard deviation; STE= presence of *Strongyloides* sp. eggs; FEC= log transformed fecal egg count ($\log_{10}$ (eggs per gram + 1)); FAM= Famacha score; BCS= body condition score.

Regarding the estimates of correlation between GEBVs, negative values were obtained between BCS and the other traits in study (Table 3). Higher GEBVs for BCS are

indicative of animals genetically more resistant, whereas for STE, FAM and LFEC, lower GEBVs indicate higher genetic merit of the individuals for resistance to worm infection. Thus, the negative estimates of correlations between BCS and the other traits were favorable. Nevertheless, the low magnitude of all correlation estimates among GEBVs indicates that the indirect selection for these traits could have low efficiency.

After the estimation of GEBVs using the BRR method, ten animals were ranked according to their genetic merit for each trait (Table 4). Four individuals were ranked among those with better GEBVs for FAM and BCS. Furthermore, two out of the sheep with higher genetic merit for FAM were also ranked in the top ten of GEBVs for LFEC.

Table 3. Correlation (above the diagonal) and probability (below the diagonal) between breeding values for traits associated with resistance to gastrointestinal nematode infections obtained using the Bayesian ridge regression method.

	BCS	FAM	STE	LFEC
BCS	1	-0.334	-0.006	-0.323
FAM	<0.0001	1	0.007	0.366
STE	0.990	0.900	1	0.016
LFEC	<0.0001	<0.0001	0.80	1

BCS= body condition score; FAM= Famacha score; STE= presence of *Strongyloides* sp. eggs; LFEC=log transformed fecal egg count ($\log_{10}$ (eggs per gram + 1)).

Table 4. Ranking of animals with the 10 best breeding values for traits associated with resistance to gastrointestinal nematode infections in Santa Inês sheep.

Ranking	LFEC	STE	FAM	BCS
1	152	229	44	44
2	13	264	76	129
3	147	74	39	65
4	44	269	271	158
5	40	176	134	271
6	228	210	19	105
7	230	63	239	203
8	153	267	203	39
9	27	107	33	186
10	76	255	65	249

LFEC=log transformed fecal egg count ($\log_{10}$ (eggs per gram + 1)); STE = presence of *Strongyloides* sp. eggs; FAM=Famacha score; BCS= body condition score.

DISCUSSION

According to de los Campos et al. (2013), most of the studies comparing genomic prediction models using real data have reported small differences in accuracy estimates between models. This could be due to the large number of parameters (P) that are usually estimated using a small sample size (n) (P > n). Consequently, there is not sufficient information for a consistent Bayesian learning process (Pérez and de los Campos, 2014), which decreases the influence of the prior distribution.

Nevertheless, it is important to mention that substantial gain in accuracy is usually obtained using Bayesian methods and other genomic approaches, in comparison to the

traditional pedigree-based BLUP method (Vallejo et al., 2017; Joshi et al., 2020). In the present study, accuracy gains above 60% were obtained for presence of *Strongyloides* sp. eggs using Bayesian methods. Also, gains above 100% were observed for accuracy of breeding values for FAM, LFEC, and BCS obtained using Bayesian methods in comparison to those obtained using the pedigree-based BLUP.

Several authors (Meuwissen et al., 2016; Usai et al., 2009) have also pointed out that Bayesian methods outperform BLUP methods used for prediction of molecular marker effects. However, a more complicated distribution of random effects, such as that used in Bayesian methods is useful only when markers are strongly associated to QTL (Zhong et al., 2009; Habier et al., 2011). According to Zhong et al. (2009), the accuracy of different methods relies on the magnitude of marker effects. Therefore, when there is high linkage disequilibrium between markers in the presence of a low number of QTL, the Bayesian methods are more accurate. On the other hand, the random regression BLUP method (RR-BLUP) is more accurate when several markers have small effects (Clark and van der Werf, 2013).

According to Resende Jr et al. (2012), higher prediction accuracies are expected when models use a reduced number of parameters, especially in the case of traits controlled by few major loci. Bayesian approaches used for markers selection, such as Bayes C, have more realistic assumptions regarding the genetic composition of a trait (VanRaden et al., 2009; Legarra et al., 2011). However, no significant differences were observed in model accuracies obtained using different Bayesian models in the present study. Thus, BRR was considered as the best model, as it used the lowest number of parameters. Superiority of BRR over other Bayesian models has been reported by several authors (Luan et al., 2009; Legarra et al., 2011; Mota et al., 2018).

Other studies have also reported that FEC (transformed or not), FAMACHA, and BCS have sufficient genetic variation to allow mass selection for worm resistance in sheep (e.g. Van Wyk and Bath, 2002; Zvinorova et al., 2016; Snyman and Fisher, 2019). However, several factors (e.g. age of animals, sample size, statistical methodology used, and environmental conditions) may influence the estimation of genetic parameters for these traits. For this reason, heritability estimates ranging from low to high magnitude have been reported in different studies.

There are few reports on genetic parameters for traits indicator of sheep resistance to gastrointestinal nematode infections using genomic information. Using the single-step method (ssGBLUP) and information of Santa Inês sheep genotyped with the Ovine SNP12k BeadChip (Illumina, Inc.), Berton et al. (2017) obtained heritability estimates of 0.11± 0.08 and 0.35 ± 0.11 for log transformed fecal egg count and Famacha score, respectively. Using the same SNP panel, the same methodology, and part of the animals used in the study mentioned above, Amorim et al. (2018) reported heritability of 0.04 ± 0.03 for BCS. To the best of our knowledge, there are no publications reporting heritability estimates for STE in sheep using genomic information. In study using a pedigree-based model, McManus et al. (2009) reported low heritability (0.09 ± 0.06) for fecal egg count of *Strongyloides* in Santa Inês sheep. For fecal egg count of other Strongyles (nematodes of the order Strongylida), Bishop et al. (2004) reported heritability estimates ranging from moderate to high magnitude (0.34 ± 0.15 to 0.43 ± 0.17) in Texel lambs.

Different heritability estimates for similar traits among different studies can be attributed to specific properties of each population, use of different procedures for trait

measurements, and distinct statistical methodologies, as mentioned above. This highlights the importance of the continuous evaluation of heritability for different traits in a specific population over time. Negative and low genetic correlations of BCS with FAM were reported by Riley and Van Wyk. (2009) and Snyman and Fisher. (2019), in Merino and Dohne Merino sheep, respectively. In Santa Inês sheep, Berton et al. (2019) reported low genetic correlation (0.23) between fecal egg count and Famacha score (n = 518).

In our study, four individuals were ranked among those with better GEBVs for FAM and BCS. Furthermore, two out of the sheep with higher genetic merit for FAM were also ranked in the top ten of GEBVs for LFEC (Table 4). This result indicates that these individuals can be selected as parents of the next generation, if breeders aim to improve the genetic resistance to worm infection in Santa Inês sheep flocks.

CONCLUSIONS

The genomic prediction tested by Bayesian methods resulted in similar estimates, not promoting large differences in the genetic merit of Santa Inês sheep for characteristics indicative of resistance to worms. In general, more reliable predictions of genetic merit for all traits were obtained using Bayesian methods, as they resulted in more accurate estimates compared to pedigree-based BLUP. The Bayesian Ridge regression model presented the best performance for estimating the effects of SNP and genomic genetic values for the traits under study.

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ETHICS APPROVAL

The experimental procedures carried out in this study were approved by the Committee on Ethics in the Use of Animals (CEUA) of the Federal University of Piauí (UFPI), Brazil (protocol number 018/2013).

DATA AVAILABILITY STATEMENT

Data available on reasonable request.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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