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ABSTRACT

The US dairy cattle genetic evaluation is currently a multistep process, including multibreed traditional BLUP estimations followed by single-breed SNP effects estimation. Single-step GBLUP (ssGBLUP) combines pedigree and genomic data for all breeds in one analysis. Unknown parent groups (UPG) or metafounders (MF) can be used to address missing pedigree information. Fertility traits are notably difficult to evaluate due to low heritabilities, changing management, and a higher recent emphasis on selection to move in a favorable direction. We assessed bias, dispersion, and accuracy of fertility traits in all-breed US dairy cattle using pedigree-based BLUP (PBLUP) and ssGBLUP with UPG or MF; with 5% or 10% residual polygenic effect. Validation methods included the linear regression method and comparison of early and late deregressed proofs for Holstein and Jersey breeds. By comparing MF or UPG in PBLUP, we observed similar results in terms of bias, dispersion, and correlations between early and recent predictions. When genomics was used, ssGBLUP with MF and 10% residual polygenic effect consistently outperformed other models regarding bias, dispersion, and correlations. Compared with multistep results, ssGBLUP with MF and 10% residual polygenic effect showed less bias and increased correlations but slightly overdispersed estimates. Overall, genomic prediction of fertility traits using ssGBLUP was accurate and unbiased, more so with MF than with UPG.

Key words: genomic predictions, pedigree-based BLUP, unknown parent groups, metafounders, daughter pregnancy rate

INTRODUCTION

The current genetic evaluation system for US dairy cattle follows a multistep process. Initially, breeding values are estimated using an all-breed traditional BLUP. Subsequently, these EBV and their reliabilities are used to create deregressed proofs and obtain a within-breed estimation of SNP effects, which in turn are used to compute direct genomic values. The final GEBV (VanRaden, 2008) combine the EBV and the direct genomic value, including a 10% residual polygenic effect from the initial pedigree-based BLUP (**PBLUP**). However, this multistep process has some drawbacks when using results from the traditional BLUP method, which is known to be biased due to the influence of genomic preselection (Patry and Ducrocq, 2011). Single-step GBLUP (**ssGBLUP**) predicts genomic breeding values by incorporating all available information, namely phenotypic, pedigree, and genomic data, in a single analysis (Legarra et al., 2009; Aguilar et al., 2010; Christensen and Lund, 2010). The single-step method is, in principle, unbiased and more accurate than BLUP (Masuda et al., 2018; Jibrila et al., 2021; Cesarani et al., 2022).

An important detail in implementing ssGBLUP in dairy cattle evaluations involves how to include unknown parent groups (**UPG**; Quaas, 1988; Tsuruta et al., 2014, 2019). The correct inclusion of UPG without double counting is complex (Misztal et al., 2013; Masuda et al., 2022; Strandén et al., 2022). A different method is metafounders (**MF**; Legarra et al., 2015), which address the incompatibility between the pedigree relationship matrix **A** and the genomic relationship matrix **G**, while simultaneously modeling the differences within and across populations.

In this study, we aimed to apply ssGBLUP to fertility traits used in the genetic evaluation of US dairy cattle. The traits under consideration include daughter pregnancy rate (**DPR**), cow conception rate (**CCR**), heifer conception rate (**HCR**), and early first calving (**EFC**).

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The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-24. Nonstandard abbreviations are available in the Notes.

These traits present a challenging case for evaluation due to their low heritability and the diverse range of records involved in phenotype determination, such as calving interval, insemination dates, and pregnancy verification (VanRaden et al., 2004, 2014). The primary objectives of this study are 2-fold: first, to assess the accuracy and potential biases of the ssGBLUP method when applied to the specific case of all-breed US fertility traits, and second, to explore various options for modeling missing parents, using either UPG or MF. We also evaluate the fraction of pedigree-based residual polygenic effect included in the predictions. Finally, we compare the results of these methods with those of the current multistep evaluation system. This comprehensive study aims to gain insights into the effectiveness and suitability of implementing ssGBLUP methodology in fertility traits for US dairy cattle.

MATERIALS AND METHODS

No animals were used in this study, so ethical approval for the use of animals was deemed unnecessary.

Data

We used domestic data from the official December 2022 multibreed US dairy genetic evaluation for fertility traits, which were provided by the Council on Dairy Cattle Breeding (**CDCB**; Bowie, MD). The phenotypic file consisted of all breeds (Ayrshire, Brown Swiss, Guernsey, Jersey [**JE**], Holstein [**HO**], Milking Shorthorn, and crossbreds) records for CCR, HCR, DPR, and EFC. The DPR predicts the percentage of nonpregnant cows that will become pregnant during each 21-d period compared with the breed base, and it is a function of days open. Both HCR and CCR measure the percentage of inseminated heifers or cows that successfully become pregnant with each service, modeling the success or failure of each reported insemination. The EFC measures the age at first calving. For further details on these traits, refer to VanRaden et al. (2004, 2014). We will focus on DPR and CCR as these are the most relevant traits for the industry. The records for DPR and EFC started in 1960, whereas data collection for CCR and HCR started in 2000; however, DPR and CCR are strongly genetically correlated traits (Legarra and VanRaden, 2023), expected to have similar genetic trends. Table 1 provides an overview of the traits. The pedigree file included 93,417,440 animals, with 417 UPG based on breed, birth year, and pathway (sex of the animal with missing parent, sex of its ancestor, and foreign or local origin).

The CDCB database at this time contained over 7 million genotypes, all imputed to a standard set of 78,964 selected SNPs, following the CDCB procedures outlined in https://uscdcb.com/genomic-evaluations/. Of these genotyped animals, only those deemed "useful" were considered, as explained next.

Table 1. Descriptive statistics of the studied traits

Trait[1]	Minimum	Maximum	Average	SD	N[2]	h^2, %
CCR	−15.64	123.03	52.44	39.25	35,212,583	1.60
HCR	−24.90	130.42	70.60	38.53	11,587,364	1.00
DPR	0.00	100.00	45.51	34.23	89,672,054	1.40
EFC	−2,273.00	−519.00	−787.04	101.15	35,412,656	2.70

[1]CCR = cow conception rate; HCR = heifer conception rate; DPR = daughter pregnancy rate; EFC = early first calving.
[2]Number of records.

In a ssGBLUP evaluation, declaring an animal "informative" or not involves some considerations. In the pedigree-based evaluation, animals with no records or with no descendants with records (we will call these "noninformative" animals) could be ignored because they did not contribute information, and their inclusion did not modify the covariance structure of the records (Henderson, 1977, 1984). This can be shown using selection index principles (Henderson, 1984). For instance, for a pedigree-based BLUP model with the usual notation, $\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$, with $Var(\mathbf{u}) = \mathbf{A}\sigma_u^2$ and $Var(\mathbf{e}) = \mathbf{R}$, EBVs are $\hat{\mathbf{u}} = \sigma_u^2\mathbf{AZ}'\mathbf{V}^{-1}\left(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}\right)$, with $\hat{\mathbf{b}} = (\mathbf{X}'\mathbf{V}^{-1})^{-1}\mathbf{X}'\mathbf{V}^{-1}\mathbf{y}$ and $\mathbf{V} = \sigma_u^2\mathbf{ZAZ}' + \mathbf{R}$ (this is a single trait proof but readily applies to multiple traits and more complex models), where adding or dropping columns and rows of **A** (and at the same time adding or dropping additional columns of **Z** filled with zeros) with noninformative animals does not change the prediction. Noninformative animals include, in particular, culled animals and newborns. This is practical because, for example, newborn animals do not need to be included in PBLUP (they can be predicted based on parent average), and pedigrees can be trimmed.

In the ssGBLUP case, the covariance matrix among records is $\mathbf{V} = \sigma_u^2\mathbf{ZHZ}' + \mathbf{R}$. If we remove noninformative animals in a pedigree-based BLUP sense, in order for ssGBLUP to give the same results, it would be necessary that matrix **H** among animals with records is not modified with the removal of genotypes of these noninformative animals. This is not always the case. The removal has no consequences only when both parents of a noninformative animal are genotyped because, in that situation, the matrix **H** is modified only for the row and column of the animal itself. This is evident from examining the columns of the product $\mathbf{A}_{12}\mathbf{A}_{22}^{-1}$, or can be understood by recognizing that all relationships with the animal and other animals are mediated by their parents. The abscense of bias in this case (when culled animals are ignored in **H** and both parents are genotyped) was also shown by Jibrila et al. (2021, 2023) using simulation. Another intui-

tive explanation is that highly selected young bulls exhibit positive Mendelian Sampling term, which is well accounted for by the difference between progeny and parents' genotypes.

However, when one or both parents of a noninformative animal are not genotyped, the genotype of the noninformative animal contributes to an improved matrix **H** among parents (informally, imputing the nongenotyped parent) and reduces bias (Shabalina et al., 2017; Jibrila et al., 2021). Shabalina et al. (2017) found that genotypes of culled bulls needed to be included in **H** when (as in their simulation) the dams of both culled and selected bulls were not genotyped. In our case, however, the dams of bulls are genotyped. In our dataset, 99% and 95%, respectively, of Holstein and Jersey bulls born since 2010 with more than 100 daughters in records have both parents genotyped. Thus, the policy for selection seems to genotype elite bulls and cows, then preselecting their offspring (candidate bulls) for selection, and then either selecting or culling them. Thus, by the nature of genomic selection, bulls with offspring in the data have both parents genotyped meaning the rows in the matrix **H** for the selected bulls will not be modified by adding their culled half-sibs.

Given that the major selection pressure is applied to bulls, we consider that in our case, there should be little or no bias, although we have not verified it. We, therefore, define noninformative animals as those that do not contribute information in a pedigree setting (i.e., no phenotype for themselves or their descendants). We prefer to use this simple rule rather than trying to track genotyped descendants of ungenotyped parents, as it is easy to implement, explain, and troubleshoot. Moreover, it is likely that including these noninformative genotyped animals would likely increase the memory needs and slow the convergence of iterative solvers.

Therefore, genotypes of animals with records or their ancestors were selected, whereas the rest were ignored (e.g., we ignored a foreign genotyped bull with no domestic genotyped daughters in records or a domestic genotyped heifer with no record yet). Out of the 7 million genotypes, 2,041,543 genotyped animals were thus extracted. Table 2 presents the number of genotyped animals per breed.

Table 2. Number of core animals per breed and sex and total number of genotypes across breed

Breed	No. of genotypes	No. of sires (dams) in core
Ayrshire	1,608	311 (1,175)
Brown Swiss	9,560	611 (4,313)
Guernsey	3,561	219 (3,258)
Holstein	1,669,795	6,890 (8,113)
Jersey	300,976	3,186 (11,883)
Crossbreds	56,528	141 (4,616)

Estimation of Pedigree-Based or Genomic Breeding Values

An all-breed, multitrait repeatability animal model incorporating all 4 traits was used to predict pedigree-based EBV or genomic-based GEBV. The pedigree-based methods were PBLUP with UPG and MF (**PBLUP$_{UPG}$**, **PBLUP$_{MF}$**). The genomic prediction methods were ssGBLUP with UPG or MF fitted using either 5% (**ssGBLUP$_{UPG5}$** or **ssGBLUP$_{MF5}$**) or 10% (**ssGBLUP$_{UPG10}$** or **ssGBLUP$_{MF10}$**) pedigree-based polygenic effect (also called residual polygenic effect). The 5% and 10% fractions are, respectively, the default in the blupf90 software suite (Misztal et al., 2014b) and the standard at CDCB multistep (**MS**) genomic prediction. In summary, the different models were PBLUP$_{UPG}$, PBLUP$_{MF}$, ssGBLUP$_{UPG5}$, ssGBLUP$_{UPG10}$, ssGBLUP$_{MF5}$, and ssGBLUP$_{MF10}$.

The results obtained from these models were compared with statistics from the official results of the dairy genetic evaluation provided by CDCB, which employs a traditional all-breed BLUP followed by within-breed GBLUP using deregressed proofs. However, due to model changes, these statistics are 1 yr delayed, as will be explained later.

When MF is used to model unknown parents, both PBLUP and ssGBLUP use an inverse relationship matrix denoted as $\mathbf{A}_{\Gamma}^{-1}$ Legarra et al. (2015), which requires the estimation of a matrix $\mathbf{\Gamma}$ of relationships among metafounders. The MF are the same as UPG (e.g., 417), with a different method that uses a relationship matrix $\mathbf{\Gamma}$. The $\mathbf{\Gamma}$ matrix was estimated similarly to Wicki et al. (2023) or Legarra and VanRaden (2023) using base allele frequencies inferred during the imputation process at CDCB. We did use the adjustment of the genetic covariance across traits ($\mathbf{G}_0$) to consider $\mathbf{\Gamma}$, as $G_{0(\text{related})} = \frac{\mathbf{G}_0}{k}$ for $k = \left(1 + \frac{\overline{\text{diag}(\mathbf{\Gamma})}}{2} - \bar{\mathbf{\Gamma}}\right)$ (Legarra et al., 2015) with a value of $k = 0.91$. This is an approximation, as it is not possible to exactly scale variance components to an all-breed situation when breeds are assumed to be related.

When using MF, genomic relationships are created as cross-products of genotype matrices, where genotypes are coded assuming allele frequencies of 0.5 (Christensen, 2012; Legarra et al., 2015). In other words, the **G** matrix is constructed as cross-products of the genotypes coded as (−1,0,1), then multiplied by $\frac{2}{m}$, for m the number of SNPs, then "blended" with a fraction (5% or 10% as described) of $\mathbf{A}_{\Gamma 22}$. The compatibility of pedigree and genomic relationships is automatic, because $\mathbf{A}_{\Gamma}$ is created using $\mathbf{\Gamma}$ as estimated for MF, which is in the same base as **G**.

When using UPG, **G** is different, where observed allele frequencies (p) are used for both the genotype coding as ($-2p$,$1-2p$, $2-2p$) and for the scaling of **G**. Then the matrix is "tuned" to resemble **A** (Christensen et al., 2012) then "blended" with A_{22}.

For BLUP and ssGBLUP, we used random UPG with a priori covariances equal to the identity matrix multiplied ($\otimes$ Kronecker product) by the genetic covariance matrix, resulting in a matrix $\mathbf{A}^*_{\#}$ (Masuda et al., 2022). For BLUP, this implies the usual inverse with UPG ($\mathbf{A}^*$) plus a block-structure in the corresponding block to UPG $\left(\mathbf{A}^*_{\#} = \mathbf{A}^* + \begin{bmatrix} 0 & 0 \\ 0 & \boldsymbol{\Sigma}^{-1} \end{bmatrix}\right)$. For ssGBLUP with UPG, we used the Altered QP model (Masuda et al., 2022), which is equivalent to adjusting J-factors (i.e., covariates accounting for different allele frequencies across populations), a special case where (in their notation) $\mathbf{Q}_2 = \mathbf{Q}_c$ (Strandén et al., 2022; Himmelbauer et al., 2024), where $\mathbf{Q}_2$ is the matrix containing fractions of UPGs and $\mathbf{Q}_c$ is the matrix containing fractions of differences from genotyped base to pedigree base.

Choice of Core Animals for APY

Given the large number of genotyped animals, the Algorithm for Proven and Young (**APY**; Misztal et al., 2014a) was employed for this study to efficiently obtain the inverse of **G**. Core animals representing genotypes from 5 pure breeds and crossbreds were included in the evaluation: Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey, and crossbred genotyped animals. Choice of the core can lead to changes in the GEBV (Misztal et al., 2020; Edel et al., 2022). Thus we tried to avoid a truly random sample, given that our dataset is structured by breed and sex. The core was selected in the following manner. In the case of Ayrshire and Guernsey, all genotyped animals born in or after 1990 were chosen due to the low number of genotyped animals in those breeds. Based on previous studies (Cesarani et al., 2022), the desired core size was 15K for Jersey and Holstein and 5K for Brown Swiss and crossbreds. Then, we proceeded as follows. First, core animals must be born in or after 1990 and have both parents known. Second, we chose bulls with more than 100 daughters in the pedigree for Brown Swiss, Jersey, and crossbreds and more than 500 daughters in the pedigree for Holstein. Last, we added genotyped cows to the core until (approximately) the desired size. Cows were added if modulo(anim_{key},n) = 0, where anim_{key} is the internal, unique ID used at CDCB and $n = \text{round}\left(\frac{\text{N}_\text{G} - \text{B}}{\text{C}}\right)$, where n is the nearest integer to the ratio of the difference between the total number of genotypes of a breed (N_G) and the number of selected bulls (B) of the same breed, and the number core animals (C) and round ($\cdot$) is the mathematical rounding function. This ensures that the process is repeatable, provided that no new information is added. The integer key anim_{key} is roughly correlative with the inclusion of new animals (i.e., in time), so our method should give an approximately balanced sampling of genotyped cows per year. The cows included in the evaluation will change from evaluation to evaluation, and this will result in small changes in their GEBVs (Misztal et al., 2020; Garcia et al., 2022). Changes are not practically relevant for old animals, but they may be important for more recent ones potentially used for selection, and this should be investigated in the long run. Changes can be minimized by keeping the same core across evaluations, but this leads to suboptimal cores that need to be updated (Garcia et al., 2022).

The reason for requiring a minimum number of daughters with records is to include both sires and cows in the core. Sires represent the next generation but are highly selected; cows represent the current population and are less selected. The combination of both should provide a good representation of the population's genetic diversity. Table 2 presents the number of core animals per breed and sex finally used to create an approximated inverse of the genomic relationship matrix $\left(\mathbf{G}^{-1}_{\text{APY}}\right)$.

Validation Methods

To evaluate the performance of BLUP and ssGBLUP, we employed 2 validation methods based on (G)EBV: linear regression (**LR**; Legarra and Reverter, 2018) and improved genomic validation (**IGV**; VanRaden, 2021). These validation approaches enable the estimation of different metrics to assess bias, dispersion, and accuracy of the estimated breeding values derived from ssGBLUP and PBLUP. To ensure fair comparisons, we expressed all (G)EBVs as deviations from the same base, which is the average (G)EBV of cows with records born in 2015.

Both validation methods involve using a whole dataset, which we have already described, and a partial dataset, which excluded records with calving dates during or after 2019 (but we did not remove genotypes or pedigree). We ran the same models for evaluations for this partial dataset. Then the respective (G)EBV predicted using "whole" (with subindex "w") or "partial" datasets (with subindex "p") are compared. For the validation process, we identified focal individuals (or validation candidates) as bulls with more than 100 daughters with records for DPR in the whole dataset and no daughters with records in the partial dataset. To simplify the process, the same set of validation bulls was selected for DPR and CCR. In total, there were 1,891 Holstein and 303 Jersey focal bulls, all born between 2012 and

2019, with the majority falling within the 2014 to 2018 range. Given the limited number of bulls meeting these criteria, no validation set was established for the other breeds.

The first validation method (LR) involves estimating 3 statistics for the validation bulls. Bias μ_{pw} was estimated as the difference in means of (G)EBV in the partial and whole datasets for the focal animals; estimations were expressed in genetic SD of each trait. Positive values imply an overestimation of early (G)EBV, whereas negative values imply an underestimation. dispersion (b_1) is measured as the regression coefficient of the (G)EBV from the whole dataset on the (G)EBV of the partial dataset. If b_1 is equal to 1, there is not over- or underdispersion. As a measure of accuracy, we computed the Pearson correlation between the (G)EBV of the validation animals between the whole and the partial dataset, whose expected value is the ratio $\frac{acc_p}{acc_w}$, where acc_p is the accuracy of the validation candidates from the partial dataset and acc_w is the accuracy of the same animals but from the whole dataset. Thus, assuming that the later prediction is highly accurate, higher correlation values mean that the "early" predictions with partial data are more accurate.

The second validation method (IGV) involves computing the deregressed (G)EBV (d(G)EBV) from the difference between (G)EBV in the whole and partial datasets (VanRaden, 2021). The resulting d(G)EBV is analogous to a record (not shrunken), and it only incorporates the information from the gain in reliability between the partial and whole datasets. The calculation of d(G)EBV is based on the following equation (VanRaden, 2021):

$$d(G)EBV = \widehat{(G)EBV}_p + \frac{\widehat{(G)EBV}_w - \widehat{(G)EBV}_p}{Rel_{diff}}, \quad (1)$$

where Rel_{diff} is the reliability of the additional information of the whole compared with the partial datasets. The value of Rel_{diff} can be calculated by transforming the 2 (G)EBV reliabilities, "whole" and "partial," to equivalent daughter contribution (**EDC**), and then the difference between the 2 EDC (whole − partial) is transformed back into reliability. Another equivalent method to directly calculate Rel_{diff} is (Harris and Johnson, 1998):

$$Rel_{diff} = \frac{Rel_w - Rel_p}{Rel_w \times Rel_p + 1 - 2Rel_p}, \quad (2)$$

in which Rel_w and Rel_p are the reliabilities of (G)EBV computed from the whole and partial datasets.

After obtaining the $d(G)EBV$ and Rel_{diff} of the focal individuals, the $d(G)EBV$ are then used in the following linear regression:

$$d(G)EBV = b_0 + b_1 \times \widehat{(G)EBV}_p + e, \quad (3)$$

where b_0 and b_1 are the unknown parameters to be estimated. The $d(G)EBV$ in Equation 3 are weighted by Rel_{diff}, so when there is no gain in reliability, that animal gets zero weight. The expected value of b_1 is 1. Additionally, we calculated standard errors of the metrics as described by Bermann et al. (2024).

To compare with existing procedures, the CDCB provided the results of these metrics using their national MS evaluation method, split into first a BLUP prediction (**MS_{BLUP}**) and second a genomic prediction (**$MS_{Genomic}$**) done within breed from de-regressed proofs from the MS_{BLUP}. These metrics were obtained for bulls chosen in the same manner as the validation animals in our study. However, there was a difference in the time span due to changes in edits and models from 2018 to 2022, rendering the respective proofs not directly comparable. Thus, the comparison was conducted 1 yr later. We selected bulls with 0 daughters in the evaluation of December 2019 and at least 100 daughters with DPR records in December 2023. In addition, bulls were chosen to not have Interbull's Multiple Across Country Evaluation (**MACE**) information (i.e., foreign bulls with 0 domestic daughters in records but with foreign daughters in December 2019 were excluded from the validation dataset). The number of selected bulls was 2,160 and 331 for Holstein and Jersey, respectively. The results from the MS methods contained domestic information, with no foreign progeny records; therefore, no MACE data.

Genetic Trends

Genetic trends (means of (G)EBV per year of birth for cows with records) were obtained via ssGBLUP and PBLUP from both whole and partial datasets for CCR and DPR in Holstein and Jersey. This visualization serves to illustrate the method's ability to accurately capture the response to selection of a particular trait. Furthermore, it offers insight into the behavior of the estimates over a specific timeframe, potentially highlighting any distortions in the curve's behavior or indicating the homogeneity of genetic progress. The genetic base year was set to cows with records born in 2015 (Norman et al., 2020). In addition, to further understand disparities between methodologies (MF and UPG), we plotted solutions (using the whole dataset) of the UPG or MF for unknown sires of foreign dams with ssGBLUP (MF10 and UPG10).

RESULTS

Validation of UPG and MF

The estimated validation metrics for bias, dispersion, and correlation for both methods (LR and IGV) are shown when using ssGBLUP and PBLUP with MF or UPG. Table 3 presents the results of bias in terms of the difference in the means of (G)EBVs between the partial and whole datasets, expressed in the standard genetic deviation of the trait.

A comparison between $PBLUP_{UPG}$ and $PBLUP_{MF}$ revealed a reduction in bias (difference closer to zero) using MF for both breeds, with a decrease ranging from 0.09 to 0.17 in favor of MF except in the case of Jersey with DPR with a difference of 0.03 in favor of UPG. In the case of $ssGBLUP_{MF5}$ and $ssGBLUP_{UPG5}$, there was a reduction in bias of 0.03 with MF in DPR and no change in CCR for Holstein. However, using MF in ssGBLUP with a 5% residual polygenic effect did not improve results for the Jersey breed, resulting in an increase of 0.11 between the 2 methods. Setting the residual polygenic effect to 10% ($ssGBLUP_{UPG10}$ and $ssGBLUP_{MF10}$) led to a significant decrease in bias with MF (i.e., in MF5), whereas in the case of UPG, the same fraction (UPG10) resulted in opposite, but sizable, bias. This suggests that UPG may be unfairly capturing management trends, which would indicate that the bias originates from the phenotypes among other factors (CDCB and USDA Animal Genomics and Improvement Laboratory, 2024) and that genomics appears to help palliate this bias.

Table 4 presents b_1 in ssGBLUP and PBLUP for both genetic group definitions and validation methods LR and IGV. Results from traditional PBLUP showed inflation in both cases (MF and UPG), as evidenced by regression coefficients lower than 1 in both methods and for all traits). The lowest b_1 for PBLUP was observed with CCR in Jersey, $PBLUP_{MF}$ yielded 0.69 with IGV and 0.76 with LR, while $PBLUP_{UPG}$ produced 0.62 and 0.72, respectively. Although MF decreased the inflation levels for PBLUP, they were still farther than ssGBLUP from the expected value of 1, perhaps due to not accounting for genomic preselection.

Notably, upon adding genomic information, an immediate increase in the regression coefficient toward 1 was observed. In the case of ssGBLUP, and considering UPG and MF, both LR and IGV regression coefficients calculations produced still inflated estimates ($b_1 < 1$) with the highest levels of inflation observed in $ssGBLUP_{UPG5}$/$ssGBLUP_{MF5}$ with 0.87 (IGV) in CCR Jersey. Both validation methods, IGV and LR, yielded similar results in Holstein and Jersey breeds with ssGBLUP, but the values changed in PBLUP depending on the breed. When MF or UPG included more polygenic fractions (5 to 10), there was an increase in the regression coefficient values, approaching 1. Although LR consistently yielded higher coefficients than IGV, the relative rankings across models were very similar.

Table 5 presents the correlations between (G)EBV derived from the whole and partial datasets for each scenario. Pedigree-based BLUP (MF and UPG) yielded low correlations, ranging between 0.49 and 0.65, which indicated that partial EBV was not a good predictor of EBV of the validation sires when the phenotypes of their daughters were added. Correlations within $PBLUP_{MF}$ were consistently higher than within $PBLUP_{UPG}$, although the differences were small (0.01–0.02), rendering it insignificant in practice. Similar to the regression

Table 3. Estimated bias, in genetic SD, of (G)EBV comparing whole and partial datasets for ssGBLUP with MF/UPG at 5% and 10% residual polygenic effect ($ssGBLUP_{UPG5}$/$ssGBLUP_{MF5}$ and $ssGBLUP_{UPG10}$/$ssGBLUP_{MF10}$), and traditional pedigree BLUP with MF and UPG ($PBLUP_{MF}$ and $PBLUP_{UPG}$)

	Bias					
	ssGBLUP[1]				PBLUP[1]	
$Breed_{Trait}$[2]	MF10	MF5	UPG10	UPG5	MF	UPG
HO_{CCR}	−0.08	−0.40	0.15	−0.40	−0.23	−0.40
HO_{DPR}	0.02	−0.13	0.22	−0.16	0.01	−0.12
JE_{CCR}	0.03	−0.30	0.20	−0.19	−0.05	−0.14
JE_{DPR}	0.05	−0.33	0.19	−0.22	0.08	−0.05

[1]SE: HO_{CCR} and HO_{DPR}: ssGBLUP ≤0.10, PBLUP ≤0.05; JE_{CCR} and JE_{DPR}: ssGBLUP ≤0.24, PBLUP ≤0.12.

[2]HO_{CCR} = CCR in Holstein; HO_{DPR} = DPR in Holstein; JE_{CCR} = CCR in Jersey; JE_{DPR} = DPR in Jersey.

Table 4. Estimated regression coefficient of (G)EBV from whole on partial datasets for ssGBLUP with UPG or MF at 5% and 10% residual polygenic effect ($ssGBLUP_{UPG5}$/$ssGBLUP_{MF5}$ and $ssGBLUP_{UPG10}$/$ssGBLUP_{MF10}$), and traditional pedigree BLUP with MF and UPG ($PBLUP_{MF}$ and $PBLUP_{UPG}$) with linear regression (LR) improved genomic validation (IGV)

	b_1					
	ssGBLUP[1]				PBLUP[1]	
$Breed_{Trait}$[2]	MF10	MF5	UPG10	UPG5	MF	UPG
LR						
HO_{CCR}	0.94	0.95	0.90	0.90	0.93	0.92
HO_{DPR}	0.95	0.93	0.91	0.90	0.81	0.82
JE_{CCR}	0.94	0.89	0.90	0.88	0.76	0.72
JE_{DPR}	0.97	0.92	0.95	0.90	0.81	0.79
IGV						
HO_{CCR}	0.93	0.94	0.89	0.89	0.91	0.88
HO_{DPR}	0.94	0.93	0.90	0.89	0.74	0.75
JE_{CCR}	0.91	0.87	0.87	0.87	0.69	0.62
JE_{DPR}	0.97	0.91	0.94	0.89	0.74	0.69

[1]SE for LR: HO_{CCR} and HO_{DPR}: ssGBLUP = 0.03, PBLUP = 0.01; JE_{CCR} and JE_{DPR}: LUP = 0.07, PBLUP = 0.02.

[2]HO_{CCR} = CCR in Holstein; HO_{DPR} = DPR in Holstein; JE_{CCR} = CCR in Jersey; JE_{DPR} = DPR in Jersey.

Table 5. Correlation of (G)EBV from whole and partial data sets for ssGBLUP with MF at 5% and 10% residual polygenic effect ($ssGBLUP_{UPG5}$/$ssGBLUP_{MF5}$ and $ssGBLUP_{UPG10}$/$ssGBLUP_{MF10}$), ssGBLUP with UPG ($ssGBLUP_{UPG}$) and traditional pedigree BLUP with MF and UPG ($PBLUP_{MF}$ and $PBLUP_{UPG}$)

	Correlation					
	ssGBLUP[1]				PBLUP[1]	
$Breed_{Trait}$[2]	MF10	MF5	UPG10	UPG5	MF	UPG
HO_{CCR}	0.87	0.87	0.86	0.85	0.54	0.53
HO_{DPR}	0.90	0.90	0.88	0.89	0.49	0.50
JE_{CCR}	0.88	0.80	0.85	0.81	0.56	0.54
JE_{DPR}	0.86	0.85	0.86	0.86	0.65	0.63

[1]SE: Holstein ≤0.02 for all traits and methods; Jersey: ≤ 0.06 for all traits and methods.

[2]HO_{CCR} = CCR in Holstein; HO_{DPR} = DPR in Holstein; JE_{CCR} = CCR in Jersey; JE_{DPR} = DPR in Jersey.

coefficients, there was a large increase in the correlation when genomic information was included. With $ssGBLUP_{MF5}$, the lowest correlation observed was 0.80 (CCR in Jersey), and the highest with $ssGBLUP_{MF10}$ was in DPR for Holstein with a value of 0.90.

Overall, the results demonstrated high correlations, indicating that GEBV of young bulls from early evaluations without daughter information are highly correlated with the GEBV when daughter information is added. Implementing MF (whether MF5 or MF10) led on average to small increases in the correlation compared with UPG (UPG5 or UPG10), with minor differences among the 4 models (UPG5, UPG10, MF5, and MF10) in Holstein for both traits. Increasing the residual polygenic effect to 10% notably benefited the Jersey breed in terms of correlations of GEBV, resulting in more accurate predictions with an increase of 0.08 in CCR with $ssGBLUP_{MF10}$ and 0.04 with $ssGBLUP_{UPG10}$.

Validation of ssGBLUP, PBLUP, and MS

In this study, we also compared the results derived from ssGBLUP (UPG5, UPG10, MF5, and MF10) and PBLUP (MF and UPG) with results obtained from the MS results (pedigree-based predictions MS_{BLUP} and within-breed genomic predictions $MS_{Genomic}$) provided by CDCB. Both validation methods were applied to $MS_{Genomic}$ and MS_{BLUP}.

Table 6 presents the validation metrics provided by the CDCB. Results from PBLUP (Tables 3, 4, and 5) and CDCB MS_{BLUP} were expected to be different. First, CDCB uses UPG, not MF. Second, in the MS_{BLUP} process, if insufficient data are associated with a UPG for accurate estimation, this UPG is automatically merged with the subsequent UPG. In contrast, with PBLUP using the blupf90 programs, such merging does not occur, and there is no genetic group redefinition. We, therefore, observed some discrepancies between PBLUP (MF and UPG) and MS_{BLUP}. A difference in the level of bias existed between PBLUP (MF and UPG) and MS_{BLUP}, with MS_{BLUP} yielding less biased results for CCR in Holstein than PBLUP, and comparable but opposite biases for Jersey (biases for MS_{BLUP} are −0.02, 0.13, 0.21, 0.27 whereas for $PBLUP_{UPG}$ are −0.40, −0.12, −0.14, −0.05, always in the order HO_{CCR}, HO_{DPR}, JE_{CCR}, and JE_{DPR}). We do not have a clear explanation for these differences.

Regarding ssGBLUP, as observed earlier, all 4 analyses (UPG5, UPG10, MF5, and MF10) yielded biased estimates (Table 3). Bias also exists with the MS method ($MS_{Genomic}$, Table 6). Interestingly enough, $ssGBLUP_{MF10}$ yielded the lowest level of bias (approaching zero) among the 5 genomic predictions (ssGBLUP with UPG5, UPG10, MF5, MF10, and $MS_{Genomic}$). There was a drop in bias for Holstein from 0.25 (CCR) and 0.25 (DPR) in $MS_{Genomic}$ to −0.08 (CCR) and 0.02 (DPR) in $ssGBLUP_{MF10}$. For Jersey, bias decreased from $MS_{Genomic}$ to $ssGBLUP_{MF10}$, although there were still slight biases, e.g., in $ssGBLUP_{MF10}$ with 0.03 for CCR and 0.05 for DPR compared with $MS_{Genomic}$ with 0.14 and 0.41, respectively.

In terms of dispersion, as anticipated, genomic estimates of CDCB were nearly unbiased (slope of $MS_{Genomic}$ nearly 1) for both LR and IGV. Still, there was inflation in traditional pedigree BLUP with slopes of MS_{BLUP} of 0.93 (IGV) and 0.94 (LR) for Holstein CCR and 0.90

Table 6. Linear regression (LR) and improved genomic validation (IGV) statistics for multistep predictions with genomics ($MS_{Genomic}$) and without genomics (MS_{BLUP})

	Bias		Correlation		b_1			
					$MS_{Genomic}$		MS_{BLUP}	
$Breed_{Trait}$[1]	$MS_{Genomic}$	MS_{BLUP}	$MS_{Genomic}$	MS_{BLUP}	IGV	LR	IGV	LR
HO_{CCR}	0.25	−0.02	0.86	0.51	1.01	1.01	0.93	0.94
HO_{DPR}	0.25	0.13	0.84	0.47	1.12	1.10	0.90	0.92
JE_{CCR}	0.14	0.21	0.82	0.53	1.02	1.01	0.73	0.78
JE_{DPR}	0.41	0.27	0.72	0.57	1.00	1.00	0.68	0.74

[1]HO_{CCR} = CCR in Holstein; HO_{DPR} = DPR in Holstein; JE_{CCR} = CCR in Jersey; JE_{DPR} = DPR in Jersey.

(IGV) and 0.92 (LR) in DPR but lower than 0.80 (IGV and LR) for Jersey for both traits. This is similar to the pattern observed in Table 4, with slopes close to 0.9 to 1.0 for ssGBLUP but much lower for PBLUP. Among the 4 ssGBLUP models (UPG5, UPG10, MF5, and MF10), the b_1 closest to 1 was observed in ssGBLUP$_{MF10}$, with the highest b_1 values for both validation methods (LR and IGV), reaching 0.97 for DPR in Jersey. These results indicated an overdispersion of breeding values with ssGBLUP$_{MF10}$ and, overall, in ssGBLUP. In contrast to the official evaluation results, the ssGBLUP regression coefficient detected inflation (Table 4). For example, in MS$_{Genomic}$, no over- or underdispersion was observed in CCR for Holstein and either CCR or DPR for Jersey, with the regression coefficients varying close to 1 for both LR and IGV. However, in ssGBLUP$_{MF10}$, the same results varied between 0.91 and 0.97. Interestingly, in the case of DPR in Holstein, deviations from 1 in the slope were detected in both ssGBLUP$_{MF10}$ and MS$_{Genomic}$. Early proofs from ssGBLUP$_{MF10}$ were overdispersed (IGV = 0.94 and LR = 0.95), whereas in MS$_{Genomic}$, early proofs were under-dispersed (IGV = 1.12 and LR = 1.10).

Correlations of (G)EBV from validation animals between whole and partial datasets were similar across our results and CDCB results, with correlations around 0.50 for MS$_{BLUP}$ and around 0.80 for MS$_{Genomic}$. The PBLUP$_{MF}$ had slightly higher correlations than MS$_{BLUP}$, with the most increase in correlation (0.08 points, MF5 and MF10) observed in DPR with Jersey. We would expect that PBLUP$_{UPG}$ and MS$_{BLUP}$ would yield similar results because both use the same UPG definitions; however, in MS$_{BLUP}$ there is UPG redefinition when a given UPG has insufficient information. There were minor differences, with the highest difference in DPR with Jersey, where PBLUP$_{UPG}$ yielded a 0.63 correlation and MS$_{BLUP}$ = 0.57. Concerning genomics, as noted earlier, ssGBLUP$_{MF10}$ exhibited the highest correlations across all traits and breeds. Compared with MS$_{Genomic}$, ssGBLUP$_{MF10}$ demonstrated a general improvement in accuracy, ranging between 0.01 and 0.14, with the most notable increase observed in DPR for Jersey (0.72 vs. 0.86).

Genetic Trends

Genetic trends for CCR and DPR in Holsteins and Jerseys were visualized by plotting the estimated (G)EBV mean per birth year of cows with phenotypes for DPR. Figure 1 depicts the analyses conducted with ssGBLUP$_{MF10}$ and PBLUP$_{MF}$. Each panel contains one breed, one trait, 2 methods (BLUP and ssGBLUP) and 2 datasets (partial and whole). Only results with MF will be presented here because similar outcomes were produced with UPG. In all cases, (G)EBV were centered at 0 for animals born in 2015.

In the case of Holsteins, the 4 trends generally exhibited a consistent direction with minor variations at the beginning and the end of the studied period. The trend for ssGBLUP$_{MF10}$ with the whole dataset was consistently higher from 2000 to 2019 than ssGBLUP$_{MF10}$ with the partial dataset, and PBLUP$_{MF}$ with the partial dataset had the lowest trend. However, there were small differences in the very last years (2015–2019), depending on the method and dataset combination. The trend for Jersey DPR in the last 5 yr (2015–2019) was essentially flat. For other traits/breeds, PBLUP$_{P}$ (pedigree-based BLUP with partial dataset) generally showed the lowest values (i.e., the lowest genetic progress since 2015), and (somewhat unexpectedly) the fastest genetic progress was not always ssGBLUP$_{MF10}$, for which we discuss possible reasons in the Discussion section.

Figure 2 compares the genetic trend (solutions) of UPG10 and MF10 of unknown sires of foreign dams for both Holstein and Jersey breeds concerning CCR with ssGBLUP$_{MF10}$ and the whole dataset. We show these solutions as an illustration of the virtues of using MF when UPG are hard to estimate. The trend represented by MF10 (depicted in yellow) exhibits a smoother, less heterogeneous behavior, providing a more straightforward interpretation for viewers. In contrast, the trends associated with UPG display more noise over time, particularly evident in the case of Jersey UPG,. The main difference here is that UPG and MF are fit as random effects, but MF are correlated with the neighboring ones, whereas UPG are just shrunken toward 0. This underscores the significance of having sufficient information to accurately estimate the effects of UPG, as inaccurate estimates lead to bias. Consequently, in April 2024, the CDCB changed its definition of UPG by merging foreign UPG (such as the one in Figure 2) with domestic ones (CDCB and USDA Animal Genomics and Improvement Laboratory, 2024).

Concerning computational resources, we used preGSf90 to build the genomic matrices and blup90iod3 for solving, using preconditioned conjugate gradients iterations (Lourenco et al., 2022). Convergence was declared when the average squared difference between the right and left-hand sides of the mixed model equations was smaller than 10^{-12}. Models using ssGBLUP took the following number of iterations to converge: around 479 rounds (MF) and 476 (UPG) for 5% residual polygenic effect, and 294 (both MF and UPG) for 10% residual polygenic effect. For the case of 5% residual polygenic

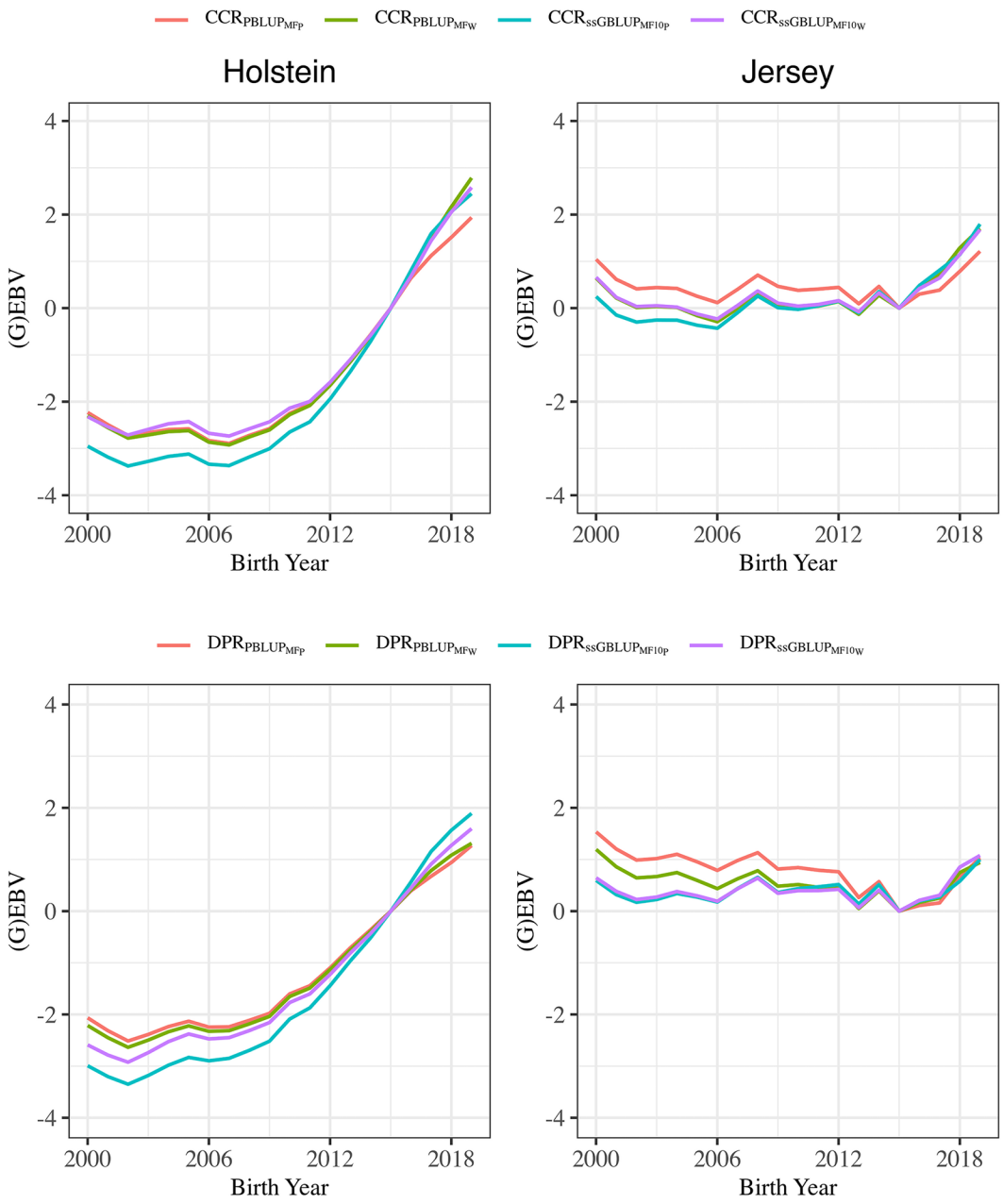

Figure 1. Genetic trend of CCR and DPR in Holstein and Jersey using Metafounders in ssGBLUP with 10% residual polygenic effect and PBLUP. $CCR_{PBLUP_{MF_w}}$, $DPR_{PBLUP_{MF_w}}$, $CCR_{ssGBLUP_{MF10_w}}$, $DPR_{ssGBLUP_{MF10_w}}$: Mean (G)EBV from the whole dataset with $PBLUP_{MF}$ and $ssGBLUP_{MF10}$ for CCR and DPR in Holstein and Jersey; $CCR_{PBLUP_{MF_p}}$, $DPR_{PBLUP_{MF_p}}$, $CCR_{ssGBLUP_{MF10_p}}$, $DPR_{ssGBLUP_{MF10_p}}$: Mean (G)EBV from the partial dataset with $PBLUP_{MF}$ and $ssGBLUP_{MF10}$ for CCR and DPR in Holstein and Jersey.

effect, computing time was 19 h for MF and 14 h for UPG, using 8 threads. This does not include the time to create the genomic matrices. Setting up $\mathbf{G}^{-1}_{APY}$ in preGSf90 (Misztal et al., 2014b) took around 5 h, using about 700 GB memory and 36 CPU. PBLUP models took around 430 rounds to converge, with a total computing time of 7.5 h for MF and 6 h for UPG. Other processes were running simultaneously, so these times are not good benchmarks and are provided as a rough guide. All computations were performed in a Linux server (x86_64) with 1.5 TB of RAM and an Intel Xeon Gold 6354 (3.00 GHz) processor (36 computing cores).

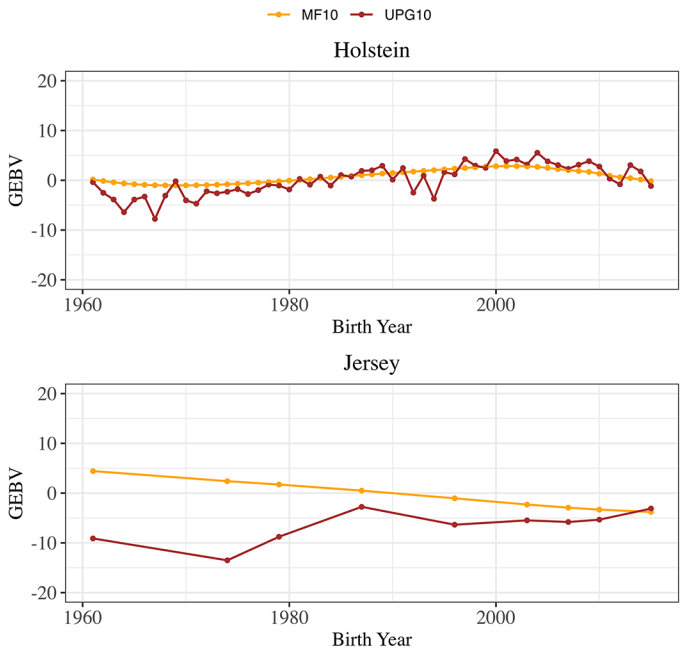

Figure 2. Estimates of genetic groups for unknown sires of foreign dams in Holstein and Jersey from the whole dataset for CCR with ssGBLUP$_{MF10}$ and ssGBLUP$_{UPG10}$ (ssGBLUP with MF/UPG and residual polygenic effect = 10%).

DISCUSSION

Choice of Core Animals for APY

Algorithm for Proven and Young requires a choice of core animals, and this choice is not without consequences. Including an animal in the core/noncore sets affects its GEBV (Misztal et al., 2020; Edel et al., 2022). The objective of this work was not to formally propose and compare the results of a core choice versus other choices. Still, we do propose a deterministic algorithm to choose a core, and this deserves some discussion. First, with our proposal, the pool of sires (with daughters in records) in the core should increase at a slow pace, whereas cows in the core will change with each evaluation.

Given that either there is a large body of genotyped animals (e.g., Holstein and Jersey) or essentially all genotyped animals are in the core (other populations), we expect few global changes from run to run. However, there is the possibility that those changes could affect small subsets of animals in some categories, such as young genomic bulls (Edel et al., 2022). Edel et al. (2022) observed more pronounced changes when the number of phenotyped offspring of young genomic bulls was larger, and the fact that we include all bulls with phenotyped offspring above a certain threshold should minimize these changes. We believe our choice of the core, admittedly heuristic, is a good compromise between fully random choice and choosing only proven sires as was initially considered. Further, choosing within breed, and then both bulls and cows, should provide a good sample of genetic diversity in the population. This is an exploratory proposal, and its consequences were not fully explored in this work. The quality of this proposal must be evaluated in the medium run, as other compromises that are often made in routine genetic evaluation.

Comparing Multistep and ssGBLUP

Single-step GBLUP has emerged as the preferred method for the genetic evaluation of genotyped and ungenotyped livestock. There is a general tendency of countries to shift national evaluations of dairy cattle to single step, with (to our knowledge in July 2024) the Czech Republic, France, Uruguay, and the Netherlands running single-step evaluations. Many other countries are on the verge of implementing it. Numerous studies in dairy cattle have explored the possibility of implementing ssGBLUP, with authors such as Alkhoder and Liu (2021), Cesarani et al. (2021), and Himmelbauer et al. (2021) reporting benefits (higher accuracy and less bias).

Our study compared the results estimated by ssGBLUP to those obtained by CDCB using a MS approach. Regarding, b_1, values in ssGBLUP are well within the range (0.9–1.1) currently accepted by the Interbull genomic validation test (Sullivan, 2023). We observed more inflated estimates with ssGBLUP than MS. This inflation was consistent across both validation methods, IGV and LR. The overdispersion was palliated when the pedigree-based part was increased from 5% to 10% (ssGBLUP$_{UPG10}$/ssGBLUP$_{MF10}$), which agrees with previous findings (e.g., Liu et al., 2011). The comparison of ssGBLUP and MS is not entirely fair, as our study compared data until 2018 (partial) with data until 2022 (whole), whereas the CDCB numbers are from evaluations until 2019 and 2023, leading to different sets of bulls being used. The number of bulls CDCB used to calculate these means was 1,489 (vs. 1,891 for ssGBLUP) in Holsteins and 270 (vs. 303 for ssGBLUP) in Jerseys. Additionally, a recent study (Mota et al., 2024) using similar CDCB data obtained slopes of the genomic validation test (IGV) for GEBVs in MS with values for CCR and DPR ~1 for Holstein (similar to ours) but ~0.80 for Jersey (whereas we obtained ~1 in Table 6). Differences were because of data editing for bulls (in our study, a stricter criterion of more than 100 daughters with records is imposed) and also because Mota et al. (2024) used truncated MACE GEBV (i.e., including MACE data from 4 yr ago). Therefore, it is essential to note that the outcomes are influenced by the subset of bulls used for validation.

Regarding bias, we observed levels closer to zero with $ssGBLUP_{MF10}$ than $MS_{Genomic}$. Increasing the residual polygenic effect from 5% ($ssGBLUP_{UPG5}$/$ssGBLUP_{MF5}$) to 10% ($ssGBLUP_{UPG10}$/$ssGBLUP_{MF10}$) resulted in less bias (approaching zero with 10% residual polygenic effect in the case of $ssGBLUP_{MF10}$). These findings align with prior studies (Liu et al., 2011; Gao et al., 2012; Su et al., 2012; Alkhoder and Liu, 2021). Pedigree-based BLUP was biased in all cases, including our PBLUP or MS_{BLUP}. Results from $PBLUP_{UPG}$ and MS_{BLUP} should theoretically align, as both analyses employ the same prediction method and UPG definitions in their models. However, differences in these findings are likely due to different UPG handling, stemming from insufficient information available to accurately estimate their effects, particularly in traits with low heritability (Bradford et al., 2019). In the case of MS_{BLUP}, when some UPG lack sufficient data, some of them are combined to avoid increasing bias; this process does not automatically occur in the case of blupf90 programs. Moreover, when comparing GEBV correlations between partial and whole data sets for ssGBLUP and $MS_{Genomic}$, the highest correlations were obtained with $ssGBLUP_{MF10}$, suggesting that this is the most accurate among the tested methods, with the additional benefit of being nearly unbiased.

Model Validation Between UPG and MF

The second objective of this study was to compare the effect of implementing UPG or MF; $PBLUP_{MF}$ slightly outperformed $PBLUP_{UPG}$ regarding bias and dispersion, consistent with previous studies (Garcia-Baccino et al., 2017; Bradford et al., 2019; Kudinov et al., 2020, 2022). Correlations between late and early proofs followed a similar trend, with $ssGBLUP_{MF10}$ yielding the highest correlations, between 0.86 and 0.90. Single-step GBLUP provided early predictions that are therefore rather accurate, given that late proofs are progeny-based. In pedigree models ($PBLUP_{MF}$ and $PBLUP_{UPG}$), EBVs with models using MF were also better correlated with the later proofs than models with UPG.

One of the main challenges in applying UPG or MF is the high number of UPG often defined in the population, which leads to poor estimates, especially in old genetic groups. Metafounders palliates this problem as it shares information across groups. Still, a careful consideration of UPG or MF assignment results in less biased estimation (Tsuruta et al., 2019; Kudinov et al., 2020).

Related to the use of UPG and MF, we did an all-breed ssGBLUP, which is unusual but not unique (e.g., Kudinov et al., 2020). This implies that SNP effects are defined simultaneously within and across breeds, so-called "uniquely defined" (Stuber and Cockerham, 1966) or "common genetic" (Christensen et al., 2015) approaches and that they are picking up breed differences. This does not seem to particularly harm the genomic prediction as it is generally similar to $MS_{Genomic}$ predictions. We can expect that Holstein predictions would "dominate" the Jersey ones (as there are many more genotyped Holsteins than Jersey). This seems to be confirmed by the fact that moving from 5% to 10% residual polygenic effect (i.e., less weight on genomics) increases the correlation for Jersey (Table 5). This deserves further investigation in other trait groups.

Genetic Trends for All Models

Plotting genetic trends of traits (Figure 1) provides a valuable means of evaluating the method's ability to accurately capture the response to selection. Both MF and UPG models show similar trends. Genomic and nongenomic models exhibit comparable trends until the last few years, consistent with findings by Meyer et al. (2018) and Kudinov et al. (2020).

The method/dataset yielding the apparent highest genetic trend in 2015 to 2019 varies across breeds and traits. It appears that there are 2 opposing effects. Because of changes in insemination practices, there is some bias not adequately accounted for in the data entering into CDCB, and this phenotypic bias leads to an upward bias in "early" (partial) predictions (CDCB, 2018). On the contrary, PBLUP is unable to account for genomic selection, resulting in a downward bias (Patry and Ducrocq, 2011). These 2 conflicting biases may explain the lack of a consistent ranking of methods across traits and breeds for recent genetic progress.

Furthermore, we plotted the estimated solutions of UPG and MF genetic groups (Figure 2). The MF solutions exhibited a smoother trend than UPG, as in Macedo et al. (2020) and Legarra and VanRaden (2023). The erratic behavior of UPG estimates may be attributed to a lack of records attributable to parent groups, leading to less accurate estimates (Tsuruta et al., 2014), and as mentioned before, it led to a redefinition of groups at CDCB.

CONCLUSIONS

This study found that ssGBLUP is a viable option for evaluating fertility traits in multibreed US dairy cattle. For the same definition of genetic groups, fitting MF resulted in slightly better genomic predictions compared with UPG, offering smoother trends for group solutions, similar or better correlations and slopes than UPG, and less bias in terms of average differences. Compared with the multistep evaluation, ssGBLUP produced less biased

estimates than BLUP, with slight inflation observed in the estimates of young, genotyped bulls.

NOTES

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Nonstandard abbreviations used: APY = Algorithm for Proven and Young; CCR = cow conception rate; CDCB = Council on Dairy Cattle Breeding; DPR = daughter pregnancy rate; EDC = equivalent daughter contribution; EFC = early first calving; HCR = heifer conception rate; HO_{CCR} = CCR in Holstein; HO_{DPR} = DPR in Holstein; IGV = improved genomic validation; JE_{CCR} = CCR in Jersey; JE_{DPR} = DPR in Jersey; LR = linear regression; MACE = Interbull's Multiple Across Country Evaluation; MF = metafounders; MS = multistep; MS_{BLUP} = MS evaluation method with BLUP prediction; $MS_{Genomic}$ = MS evaluation method with genomic prediction;PBLUP = pedigree-based BLUP; $PBLUP_{MF}$ = PBLUP with MF; $PBLUP_{UPG}$ = PBLUP with UPG; RPE = residual polygenic effect; ssGBLUP = single-step GBLUP; $ssGBLUP_{MF5}$ = ssGBLUP with MF fitted using 5% pedigree-based polygenic effect; $ssGBLUP_{MF10}$ = ssGBLUP with MF fitted using 10% pedigree-based polygenic effect; $ssGBLUP_{UPG5}$ = ssGBLUP with UPG fitted using 5% pedigree-based polygenic effect; $ssGBLUP_{UPG10}$ = ssGBLUP with UPG fitted using 10% pedigree-based polygenic effect; UPG = unknown parent groups.

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