Application of single-step genomic evaluation using multiple-trait random regression test-day models in dairy cattle

H. R. Oliveira,^{1,2*} D. A. L. Lourenco,³ Y. Masuda,³ I. Misztal,³ S. Tsuruta,³ J. Jamrozik,^{1,4} L. F. Brito,^{1,5}
F. F. Silva,² and F. S. Schenkel¹

¹Centre for Genetic Improvement of Livestock, Department of Animal Biosciences, University of Guelph, Guelph, Ontario, N1G 2W1, Canada

²Department of Animal Science, Universidade Federal de Viçosa, Viçosa, Minas Gerais, 36570-000, Brazil

³Department of Animal and Dairy Science, University of Georgia, Athens 30602

⁴Canadian Dairy Network, Guelph, Ontario, N1K 1E5, Canada

⁵Department of Animal Sciences, Purdue University, West Lafayette, IN 47907

ABSTRACT

Test-day traits are important for genetic evaluation in dairy cattle and are better modeled by multiple-trait random regression models (RRM). The reliability and bias of genomic estimated breeding values (GEBV) predicted using multiple-trait RRM via single-step genomic best linear unbiased prediction (ssGBLUP) were investigated in the 3 major dairy cattle breeds in Canada (i.e., Ayrshire, Holstein, and Jersey). Individual additive genomic random regression coefficients for the test-day traits were predicted using 2 multiple-trait RRM: (1) one for milk, fat, and protein yields in the first, second, and third lactations, and (2) one for somatic cell score in the first, second, and third lactations. The predicted coefficients were used to derive GEBV for each lactation day and, subsequently, the daily GEBV were compared with traditional daily parent averages obtained by BLUP. To ensure compatibility between pedigree and genomic information for genotyped animals, different scaling factors for combining the inverse of genomic ($\mathbf{G}^{-1}$) and pedigree ($\mathbf{A}_{22}^{-1}$) relationship matrices were tested. In addition, the inclusion of only genotypes from animals with accurate breeding values (defined in preliminary analysis) was compared with the inclusion of all available genotypes in the analyses. The ssGBLUP model led to considerably larger validation reliabilities than the BLUP model without genomic information. In general, scaling factors used to combine the $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ matrices had small influence on the validation reliabilities. However, a greater effect was observed in the inflation of GEBV. Less inflated GEBV were obtained by the ssGBLUP compared with the parent average from traditional BLUP when using

optimal scaling factors to combine the $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ matrices. Similar results were observed when including either all available genotypes or only genotypes from animals with accurate breeding values. These findings indicate that ssGBLUP using multiple-trait RRM increases reliability and reduces bias of breeding values of young animals when compared with parent average from traditional BLUP in the Canadian Ayrshire, Holstein, and Jersey breeds.

Key words: Ayrshire, Holstein, Jersey, longitudinal trait

INTRODUCTION

Random regression models (RRM; Schaeffer, 2004) allow taking into account the well-structured covariance pattern among the repeated measurements in genetic analysis of test-day traits. The RRM are especially useful under a multiple-trait approach because it takes into account genetic and environmental correlations between different traits or lactations (or both) over DIM, which enable the identification, for instance, of the time periods that would yield the most favorably correlated genetic responses (Oliveira et al., 2016). Including genomic information to evaluate test-day traits using multiple-trait RRM may result in more accurate breeding values at a young age and, therefore, facilitate the identification and selection of animals with better-shaped lactation curves.

Nowadays, the majority of the breeding programs have implemented genomic selection based on a multiple-step approach (Interbull, 2017). In brief, the prediction of genomic estimated breeding values (GEBV) based on the multiple-step evaluation for test-day traits requires (1) prediction of traditional EBV for each day, based on RRM; (2) estimation of the accumulated yield EBV and subsequent de-regression; (3) prediction of the accumulated direct genomic values (DGV); and (4) combination of accumulated DGV and parent

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*Corresponding author: holivier@uoguelph.ca

average (**PA**) to generate accumulated GEBV. Thus, even though RRM have routinely been used in genetic evaluation of test-day traits in several countries (Interbull, 2018), usually GEBV have been obtained for the accumulated yield, which does not allow selecting for lactation curve pattern. Furthermore, using RRM in all steps of the multiple-step evaluations to estimate GEBV for all DIM does not seem to substantially increase the reliability of the genomic predictions when compared with the reliability of accumulated GEBV (Oliveira et al., 2018).

Relevant studies have shown that simultaneously combining phenotypic records, pedigree, and genomic information in the single-step genomic best linear unbiased prediction approach (**ssGBLUP**) can lead to more accurate and less biased GEBV (Misztal et al., 2009; Aguilar et al., 2010; Christensen and Lund, 2010). In this context, Legarra et al. (2009) showed that genomic relationships are propagated to nongenotyped animals that are related to the genotyped ones through the **H** matrix, which combines the pedigree (**A**) and genomic (**G**) relationship matrices. However, sometimes **A** and **G** are not in the same scale (Misztal, 2017), which requires the use of optimal scaling factors to blend $\mathbf{G}^{-1}$ with the inverse of the pedigree relationship matrix for genotyped animals ($\mathbf{A}_{22}^{-1}$; Vitezica et al., 2011; Misztal et al., 2013). Previous studies already investigated the best combination of scaling factors for the evaluation of milk-related traits using RRM in Nordic Red (Koivula et al., 2015) and Chinese (Kang et al., 2018) dairy cattle. However, ideal scaling factors can be population specific and are not available yet for the most important breeds in Canada.

The use of ssGBLUP based on RRM enable the estimation of GEBV for all DIM, which can increase the reliability of genomic predictions for test-day traits (Koivula et al., 2015; Kang et al., 2018). Despite the improvement in reliability, one of the main constraints for using ssGBLUP based on RRM in national genomic evaluations is the computing time needed to analyze large data sets (Kang et al., 2017). Koivula et al. (2015) suggested that the number of genotyped animals may influence the number of iterations needed for ssGBLUP to converge, which is reflected in the computing time. Thus, including only genotypes from animals with accurate EBV in the analyses might optimize the computational efficiency of the ssGBLUP method. Notwithstanding, the effect of including only genotypes from animals with accurate EBV instead of all available genotypes when performing ssGBLUP analyses on the GEBV predictions is still unknown, especially when using complex models, such as multiple-trait RRM. Therefore, this study aimed to (1) investigate the reli-

ability and bias of GEBV predicted using ssGBLUP and test-day traits in Canadian Ayrshire, Holstein, and Jersey breeds, and (2) evaluate the effect on computing time, reliability, and bias of including only genotypes from animals with accurate EBV in the analyses.

MATERIALS AND METHODS

Data Sets and Quality Control

The Canadian Dairy Network (**CDN**; Guelph, ON, Canada) provided the December 2016 official pedigree, genotypes, and milk, fat and protein yields, and SCC test-day records from the first 3 lactations of Ayrshire, Holstein, and Jersey breeds. Traits within each breed were coded as MY1, FY1, PY1, SCC1, MY2, FY2, PY2, SCC2, MY3, FY3, PY3, and SCC3, where **MY**, **FY**, **PY**, and **SCC** refer to milk, fat, and protein yields, and SCC, respectively, and 1, 2, and 3 refer to the first, second, and third lactations. To analyze all traits assuming a Gaussian distribution, SCC was converted to SCS, using the standard definition implemented in the Canadian official genetic evaluations, which can be described as (Jamrozik et al., 2010; Jamrozik and Schaeffer, 2011; Do et al., 2018):

$$\text{SCS} = \log_2(\text{SCC}/100,000) + 3.$$

Thereafter, SCS have also been coded as SCS1, SCS2, and SCS3 to refer to the first, second, and third lactations, respectively. Outlier phenotypes for each trait ($\mu \pm 3$ SD, within each contemporary group, which were defined by the combination of herd and test-day) were removed from further analyses. Considering all traits together, a total of 8,260 (0.30%), 84,040 (0.12%), and 13,185 (0.71%) test-day records were identified as outliers (and consequently removed from the analyses) for the Ayrshire, Holstein, and Jersey breeds, respectively. In addition, it was required that each contemporary group had at least 3 animals. This quality control filtering excluded 71,740 (2.85%), 444,365 (0.61%), and 151,711 (7.18%) test-day records for Ayrshire, Holstein, and Jersey breeds, respectively. No restriction was imposed on the minimum number of records per lactation per animal. Test-day trait means for all breeds are shown in Supplemental Table S1 (<https://doi.org/10.3168/jds.2018-15466>).

The number of animals genotyped with low-density (<20K) SNP panels was 300, 2,270, and 202; with medium-density (>20K and <60K) SNP panels was 944, 17,105, and 1,157; and with high-density (>60K) SNP panels was 749, 2,459, and 158, for Ayrshire, Holstein, and Jersey, respectively. All analyses in this study were

performed using 50K SNP panel. Therefore, only SNP present on the 50K panel were kept for the animals genotyped using high density panels. In addition, animals genotyped with low- and medium-density panels were imputed by CDN to 50K using the FImpute software (Sargolzaei et al., 2011), for each breed separately. For the imputation process, SNP were not filtered for minor allele frequency. After the genotype imputation process performed by CDN, SNP with Mendelian conflicts, call rate less than 0.90, minor allele frequency less than 0.05, and with a difference between observed and expected heterozygosity higher than 0.15 (Wiggans et al., 2009) were removed using the preGSF90 software (Aguilar et al., 2014; Misztal et al., 2014b). The total number of SNP on the 29 BTA that remained after the quality control was 38,096, 40,658, and 34,500, for the Ayrshire, Holstein, and Jersey breeds, respectively.

After the quality control, a reduced data set was created from the full data set (i.e., from the data set that included all information up to December 2016) by excluding the last 4 yr. Therefore, the reduced data set included all phenotypic information available until 2012 and it was used to predict GEBV using ssGBLUP, and EBV (or PA for validation animals) using the traditional BLUP. The full data set was used to predict current EBV, which were used as a benchmark to validate GEBV and PA obtained from the reduced data set for validation animals by assessing the reliability and bias of genomic predictions. Validation animals were defined as genotyped bulls with minimum trait EBV reliability of 0.65 for the Ayrshire and Jersey breeds, and 0.80 for the Holstein breed. In addition, validation bulls were required to be born from 2007 to 2010 and to have only daughters born after 2012. A total of 97, 1,160, and 88 bulls were used as validation animals for Ayrshire, Holstein, and Jersey, respectively, in the multiple-trait analyses of MY, FY, and PY. For SCS, a total of 87, 1,083, and 82 bulls were used as validation animals for Ayrshire, Holstein, and Jersey, respectively. We have opted for using small validation populations of animals with more reliable trait EBV in this study due to the small benefit of including animals with less reliable EBV to increase the validation population's size, as reported by Oliveira et al. (2018). Details on the approach used to evaluate the prediction reliability and bias for the validation animals are given in the Prediction Reliability and Bias section.

Animals that were not considered as validation bulls and that were born from 1957 to 2010 were included in the training population. It is worth noting that not all animals included in the training population have both phenotype and genotype information. To evaluate the effect of including in the training population genotypes from animals with accurate EBV only, 2 scenarios were

created based on the training animals: (1) including only genotypes from animals with accurate EBV (i.e., genotypes were included in the analyses when the EBV reliability for PY or SCS, estimated in a preliminary analyses, was higher than 0.50 for the Ayrshire and Jersey breeds and higher than 0.65 for the Holstein breed), and (2) including genotypes from all genotyped animals. These preliminary analyses were conducted using animal model and the traditional BLUP method, based on the same RRM used in this study (the model is described in details in the Statistical Analyses section). Thereafter, the EBV reliabilities were estimated as an approximation of reliability of 305-d yield, as described in Jamrozik et al. (2000). Animals that did not satisfy the criteria to be included either in the validation (i.e., genotyped bulls born from 2007 to 2010 that had daughters born only after 2012, and with minimum EBV reliability of 0.65 for the Ayrshire and Jersey breeds, and 0.80 for the Holstein breed) or in the training (i.e., animals that were not considered as validation bulls and that were born from 1957 to 2010) populations were excluded from the analyses. Average EBV reliabilities, standard deviations, and the corresponding 95% confidence interval for the first and second scenarios estimated in the preliminary analyses are shown in Supplemental Table S2 (<https://doi.org/10.3168/jds.2018-15466>). The total number of training animals and test-day records in the reduced and full data sets, and the number of genotyped animals in each scenario, for the different analyses and breeds, are given in Table 1.

It is worth mentioning that the number of test-day records and animals in the pedigree file of the Holstein breed used in this study are higher than the number used in Kang et al. (2018), who analyzed Chinese Holstein (2.8 million test-day records and 0.3 million animals in the pedigree file). The data sets used by Koivula et al. (2015), 85 million test-day records and 5.1 million animals in the pedigree file, are similar to the Holstein data sets used in the current study. However, Koivula et al. (2015) studied Nordic Red Dairy cattle, whereas in this study the focus was on the 3 main dairy cattle breeds in Canada (i.e., Ayrshire, Holstein, and Jersey). In addition, Koivula et al. (2015) and Kang et al. (2018) did not analyze SCS.

Statistical Analyses

Individual additive genetic random regression coefficients for each trait were predicted by the traditional BLUP method, using 2 different multiple-trait RRM: one considering MY, FY, and PY in the first 3 lactations; and another considering SCS in the first 3 lactations. The RRM (Schaeffer et al., 2000) used in

this study were similar to the multiple-trait RRM used in official genetic evaluations performed by CDN in Canada (Interbull, 2018). In general, the multiple-trait RRM used for each breed can be described as

$$y_{ijklm} = \text{HTD}_{ijl} + \sum_{o=1}^5 \beta_{ojkl} z_{ojkl} + \sum_{o=1}^5 \delta_{ojl} z_{ojkl} + \sum_{o=1}^5 \alpha_{ojkl} z_{ojkl} + \sum_{o=1}^5 \rho_{ojkl} z_{ojkl} + e_{ijklm},$$

where y_{ijklm} is the m th phenotypic test-day record of animal k , for the trait l (i.e., MY, FY, PY, or SCS), in the lactation j (i.e., first, second, or third lactation); HTD_{ijl} is the effect of the i th herd-test day for the trait l in the lactation j ; β_{ojl} is the fixed regression coefficient for age-parity-season of calving effect for the trait l in the lactation j ; δ_{ojl} is the random regression coefficient for herd-year of calving effect for the trait l in the lactation j ; α_{ojkl} is the random regression coefficient for the animal additive genetic effect for the animal k , trait l in the lactation j ; ρ_{ojkl} is the random regression coefficient for the permanent environmental effect for the animal k , trait l in the lactation j ; z_{ojkl} is the o th covariate related to the fifth-order Legendre orthogonal polynomials (Kirkpatrick et al., 1990) for animal k , trait l , and lactation j ; and e_{ijklm} is the residual effect. The model assumptions were

$$E[\mathbf{y}] = \mathbf{X}\boldsymbol{\beta} \text{ and } \text{Var} \begin{bmatrix} \boldsymbol{\delta} \\ \boldsymbol{\alpha} \\ \boldsymbol{\rho} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{I} \otimes \mathbf{H}\mathbf{Y}_0 & 0 & 0 & 0 \\ 0 & \mathbf{A} \otimes \mathbf{G}_0 & 0 & 0 \\ 0 & 0 & \mathbf{I} \otimes \mathbf{P}_0 & 0 \\ 0 & 0 & 0 & \mathbf{R} \otimes \mathbf{R}_0 \end{bmatrix},$$

where $E[\mathbf{y}]$ is the expectation of $\mathbf{y}$, $\mathbf{y}$ is the vector of trait phenotypes sorted by test-day and trait/lactation within each animal, $\mathbf{X}$ is the incidence matrix for the fixed effects in the vector $\boldsymbol{\beta}$; $\mathbf{H}\mathbf{Y}_0$, $\mathbf{G}_0$, and $\mathbf{P}_0$ are the variance-covariance matrices among traits due to herd-year of calving, additive genetic, and permanent environmental random effects, respectively; and $\mathbf{R}_0$ is the variance-covariance matrix of residual effects among traits. The $\mathbf{I}$ is an identity matrix, $\mathbf{A}$ is the numerator relationship matrix obtained from pedigree information, and $\mathbf{R}$ is a diagonal matrix of residual variances sorted by test-day and trait/lactation, modeling the heterogeneity of residual variance in 10 different classes of DIM (first: 5 to 35 DIM; second: 36 to 65 DIM; third: 66 to 95 DIM; and so on).

In the ssGBLUP, the $\mathbf{A}$ was replaced by the $\mathbf{H}$ matrix, which combines the pedigree and genomic information. Usually the $\mathbf{H}$ is computationally demanding to compute; however, its inverse has a simple structure (Aguilar et al., 2010; Christensen and Lund, 2010):

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \tau(0.95\mathbf{G} - 0.05\mathbf{A}_{22})^{-1} - \omega\mathbf{A}_{22}^{-1} \end{bmatrix},$$

where $\mathbf{G}^{-1}$ is the inverse of the genomic relationship matrix (calculated using the first method presented in VanRaden, 2008), $\mathbf{A}^{-1}$ is the inverse of the traditional relationship matrix, and $\mathbf{A}_{22}^{-1}$ is the inverse of the section of $\mathbf{A}$ related to genotyped animals. The $\mathbf{A}^{-1}$ included animals up to 10 generations back, and it accounted for inbreeding coefficients. To make $\mathbf{G}$ invertible, 0.05 of $\mathbf{A}_{22}^{-1}$ was added to 0.95 of $\mathbf{G}$. The τ and ω parameters (i.e., scaling factors) were used to account

Table 1. Total number of animals included in the final pedigree file, number of test-day records (phenotypes) in the reduced and full data sets, and number of genotyped animals in both analyzed scenarios

Trait ¹			Ayrshire	Holstein	Jersey
MY, FY, and PY	Pedigree ²	Reduced	204,429	5,085,542	157,718
		Full	221,533	5,976,711	185,737
	Phenotypes ²	Reduced	2,143,941	59,724,786	1,353,185
		Full	2,446,662	72,363,090	1,688,987
	Genotypes ³	Scenario 1	1,716 (542)	8,865 (7,370)	917 (547)
		Scenario 2	1,827 (634)	20,663 (8,517)	1,427 (849)
SCS	Pedigree ²	Reduced	195,099	4,983,668	154,123
		Full	212,141	5,868,988	182,198
	Phenotypes ²	Reduced	1,856,634	54,532,924	1,211,483
		Full	2,153,882	66,752,684	1,541,168
	Genotypes ³	Scenario 1	1,141 (526)	7,329 (7,098)	524 (430)
		Scenario 2	1,827 (634)	20,663 (8,517)	1,427 (849)

¹Milk (MY), fat (FY), and protein (PY) yields in the first, second, and third lactations were analyzed separately from SCS in the first, second, and third lactations.

²Pedigree and phenotypes are shown for the reduced data set (all available information excluding the last 4 yr) and for the full data set.

³Genotype scenarios: (1) including genotypes from animals with accurate EBV only; (2) including genotypes from all genotyped animals; numbers in parentheses show the number of genotyped bulls.

for the reduced genetic variance and for different depths of pedigree, respectively, to make $\mathbf{G}^{-1}$ compatible with $\mathbf{A}_{22}^{-1}$ and also $\mathbf{A}^{-1}$. To evaluate the effect of including only genotypes from animals with accurate EBV in the analyzes or genotypes from all animals, no scaling factors were used to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ in these 2 scenarios. After the definition of the best scenario with respect to the inclusion of genotyped animals in the training population (based on validation reliabilities and regression coefficients), a total of 3 different values were tested for τ (i.e., 1.0, 1.5, and 2.0) and 5 for ω (i.e., 0.6, 0.7, 0.8, 0.9, and 1.0). Values for τ and ω were defined based on the literature, and the best combination of τ and ω parameters for each analyze of each breed was chosen according to the validation reliabilities and regression coefficients (bias).

The additive genetic (estimated by BLUP) and genomic (estimated by ssGBLUP) random regression coefficients were used to derive EBV and GEBV for each DIM, respectively. The vectors of EBV and GEBV for all DIM of each animal were obtained as follows:

$$\text{EBV}_{jkl} = \mathbf{T}\hat{\alpha}_{jkl} \text{ and } \text{GEBV}_{jkl} = \mathbf{T}\hat{\delta}_{jkl},$$

where $\hat{\alpha}_{jkl}$ is the vector of predicted additive genetic coefficients for each animal k , trait l , and lactation j ; $\hat{\delta}_{jkl}$ is the vector of predicted genomic coefficients for each animal k , trait l , and lactation j ; and $\mathbf{T}$ is a matrix of independent covariates for every DIM (ranging from 5 to 305 d), associated with the Legendre polynomial function.

The BLUP90IOD software (Misztal et al., 2002, 2014b), which is based on iteration on data and on the preconditioned conjugate gradient algorithm (PCG; Strandén and Lidauer, 1999; Tsuruta et al., 2001), was used to obtain the solutions of the mixed model equations for all analyses. The PCG algorithm converged when the relative difference between the right-hand and left-hand sides of the mixed model equations for all equations describing the genetic animal effects was smaller than 10^{-12} . The variance components used in this study for both BLUP and ssGBLUP analyses were those estimated in the December 2015 official genetic evaluation performed by CDN using the traditional BLUP. Several ssGBLUP studies have also used the same variance components as the traditional BLUP evaluations (e.g., Koivula et al., 2012; Kang et al., 2017, 2018). The average heritabilities over DIM for MY1, FY1, PY1, SCS1, MY2, FY2, PY2, SCS2, MY3, FY3, PY3, and SCS3, as estimated by CDN, are shown in Supplemental Table S3 (<https://doi.org/10.3168/jds.2018-15466>).

Prediction Reliability and Bias

A proxy of the validation reliability for each trait was calculated as the squared Pearson correlation coefficient between daily GEBV estimated based on the reduced data set and daily EBV estimated based on the full data set, considering only animals in the validation populations. To assess the genomic prediction bias (i.e., inflation or deflation of the GEBV relative to EBV), regression coefficients (b_1) were estimated using a linear regression of the daily EBV estimated based on the full data set on the daily GEBV estimated based on the reduced data set (i.e., $\text{EBV} = b_0 + b_1 \times \text{GEBV}$, where b_0 is the intercept), considering only animals in the validation population and all DIM together. To compare prediction reliability and bias of GEBV to those of PA from traditional genetic evaluation, validation reliabilities and regression coefficients were also calculated using daily PA and daily EBV for the animals in the validation population, estimated based on the reduced and full data sets, respectively (i.e., squared Pearson correlation coefficient between EBV and PA, and b_1 was obtained from $\text{EBV} = b_0 + b_1 \times \text{PA}$).

Computational Demand

To evaluate the feasibility of the use of ssGBLUP based on RRM, the computational demand was also investigated. The number of rounds (iterations) used by the PCG algorithm until the convergence, the average number of cores (processors), and the total computing time were recorded for each analysis. Total computing time was estimated as the amount of central processing unit (CPU) time spent within the process regarding all cores used: in other words, the amount of CPU time spent in user-mode code plus the amount of CPU time spent in the kernel, divided by the average number of cores that were used in the analysis. For the ssGBLUP analyses considering scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$, only the computational demand for the optimal scaling factor of each analysis was reported.

RESULTS

Genotypes from Animals with Accurate EBV Only Versus from All Genotypes

Overall, similar validation reliabilities and regression coefficients (bias) were observed when considering genotypes from only animals with accurate EBV or from all genotyped animals (Tables 2 and 3). Including all available genotypes slightly increased the reliability for the Holstein and Jersey breeds. However, for the Ayr-

Table 2. Validation reliabilities for genomic EBV using genotypes from animals with accurate EBV only ($r_{\text{GEBV}_{\text{acc}}}^2$) and from all ($r_{\text{GEBV}_{\text{all}}}^2$) genotyped animals for Ayrshire, Holstein, and Jersey breeds¹

Trait	Ayrshire		Holstein		Jersey	
	$r_{\text{GEBV}_{\text{acc}}}^2$	$r_{\text{GEBV}_{\text{all}}}^2$	$r_{\text{GEBV}_{\text{acc}}}^2$	$r_{\text{GEBV}_{\text{all}}}^2$	$r_{\text{GEBV}_{\text{acc}}}^2$	$r_{\text{GEBV}_{\text{all}}}^2$
MY1	0.40	0.39	0.62	0.65	0.56	0.58
MY2	0.45	0.44	0.58	0.60	0.48	0.50
MY3	0.48	0.47	0.57	0.59	0.46	0.48
FY1	0.45	0.43	0.57	0.58	0.62	0.62
FY2	0.44	0.44	0.57	0.58	0.60	0.59
FY3	0.46	0.45	0.58	0.59	0.55	0.54
PY1	0.55	0.54	0.66	0.67	0.67	0.68
PY2	0.49	0.48	0.64	0.65	0.61	0.61
PY3	0.51	0.49	0.64	0.64	0.56	0.58
SCS1	0.42	0.43	0.42	0.45	0.28	0.31
SCS2	0.50	0.47	0.46	0.48	0.26	0.28
SCS3	0.49	0.45	0.44	0.46	0.36	0.37

¹Traits: milk (MY1, MY2, MY3), fat (FY1, FY2, FY3), and protein (PY1, PY2, PY3) yield, and SCS (SCS1, SCS2, SCS3) in the first, second, and third lactation, respectively. $r_{\text{GEBV}_{\text{acc}}}^2$ included genotypes from animals with accurate EBV only (EBV reliability for PY or SCS higher than 0.50 for the Ayrshire and Jersey breeds, and higher than 0.65 for the Holstein breed).

shire breed, a small decrease in reliability was observed, as shown in Table 2.

With respect to the regression coefficients, a slight increase in bias of GEBV (i.e., regression coefficients deviating from 1.0) was observed using all available genotypes for SCS in the Ayrshire breed (average regression coefficients considering only accurate and all animals were 0.93 and 0.89, respectively), MY, FY, and PY in the Holstein breed (0.74 and 0.73 for MY, 0.66 and 0.64 for FY, and 0.69 and 0.68 for PY, respectively), and FY and PY in the Jersey breed (0.96 and 0.94 for FY, and 0.85 and 0.84 for PY, respectively). The GEBV were less biased for SCS when using all available genotypes in the Holstein and Jersey breeds (average

regression coefficients considering only accurate and all animals were 0.70 and 0.71 in Holstein, and 0.76 and 0.79 in Jersey, respectively). No difference in average regression coefficients were observed for MY, FY, and PY in the Ayrshire breed, and for MY in the Jersey breed (Table 3) using genotypes from all or accurate animals only.

ssGBLUP Versus Traditional Evaluation of Test-Day Traits and Effect of Scaling Factors

For almost all traits and breeds, the ssGBLUP yielded considerably higher validation reliabilities compared with the model without genomic information,

Table 3. Regression coefficients ($\pm$ SE) for genomic EBV using genotypes from animals with accurate EBV only ($b_{\text{GEBV}_{\text{acc}}}$) and from all ($b_{\text{GEBV}_{\text{all}}}$) genotyped animals for the Ayrshire, Holstein, and Jersey breeds¹

Trait	Ayrshire		Holstein		Jersey	
	$b_{\text{GEBV}_{\text{acc}}}$	$b_{\text{GEBV}_{\text{all}}}$	$b_{\text{GEBV}_{\text{acc}}}$	$b_{\text{GEBV}_{\text{all}}}$	$b_{\text{GEBV}_{\text{acc}}}$	$b_{\text{GEBV}_{\text{all}}}$
MY1	0.65 $\pm$ 0.005	0.64 $\pm$ 0.005	0.76 $\pm$ 0.001	0.75 $\pm$ 0.001	0.89 $\pm$ 0.005	0.89 $\pm$ 0.005
MY2	0.67 $\pm$ 0.004	0.67 $\pm$ 0.004	0.73 $\pm$ 0.001	0.73 $\pm$ 0.001	0.83 $\pm$ 0.005	0.83 $\pm$ 0.005
MY3	0.67 $\pm$ 0.004	0.67 $\pm$ 0.004	0.73 $\pm$ 0.001	0.71 $\pm$ 0.001	0.78 $\pm$ 0.005	0.79 $\pm$ 0.005
FY1	0.66 $\pm$ 0.004	0.65 $\pm$ 0.004	0.64 $\pm$ 0.001	0.62 $\pm$ 0.001	0.99 $\pm$ 0.005	0.98 $\pm$ 0.005
FY2	0.67 $\pm$ 0.004	0.68 $\pm$ 0.004	0.66 $\pm$ 0.001	0.65 $\pm$ 0.001	0.96 $\pm$ 0.005	0.94 $\pm$ 0.005
FY3	0.67 $\pm$ 0.004	0.67 $\pm$ 0.004	0.68 $\pm$ 0.001	0.66 $\pm$ 0.001	0.92 $\pm$ 0.005	0.90 $\pm$ 0.005
PY1	0.70 $\pm$ 0.004	0.70 $\pm$ 0.004	0.68 $\pm$ 0.001	0.67 $\pm$ 0.001	0.89 $\pm$ 0.004	0.88 $\pm$ 0.004
PY2	0.70 $\pm$ 0.004	0.70 $\pm$ 0.004	0.69 $\pm$ 0.001	0.69 $\pm$ 0.001	0.86 $\pm$ 0.004	0.85 $\pm$ 0.004
PY3	0.69 $\pm$ 0.004	0.69 $\pm$ 0.004	0.69 $\pm$ 0.001	0.68 $\pm$ 0.001	0.81 $\pm$ 0.004	0.80 $\pm$ 0.004
SCS1	0.97 $\pm$ 0.007	0.95 $\pm$ 0.007	0.68 $\pm$ 0.001	0.70 $\pm$ 0.001	0.76 $\pm$ 0.008	0.77 $\pm$ 0.007
SCS2	0.93 $\pm$ 0.006	0.87 $\pm$ 0.006	0.71 $\pm$ 0.001	0.73 $\pm$ 0.001	0.74 $\pm$ 0.008	0.76 $\pm$ 0.008
SCS3	0.90 $\pm$ 0.005	0.84 $\pm$ 0.006	0.70 $\pm$ 0.001	0.71 $\pm$ 0.001	0.79 $\pm$ 0.007	0.83 $\pm$ 0.007

¹Traits: milk (MY1, MY2, MY3), fat (FY1, FY2, FY3), and protein (PY1, PY2, PY3) yield, and SCS (SCS1, SCS2, SCS3) in the first, second, and third lactation, respectively. $b_{\text{GEBV}_{\text{acc}}}$ included genotypes from animals with accurate EBV only (EBV reliability for PY or SCS higher than 0.50 for the Ayrshire and Jersey breeds, and higher than 0.65 for the Holstein breed).

even when using no scaling factors (default; $\tau_{1.0}$, $\omega_{1.0}$) to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ (Supplemental Tables S4, S5, and S6; <https://doi.org/10.3168/jds.2018-15466>). However, regression coefficients deviating from 1.0 were obtained for the default ssGBLUP when compared with PA for Ayrshire and Jersey (except for FY in Jersey, where the PA usually had regression coefficients deviating from 1.0 for all lactations). On the other hand, regression coefficients obtained for the default ssGBLUP were closer to 1.0 when compared with PA for the Holstein breed (except for SCS2 and SCS3).

Scaling factors used to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ had, in general, a small influence on the validation reliabilities. However, a greater effect was observed in the regression coefficients. Less biased GEV were obtained from the ssGBLUP method compared with the PA when scaling factors were applied to the $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ for all traits and breeds (Supplemental Tables S4, S5, and S6; <https://doi.org/10.3168/jds.2018-15466>). The scaling factors used to combine $\mathbf{G}^{-1}$ (τ) and $\mathbf{A}_{22}^{-1}$ (ω) that produced the least biased predictions and the highest validation reliabilities were different for each breed and trait. For genomic evaluation of MY, FY, and PY, $\tau = 2.0$ and $\omega = 0.6$ for the Ayrshire, $\tau = 1.5$ and $\omega = 0.6$ for the Holstein, and $\tau = 1.5$ and $\omega = 0.9$ for the Jersey breed yielded the least biased predictions and the highest validation reliabilities. For SCS, the optimal scaling factors were $\tau = 1.0$ and $\omega = 0.9$ for the Ayrshire, $\tau = 2.0$ and $\omega = 0.6$ for the Holstein, and $\tau = 1.0$ and $\omega = 0.6$ for the Jersey breed. Validation reliabilities and regression coefficients estimated using the optimal scaling factors for each breed are shown in Table 4.

The validation reliability patterns of GEV over DIM, for each trait and breed (using all genotyped animals and the optimal scaling factors to combine $\mathbf{G}^{-1}$

and $\mathbf{A}_{22}^{-1}$ for each analysis), are shown in Figure 1. In general, slightly different validation reliability patterns were observed among traits, lactations, and breeds.

Computational Demand

A server with 512G memory and 88 cores [Intel Xeon CPU E5-2699 v4 @ 2.20GHz] was used in all analysis. The total number of rounds to achieve the convergence, the average number of cores, and the total CPU time used for each analysis is shown in Table 5. As expected, including genomic information increased the number of rounds, the number of cores, and the CPU time to complete the analyses. The increase in the number of rounds, cores, and CPU time was higher when including all genotypes available compared with including genotypes only for animals with accurate EBV. However, when comparing ssGBLUP using or not using scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$, a reduction in the total CPU time was observed when including the optimal scaling factors in all analyses (i.e., GEV_{allw} and GEV_{all} in the Table 5).

DISCUSSION

Genotypes from Animals with Accurate EBV Only Versus from All Genotypes

The changes in validation reliabilities due to the inclusion of all available genotypes are linked to the proportion of new genotypes included in the analysis (Table 1) and how accurate the EBV of the additional animals included in the analyses are. For instance, in the genomic evaluation of MY, FY, and PY in the Holstein and Jersey breeds, approximately 133 and

Table 4. Validation reliabilities (r^2) and regression coefficients ($\hat{b}_1 \pm \text{SE}$) for genomic breeding value estimated using all available genotypes and assuming the optimal¹ scaling factors (τ and ω) to blend $\mathbf{A}_{22}^{-1}$ and $\mathbf{G}^{-1}$ for Ayrshire, Holstein, and Jersey breeds

Breed	Lactation	Milk yield		Fat yield		Protein yield		SCS	
		r^2	$\hat{b}_1 \pm \text{SE}$	r^2	$\hat{b}_1 \pm \text{SE}$	r^2	$\hat{b}_1 \pm \text{SE}$	r^2	$\hat{b}_1 \pm \text{SE}$
Ayrshire	First	0.40	0.85 ± 0.006	0.48	0.89 ± 0.005	0.59	0.91 ± 0.004	0.46	1.06 ± 0.007
	Second	0.46	0.90 ± 0.006	0.48	0.90 ± 0.005	0.52	0.89 ± 0.005	0.50	0.97 ± 0.006
	Third	0.49	0.91 ± 0.005	0.49	0.91 ± 0.005	0.53	0.88 ± 0.005	0.49	0.96 ± 0.006
Holstein	First	0.66	0.88 ± 0.001	0.59	0.75 ± 0.001	0.69	0.77 ± 0.001	0.44	0.94 ± 0.002
	Second	0.61	0.86 ± 0.001	0.60	0.78 ± 0.001	0.67	0.79 ± 0.001	0.50	0.97 ± 0.001
	Third	0.61	0.85 ± 0.001	0.61	0.80 ± 0.001	0.66	0.78 ± 0.001	0.48	0.96 ± 0.002
Jersey	First	0.60	1.00 ± 0.005	0.64	1.12 ± 0.005	0.70	0.99 ± 0.004	0.33	0.97 ± 0.009
	Second	0.52	0.95 ± 0.005	0.61	1.08 ± 0.005	0.63	0.96 ± 0.004	0.29	0.98 ± 0.010
	Third	0.51	0.91 ± 0.005	0.56	1.04 ± 0.006	0.59	0.91 ± 0.005	0.40	1.04 ± 0.008

¹ τ = scaling factor used for genomic relationship matrix ($\mathbf{G}^{-1}$); ω = scaling factor used for pedigree relationship matrix ($\mathbf{A}_{22}^{-1}$). For genomic evaluation of milk, fat, and protein yields, the optimal scaling factors were $\tau = 2.0$ and $\omega = 0.6$ for Ayrshire, $\tau = 1.5$ and $\omega = 0.6$ for Holstein, and $\tau = 1.5$ and $\omega = 0.9$ for Jersey. For genomic evaluation of SCS, the optimal scaling factors were $\tau = 1.0$ and $\omega = 0.9$ for Ayrshire, $\tau = 2.0$ and $\omega = 0.6$ for Holstein, and $\tau = 1.0$ and $\omega = 0.6$ for Jersey.

Figure 1. Pattern of validation reliabilities of genomic EBV through DIM, using all genotyped animals, for milk (solid line), fat (dotted line), and protein yield (dashed line), and SCS (dashed-dotted line) from the first (a, d, and g), second (b, e, and h), and third (c, f, and i) lactations of Ayrshire, Holstein, and Jersey breeds, respectively [considering the scaling factors to combine $\mathbf{G}^{-1}$ (τ) and $\mathbf{A}_{22}^{-1}$ (ω) that produced the least biased predictions and the highest validation reliabilities for each breed]. For genomic evaluation of milk, fat, and protein yields: $\tau = 2.0$ and $\omega = 0.6$ for Ayrshire, $\tau = 1.5$ and $\omega = 0.6$ for Holstein, and $\tau = 1.5$ and $\omega = 0.9$ for Jersey were used. For genomic evaluation of SCS: $\tau = 1.0$ and $\omega = 0.9$ for Ayrshire, $\tau = 2.0$ and $\omega = 0.6$ for Holstein, and $\tau = 1.0$ and $\omega = 0.6$ for Jersey were used.

56% new genotypes were included when considering all available genotypes in the population, respectively. For the evaluation of SCS, these proportions increased to approximately 182% for Holstein and 172% for Jersey. In both cases, the accuracy of the EBV and proportion of genotypes included were enough to increase the validation reliabilities (Table 2). These findings are in agreement with Shabalina et al. (2017), who concluded that information from culled animals improved the accuracy of GEBV based on ssGBLUP, and with Patry and Ducrocq (2011), who reported that it is necessary to include information from all genotyped animals in the ssGBLUP evaluation.

For the analysis of MY, FY, and PY in the Ayrshire breed, only 6% new genotypes were included when considering all available genotypes in the analyses (second scenario), which did not contribute to increase the validation reliability. In fact, a slight decrease in the validation reliabilities for the Ayrshire breed was observed, probably due to the inclusion of a low number of animals with extremely low EBV reliability, which increased the amount of noise in the analyses (average reliability for the 1,716 genotyped animals with accurate EBV and for the 111 additional genotyped animals was 0.75 and 0.42 for MY, 0.72 and 0.39 for FY, and 0.72 and 0.39 for PY, respectively). Average

EBV reliability for all traits and breeds, in both scenarios, are shown in Supplemental Table S2 (<https://doi.org/10.3168/jds.2018-15466>). Also, no increase was observed in the validation reliabilities estimated for the evaluation of SCS in the Ayrshire breed, even with approximately 60% new genotypes included in the second scenario. This might be due to the lower heritability for SCS compared with the heritability estimates for MY, FY, and PY. In the case of lower heritability traits (e.g., SCS), the number of animals required to provide additional increase in prediction reliability should be greater than for high heritability traits. The minimum proportion of genotyped animals with low EBV accuracy needed to improve validation reliabilities for different traits should be determined in future studies, especially for small-sized populations such as Ayrshire and Jersey breeds.

Regression coefficients lower than 1.0 were observed for both analyzed scenarios (Table 3), which indicates that the genomic predictions are inflated and that the predicted differences in the genetic merit are biased upward compared with the observed future performance. Regression coefficients deviating from 1.0 were also observed in the second scenario, including all available genotypes, for the majority of traits and breeds. This bias might originate from the use of animals with EBV of low accuracy, which might introduce more noise into the analysis. In addition, pedigree depth for those animals may also contribute to increase the bias, if they have an incomplete pedigree (Misztal, 2017). Koivula et al. (2018) investigated the effect of including genotypes of animals without progeny in the evaluation of Nordic

Red Dairy cattle and concluded that the inclusion of genotypes of the culled bull calves may increase bias in the ssGBLUP evaluation.

The inclusion of all available genotypes is a reasonable principle and follows the BLUP theory, where all information used for making selection decisions should be accounted for in the evaluation (Henderson, 1984). Thus, as the performance of ssGBLUP evaluations that included genotypes from only animals with accurate EBV and from all genotyped animals were similar, all genomic information available was further used to define the most appropriate scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ in this study, for all analyzed breeds.

ssGBLUP Versus Traditional Evaluation of Test-Day Traits and Effect of Scaling Factors

Validation reliabilities estimated for GEBV were generally higher than the validation reliabilities estimated for PA, even when using no scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ (Supplemental Tables S4, S5, and S6; <https://doi.org/10.3168/jds.2018-15466>). These results are in agreement with other studies reported in the literature, such as Koivula et al. (2015) and Baba et al. (2017) that also concluded that ssGBLUP based on RRM increased the validation reliabilities compared with the traditional genetic evaluations based on RRM. Regression coefficients obtained for the default ssGBLUP were closer to 1.0 when compared with PA for all traits in the Holstein breed (except for SCS2 and SCS3), and for FY in the Jersey breed. However, for all traits in the Ayrshire breed, for SCS2 and SCS3 in Holstein

Table 5. Total number of rounds to achieve the convergence, average number of cores, and total central processing unit (CPU) time used for each analyses of each breed¹

Computational parameter	Analysis	MY, FY, and PY			SCS		
		Ayrshire	Holstein	Jersey	Ayrshire	Holstein	Jersey
No. of rounds	EBV _r	1,162	1,251	2,365	1,184	1,188	916
	GEBV _{acc}	1,643	2,317	2,776	1,319	2,027	977
	GEBV _{all}	2,365	3,140	4,670	2,454	3,162	1,626
	GEBV _{allw}	2,126	3,164	4,457	2,277	3,843	1,146
Average no. of cores	EBV _r	5.28	3.59	6.91	8.13	3.10	6.84
	GEBV _{acc}	9.39	6.67	8.81	11.04	3.77	11.84
	GEBV _{all}	10.15	11.81	10.83	11.32	6.43	13.31
	GEBV _{allw}	10.69	12.67	11.38	12.88	7.52	13.80
Total CPU time (d)	EBV _r	0.15	5.10	0.20	0.05	1.26	0.03
	GEBV _{acc}	0.22	10.39	0.25	0.05	2.20	0.03
	GEBV _{all}	0.33	16.08	0.41	0.11	3.50	0.06
	GEBV _{allw}	0.30	15.90	0.38	0.10	3.16	0.04

¹Computational parameters were recorded for analyses conducted based on the reduced data set (all information available until 2012) to estimate breeding value (EBV_r) and genomic breeding values using genotypes from animals with accurate EBV only (GEBV_{acc}), using all genotypes available (GEBV_{all}), and using all genotypes and the optimal scaling factors to combine genomic and pedigree information (GEBV_{allw}). The optimal scaling factors assumed for genomic evaluation of milk (MY), fat (FY), and protein (PY) yields were $\tau = 2.0$ and $\omega = 0.6$ for Ayrshire, $\tau = 1.5$ and $\omega = 0.6$ for Holstein, and $\tau = 1.5$ and $\omega = 0.9$ for Jersey. For genomic evaluation of SCS, the optimal scaling factors were $\tau = 1.0$ and $\omega = 0.9$ for Ayrshire, $\tau = 2.0$ and $\omega = 0.6$ for Holstein, and $\tau = 1.0$ and $\omega = 0.6$ for Jersey. For GEBV_{acc} and GEBV_{all}, both τ and ω were defined as 1.0 for all traits and breeds.

breed, and for MY, PY, and SCS in the Jersey breed, regression coefficients were found to deviate more from 1.0 for GEBV than for PA.

The $\mathbf{H}^{-1}$ matrix used in ssGBLUP (as presented in Aguilar et al., 2010) assumes the correct model, which is only approximated in practice. Thus, additional parameters are usually required for a better model fit. Tsuruta et al. (2011) used τ and ω parameters multiplied by $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$, respectively; they concluded that ω improved convergence and reduced bias in ssGBLUP analysis. Misztal et al. (2013) suggested that optimal scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ decrease the possible inflation of GEBV estimated by ssGBLUP. In fact, regression coefficients closer to 1.0 were obtained in the current study by ssGBLUP using scaling factors compared with the traditional genetic evaluation (Supplemental Tables S4, S5 and S6; <https://doi.org/10.3168/jds.2018-15466>). This suggests that GEBV obtained based on ssGBLUP may be less biased compared with PA. However, it is essential to determine the best scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$, as different optimal scaling factors were obtained for the different breeds and analyses. This is most likely due to differences in genotyping strategies, pedigree depth, and genetic architecture of the traits. The use of a genomic relationship matrix that weights markers according to the trait being analyzed (e.g., VanRaden, 2008; Makgahlela et al., 2013) may better account for differences in genetic architecture of the traits and, consequently, increase reliability and decrease bias, especially for small populations (Lourenco et al., 2017), such as Canadian Ayrshire and Jersey breeds. Additionally, Meuwissen et al. (2011) showed that relationships estimated by markers in $\mathbf{G}$ contain estimation errors, and that a better estimate may be obtained by regressing $\mathbf{G}$ back to $\mathbf{A}$, which maximized the accuracy and removed the bias in the GEBV. However, these authors commented that this method is computationally much more demanding than traditional methods used to construct $\mathbf{G}$.

In general, changes in the τ parameter seems to have a small effect on the regression coefficients, unlike changes in the ω parameter (Supplemental Tables S4, S5 and S6; <https://doi.org/10.3168/jds.2018-15466>). Decreasing ω increases the importance of the pedigree information in the GEBV prediction, and it is also dependent on the completeness of the pedigree in each breed. Misztal et al. (2013) and Misztal (2017) related the ω parameter to incomplete pedigree and unaccounted inbreeding effect in $\mathbf{A}_{22}^{-1}$, respectively. These findings support the conclusions that ssGBLUP evaluations are inflated when the pedigree is deep, but incomplete (Misztal, 2017). In this study, ω lower than

1.0 yielded less biased predictions for all breeds. Regarding to the τ parameter, genomic evaluation of MY, FY, and PY for all breeds and SCS for the Holstein breed were less biased and led to higher validation reliabilities when τ was higher than 1.0. When τ is higher than 1.0, the genetic variance is reduced to make $\mathbf{G}^{-1}$ to have approximately the same variance as $\mathbf{A}^{-1}$. This suggests that the genetic variance in genotyped animals is reduced and that for unknown animals an inbreeding level of 0 is assumed instead of that of their contemporaries. In contrast, for the genomic evaluation of SCS in the Ayrshire and Jersey breeds, the optimal τ was equal to 1.0. This indicates that selection has not been very intense for these traits (i.e., SCS1, SCS2, and SCS3) in the Ayrshire and Jersey breeds. Additional information about the theoretical background of τ and ω can be found in Martini et al. (2018).

Regardless of the fact that the use of scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ have decreased bias for all traits compared with the ssGBLUP with no scaling (Supplemental Tables S4, S5, and S6; <https://doi.org/10.3168/jds.2018-15466>), both traditional and genomic evaluations generated mostly biased breeding values for the majority of traits analyzed in this study. Mäntysaari and Koivula (2012) showed that several factors may contribute to the bias in genomic predictions, such as the nonrandom selection of validation bulls. Thus, currently Interbull requires national GEBV to be validated by the GEBV test before their inclusion in the international comparisons (Interbull, 2016). In summary, the GEBV test evaluates the bias in the genomic evaluations and the improvement in accuracy from the use of GEBV compared with EBV (Interbull, 2016). In our study, gains in reliabilities were obtained when genomic information was included, even when no scaling factors to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ were used (Supplemental Tables S4, S5, and S6; <https://doi.org/10.3168/jds.2018-15466>). However, the need for re-scaling the GEBV and EBV should be evaluated to meet the Interbull's bias requirements if ssGBLUP become a standard procedure for official evaluations in Canada, especially for the Ayrshire and Holstein breeds.

The current implementation of ssGBLUP does not allow different values for τ and ω for each trait in multiple-trait models. Therefore, the optimal values in this study were those that yielded high validation reliabilities and less biased regression coefficients across all traits analyzed. The pattern of GEBV reliabilities through DIM considering the optimal scaling factors for each analysis was slightly different across traits, lactations, and breeds (Figure 1), suggesting that there may be DIM for which higher genetic gain is possible compared with others. Similar pattern of GEBV reli-

abilities through DIM were obtained by Oliveira et al. (2018) using RRM in both steps of a 2-step genomic prediction for the Holstein breed. These results may be relevant for traits that summarize the lactation curve pattern, such as lactation persistency. Thus, new studies to define the optimal way to measure lactation persistency should be done taking into account the genomic information.

Computational Demand

The current study shows that incorporating genomic information into ssGBLUP based on RRM increases the computational demand for the evaluation of MY, FY, PY, and SCS. The inclusion of genomic information affects convergence because the variance structure of genotyped animals in the $\mathbf{G}^{-1}$ is less diagonally dominant than in $\mathbf{A}^{-1}$ (Koivula et al., 2015), which requires more iterations to achieve convergence and, consequently, increases the CPU time. However, despite its high computational requirements, the ssGBLUP method seems to be suitable to analyze test-day traits of Canadian Ayrshire, Holstein, and Jersey breeds, since all analyses achieved the convergence criteria.

It is important to notice that this was the first time that programs from the blupf90 family (Misztal et al., 2002, 2014b) were applied to RRM in ssGBLUP. Therefore, the version of BLUP90IOD software used in this study was not fully optimized for RRM using genomic information. Although it uses a different number of threads to read the data and pedigree in parallel, most of the computing time was spent on accessing the data from the disk (i.e., iteration on data). Thus, further improvements may reduce computational time, such as the use of a more efficient parallel computing/multi-threading, and converting from iteration on data in the disk to in the memory. Another optimization could be the development of an appropriate preconditioner for RRM. An initial test of BLUP90IOD using a block preconditioner with dimension of the polynomial order times the number of traits was able to reduce the computing time from 16.08 to 4.19 d, using all genotypes available for the Holstein breed (results not shown). Improvements to reduce computational time are required especially to allow weekly ssGBLUP evaluations.

Using a more efficient algorithm to approximate the inversion of $\mathbf{G}$ based on genomic recursions may also help to decrease the computational time required in the analyses. In this regard, the algorithm for proven and young animals (APY) allows the inversion of $\mathbf{G}$ for millions of genotyped animals using a reduced number of iterations (Misztal et al., 2014a). In summary, in the

APY procedure GEBV of noncore animals (e.g., young genotyped animals) are conditioned on GEBV of core animals (e.g., their ancestors). Masuda et al. (2016), evaluating the computational costs of the APY algorithm for analyzing a nonlongitudinal trait for more than 500,000 genotyped animals, reported that the validation reliability reached a plateau when the number of core animals was 10,000 and that small differences in reliability were observed when different groups of core animals were used. Moreover, the referred authors estimated that the computing time to invert $\mathbf{G}$ using the APY procedure for 2 million genotyped animals (assuming 10,000 core animals) would be only 4.5 h. However, for longitudinal traits, no studies using APY, RRM, and ssGBLUP were found in the literature.

To our best knowledge, no studies comparing the computational demand of ssGBLUP to multiple-step GBLUP are available in the literature for RRM. Among the reasons for this is the fact that RRM have not been routinely used in multiple-step genomic evaluations, because they do not seem to increase the reliability of the genomic predictions compared with the use of accumulated yield (Oliveira et al., 2018). However, in a simulation study using RRM, Kang et al. (2017) showed that ssGBLUP was more accurate, less biased, and had better persistency of accuracy over generations than multiple-step GBLUP.

CONCLUSIONS

Our findings indicate that including all available genotypes or only genotypes from animals with accurate EBV yields similar genomic predictions in terms of daily validation reliability and bias, especially for populations with a small number of genotyped animals. The use of ssGBLUP to predict genomic breeding values for test-day traits based on random regression models increases reliability and reduces bias of breeding values compared with traditional parentage average from BLUP in the Canadian Ayrshire, Holstein, and Jersey breeds. However, the scaling factors used to combine $\mathbf{G}^{-1}$ and $\mathbf{A}_{22}^{-1}$ should be carefully chosen.

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