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Approximating reliabilities of indirect predictions using single nucleotide polymorphism effects from large single-step genomic best linear unbiased predictor evaluations

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ABSTRACT

Reliability (REL) is a metric used to assess how accurately breeding values are predicted. Calculating theoretical REL requires the prediction error variance from the inverse of the coefficient matrix of the mixed model equations, which is computationally intensive for large populations or complex models. In such cases, REL are approximated. In routine genetic evaluations it is not feasible to evaluate animals received between evaluation cycles. As an interim solution, these individuals would rely on indirect predictions (IP) based on SNP effects, and their associated reliability approximated based on the variance of estimated SNP effects. This study aimed to approximate IP reliabilities when SNP effects are estimated from multi- and single-breed single-step genomic evaluations. Two reliability approximations were compared: 1) REL_{IP} , based on an approximated prediction error covariance (PEC) of estimated SNP effects, and 2) REL_{GEBV} , a benchmark REL calculated in routine genetic evaluations. In the multibreed analysis, the regression slope of REL_{GEBV} on REL_{IP} was ~ 1 , and the intercept was equal to zero for Holstein (HO). For Jersey (JE), slopes were 0.60 (males) and 0.78 (females), and intercepts were 0.32 (males) and 0.15 (females). For Brown Swiss (BS), slopes were 0.88 (males) and 0.82 (females), and intercepts were 0.03 (males) and 0.08 (females). Correlations between both reliabilities were higher than 0.96 for HO and BS, 0.79 (males) and 0.69 (females) for JE. In the single-breed analysis, JE showed no dispersion issues, with slopes of 1 and intercepts of zero, and correlations equal to 0.99 for both sexes. For BS, reliabilities were slightly under-dispersed, with slopes of 1.14 (males) and 1.08 (females). Additionally, single-breed evaluations yielded more consistent reliability averages within each

breed. In contrast, multibreed evaluation showed that dominant breeds disproportionately influenced reliability estimates of smaller breeds, highlighting the importance of approximating the PEC within-breed to avoid biased reliability estimates.

Key words: indirect prediction, algorithm for proven and young, prediction error (co)variance

INTRODUCTION

To select animals, breeders rely not only on EBV but on the reliability accompanying those estimates. The reliability reflects the amount of information used to estimate an animal's breeding value and helps breeders make informed mating and culling decisions within their herd (Harris and Johnson, 1998; Tier and Meyer, 2004). In the mixed model theory, reliabilities can be derived from the elements of the inverse of the coefficient matrix of the mixed model equations (MME), namely, from the prediction error variance (PEV) associated with the genetic effect (Henderson, 1984).

Since its introduction, genomic selection has led to more reliable BV (VanRaden, 2008; VanRaden et al., 2009; Legarra et al., 2014). As the value of using GEBV increased, so did the interest of genotyping animals (Wiggins and Carrillo, 2022). Recently, the Council of Dairy Cattle Breeding (CDCB; Bowie, MD) registered its 10-millionth genotyped animal (<https://wxw.uscdcb.com/10m-animal-genotypes-in-national-cooperator-database/>). Several methods have been developed to manage large-scale genomic datasets in single-step evaluations (Liu et al., 2014; Misztal et al., 2014a; Mäntysaari et al., 2017). This includes algorithms for computing reliabilities (Liu et al., 2017; Ben Zaabza et al., 2022; Bermann et al., 2022b; Gao et al., 2023), which are impossible to obtain in large, genotyped populations because they rely on elements of the inverse of the MME coefficient matrix, an intensive operation. Liu et al. (2017) proposed a method based on SNPBLUP, whereas Gao et al. (2023) extended

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the works of Ben Zaabza et al. (2022) with derivations based on GBLUP and SNPBLUP. Bermann et al. (2022b) extended the algorithm for proven and young (APY), originally introduced by Misztal et al. (2014a), and developed an efficient method to approximate genomic reliabilities within the single-step GBLUP (ssGBLUP) framework, thereby addressing the challenges posed by the growing amount of genomic information. When comparing their approximated genomic reliability to exact values derived from the inverse of the MME coefficient matrix, they found minor overestimation. Similarly, Ramos et al. (2024) reported that the approximated reliabilities were slightly overestimated compared with the exact values.

In many selection schemes, routine genetic evaluations are performed only a few times yearly (e.g., quarterly), yet new genotypes are received daily. Due to the high computational demands of the genetic evaluation, these newly genotyped animals would receive interim predicted breeding values and associated reliabilities before the subsequent official genetic evaluation. Such predictions are referred to as direct genomic values or indirect predictions (IP) and can be obtained using SNP effects estimated from the latest genetic evaluation. However, estimating the reliability of IP also requires the variances of the estimated SNP effects (Strandén and Christensen, 2011).

Garcia et al. (2022) obtained the variance of estimated SNP effects under the ssGBLUP model by backsolving the prediction error covariance (PEC) of GEBV. Then, they evaluated the reliabilities of indirect predictions (REL_{IP}) using the PEC from an APY ssGBLUP evaluation with various core sizes and definitions and observed no significant effect on reliability estimates; however, they relied on the inverse of the MME, and the study was limited to a maximum of 60k genotyped animals because of computing costs. To reduce computing costs, the authors suggested solving the MME with a smaller subset of genotyped animals (i.e., the core animals in APY) to obtain the PEC of GEBV. Although the correlations between the reliabilities from the inverse of the MME based on all genotyped animals or only core animals were greater than 0.99 with 20k or more core animals (Garcia et al., 2022), this method is still limited to a data size where the inverse is possible. If the data contain millions of animals or multiple traits and many random effects, the inverse of MME may not be possible with over 10k genotyped animals.

With the objective of computing variances of estimated SNP effects for obtaining P -values in single-step GWAS, Leite et al. (2024) combined the equivalence between APY ssGBLUP and APY ssSNPBLUP described in Bermann et al. (2022a) with intermediate steps of the algorithm proposed by Bermann et al. (2022b) presented to compute the reliability of GEBV. This allowed for the

approximation of the PEC of GEBV, avoiding the need to invert the MME. Additionally, the equivalence between APY ssGBLUP and APY ssSNPBLUP simplified the computations, as the variance of estimated SNP effects is based on PEC of GEBV of core animals only. Leite et al. (2024) compared this approximated PEC to the exact PEC based on the inverse of the MME when using the genomic relationship matrix (G^{-1}) or its sparse representation (G_{APY}^{-1}), they found that SNP P -values produced by the 3 methods were similar. Although only the diagonal values of the matrix of variance of estimated SNP effects are used for the SNP P -values, the full matrix would be needed to compute the reliabilities of IP.

Hence, this study aimed to: (1) build upon the developments of Leite et al. (2024) and use the approximated PEC of GEBV based only on core animals to obtain the variance of estimated SNP effects and to approximate the reliability of IP; (2) assess the quality of approximated IP reliabilities in single-trait dairy cattle evaluations conducted under both multi- and single-breed settings. Specifically, we compared within-breed GEBV reliabilities to IP reliabilities under multi- and single-breed evaluations.

MATERIALS AND METHODS

Data and Model

Ethical approval for this study was not needed because the data came from existing databases. Data from the official multibreed genomic evaluation in the US dairy cattle population was provided by the CDCB. The dataset consisted of 98,938,654 records (first 5 lactations) for milk yield (MY), dating from February 1963 to June 2021. These records covered all breeds used in the official evaluation: Ayrshire (AY), Brown Swiss (BS), Guernsey (GU), Holstein (HO), Jersey (JE), Milking Shorthorn (MS) and crossbreds (XX). The genotypic dataset was comprised of 1,877,704 genotyped animals, imputed to a standard set of 78,964 SNP (Table 1), following the CDCB procedures as described at <https://uscdcb.com/genomic-evaluations/>. The total number of animals in the pedigree was 49,585,192.

A single-trait multibreed (MB) repeatability animal model was applied as follows:

$$y = X\beta + Z_h h + Z_u u + Z_p p + e, \quad [1]$$

where y is the vector of MY records, β is the vector of fixed effects comprised of herd-management, age-parity interaction, and inbreeding coefficient and heterosis as linear covariate, h is the vector of random herd-by-sire interaction effects, u is the vector of random animal additive genetic effects, p is the vector of random permanent

Table 1. Distribution of phenotypes and genotypes per breed¹

Breed	Phenotypes	Genotypes
AY	216,122	12,822
BS	366,892	58,271
GU	637,022	6,964
HO	34,112,088	1,523,968
JE	2,894,825	268,278
MS	57,159	0
XX	571,995	7,401

¹AY = Ayrshire; BS = Brown Swiss; GU = Guernsey; HO = Holstein; JE = Jersey; MS = Milking Shorthorn; XX = Crossbreds.

environmental effects, and **e** is the vector of residuals. The **X**, **Z_h**, **Z_u**, **Z_p** are incidence matrices relating the phenotypic data to the effects in **β**, **h**, **u**, and **p**, respectively. The random effects (co)variance matrix is given by:

$$Var \begin{bmatrix} \mathbf{h} \\ \mathbf{u} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_h^2 & 0 & 0 & 0 \\ 0 & \mathbf{H}\sigma_u^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_p^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}, \quad [2]$$

where **I** is an identity matrix, **H** is the realized relationship matrix, which combines pedigree and genomic information (Legarra et al., 2009; Aguilar et al., 2010; Christensen and Lund, 2010). The genomic relationship (**G**) was built using VanRaden (2008) type 1, the gene content matrix was centered by twice the current allele frequencies (i.e., of the genotyped population). Compatibility issues were solved by tuning **G** as in Vitezica et al. (2011). The variance components used in the model were: σ_h^2 , σ_u^2 , σ_p^2 , and σ_e^2 belonging to the herd-by-sire interaction effects, animal additive genetic effects, permanent environmental effects, and residuals, respectively. Additionally, we ran 2 single-breed (**SB**), single-trait ss-GBLUP models for JE and BS populations. These models were run to compare the changes in reliabilities between the MB and SB evaluations. In SB evaluations, allele frequencies and tuning were based on within-breed genotyped population (i.e., either genotypes of JE or BS).

Given the large number of genotyped animals, the APY was used (Miszta et al., 2014a). Core animals were randomly selected within-breed based on Cesarani et al. (2022), with a 50% sex ratio (except for GU, which lacked sufficient genotyped males). The number of core animals per breed and sex is shown in Table 2. In the SB evaluations, the same core animals selected for each breed were used in their respective evaluations (e.g., JE core animals from MB were used as core for JE SB).

Table 2. Number of core animals per breed and sex and total number of genotypes across breed used in single- and multibreed evaluations¹

Breed	Number of core animals	
	Males	Females
AY	2,500	2,500
BS	2,500	2,500
GU	1,490	3,510
HO	7,500	7,500
JE	7,500	7,500
MS	2,500	2,500

¹AY = Ayrshire; BS = Brown Swiss; GU = Guernsey; HO = Holstein; JE = Jersey; MS = Milking Shorthorn; XX = Crossbreds.

Computation of Genomic and IP Reliabilities

Reliabilities were assessed for animals born between 2019 and 2021 (focal animals). Those were the youngest genotyped males and females, totaling 3,696 animals for HO, 3,888 for JE, and 842 for BS. These focal animals had their pedigree, own, and progeny phenotypes excluded from the analyses. These animals were not chosen as core animals.

Two different reliabilities were computed:

- I. REL_{GEBV} : calculated by including the genotypes of focal animals in the main evaluation, as if they were part of the official genetic evaluation and used as the benchmark reliability. This can be viewed as a genomic breeding value reliability because the focal animals contributed only their genotypes to the evaluation. The $REL_{GEBV,MB}$ refers to REL_{GEBV} obtained from the MB evaluation, and $REL_{GEBV,SB}$ from the SB evaluation.
- II. REL_{IP} : calculated by excluding genotypes of the focal animals and having their IP and corresponding reliabilities computed afterward. This approach relied on the variances of estimated SNP effects without any direct contribution from the focal animals. The $REL_{IP,MB}$ refers to REL_{IP} obtained from the MB evaluation, and $REL_{GEBV,SB}$ from the SB evaluation.

In both analyses, we used the same set of core animals to ensure that any differences were not due to changes in core animal selection.

Calculating REL_{GEBV}

1. Constructing $\mathbf{G}_{APY}^{-1}$ with focal animals:

For core (**c**) and noncore (**n**) animals, $\mathbf{G}_{APY}^{-1}$ (Miszta et al., 2014a) is constructed as:

$$\mathbf{G}_{APY}^{-1} = \begin{bmatrix} \mathbf{G}_{cc}^{-1} & 0 \\ 0 & 0 \end{bmatrix} + \begin{bmatrix} -\mathbf{G}_{cc}^{-1}\mathbf{G}_{cn} \\ \mathbf{I} \end{bmatrix} \mathbf{M}_{nn}^{-1} \begin{bmatrix} -\mathbf{G}_{nc}\mathbf{G}_{cc}^{-1} & \mathbf{I} \end{bmatrix}, \quad [3]$$

where $\mathbf{G}_{cc}^{-1}$ is the inverse of $\mathbf{G}$ for core animals, $\mathbf{G}_{cn}$ is the genomic relationship matrix relating c and n animals, and $\mathbf{M}_{nn} = \text{diag}(\mathbf{G}_{nn} - \mathbf{G}_{nc}\mathbf{G}_{cc}^{-1}\mathbf{G}_{cn})$.

In this case, the focal animals are treated as n animals.

2. Saving $\mathbf{G}_{APY}^{-1}$:

The $\mathbf{G}_{APY}^{-1}$ was saved using preGSf90 (Misztal et al., 2014b).

3. Calculating REL_{GEBV} using accf90GS3 (Bermann et al., 2022b):

The algorithm implemented in accf90GS3 calculates pedigree reliabilities based on Tier and Meyer (2004) and genomic reliabilities based on Bermann et al. (2022b). It requires $\mathbf{G}_{APY}^{-1}$ to obtain the PEV as $\text{diag}(\mathbf{D} + \mathbf{G}_{APY}^{-1}\lambda)^{-1}$:

$$REL_{GEBV_i} = 1 - \frac{PEV_i}{g_{ii}\sigma_u^2}, \quad [4]$$

where g_{ii} is the diagonal element of the genomic relationship matrix of the i th animal, and $\mathbf{D}$ is a diagonal matrix of effective record contributions (Misztal and Wiggans, 1988).

Calculating REL_{IP}

1. Construct and save $\mathbf{G}_{APY}^{-1}$ by excluding genotypes of focal animals.
2. Obtain GEBV with BLUP90IOD3 (Misztal et al., 2014b), reading saved matrices from previous step.
3. Compute and store the PEC matrix ($\mathbf{PEC}_{cc}$) for core animals with accf90GS3 (Bermann et al., 2022b): The $\mathbf{PEC}_{cc}$ is the approximated prediction error covariance for core animals:

$$\mathbf{PEC}_{cc} = \left(\mathbf{D}_c + \lambda \mathbf{G}^{cc} - \lambda \mathbf{G}^{cn} \left(\lambda \mathbf{M}_{nn}^{-1} + \mathbf{D}_n \right)^{-1} \lambda \mathbf{G}^{nc} \right)^{-1}, \quad [5]$$

where $\mathbf{D}_c$ and $\mathbf{D}_n$ are the c and n blocks of the diagonal matrix based on effective record contributions ($\mathbf{D}$) and $\lambda = \frac{\sigma_e^2}{\sigma_u^2}$.

4. Compute SNP variances associated with estimated SNP effects with postGSf90 (Misztal et al., 2014b).

Using APY, SNP effect estimations ($\hat{\mathbf{a}}$) only depend on the core animals (Bermann et al., 2022a)

$$\hat{\mathbf{a}} = E(\mathbf{a} | \hat{\mathbf{u}}_c) = (1 - \alpha)b \frac{1}{2 \sum p_l (1 - p_l)} \mathbf{Z}_c' \mathbf{G}_{cc}^{-1} \hat{\mathbf{u}}_c, \quad [6]$$

where $\hat{\mathbf{u}}_c$ is the vector of GEBV of core animals from step 5; p_l is the l th allele frequency based on the allele frequencies of all the genotyped animals; $\mathbf{Z}_c$ is the centered gene content matrix based on the allele frequencies of all the genotyped animals; $\mathbf{G}_{cc}^{-1}$ is the inverse of the genomic relationship matrix for the core animals; α is the blending parameter, which equals 0.05 (also known as the residual polygenic effect); and b is the tuning parameter computed as in Vitezica et al. (2011) based on the current genotyped population.

Estimated SNP effects are required for computing IP, although not directly needed for calculating REL_{IP} . However, in routine evaluations, IP are typically obtained first, and their associated reliabilities are then derived. Hence, once $\hat{\mathbf{a}}$ is obtained, its variance is computed as in Leite et al. (2024):

$$\begin{aligned} \text{Var}(\hat{\mathbf{a}}) &= (1 - \alpha)b \frac{1}{2 \sum p_l (1 - p_l)} \mathbf{Z}_c' \mathbf{G}_{cc}^{-1} (\mathbf{G}_{cc} \sigma_u^2 - \mathbf{PEC}_{cc}) \\ &\mathbf{G}_{cc}^{-1} \mathbf{Z}_c \frac{1}{2 \sum p_l (1 - p_l)} (1 - \alpha)b, \end{aligned} \quad [7]$$

where $\mathbf{PEC}_{cc}$ is stored in step 6.

5. Compute REL_{IP} using pred90 (Misztal et al., 2014b):

$$REL_{IP_i} = \frac{\mathbf{z}_{fi}' \text{Var}(\hat{\mathbf{a}}) \mathbf{z}_{fi}}{g_{ii} \sigma_u^2}, \quad [8]$$

where $\mathbf{z}_{fi}$ is the centered gene content vector of i th focal animals based on the allele frequencies of all the genotyped animals used to compute $\mathbf{G}_{APY}^{-1}$.

Assessing Reliabilities

To evaluate the relationship between REL_{GEBV} and REL_{IP} , the following linear regression was used in both MB and SB evaluations:

$$REL_{GEBV_i} = b_0 + b_1 REL_{IP_i} + e_i, \quad [9]$$

where REL_{GEBV_i} is the reliability of GEBV for the i th focal animal; REL_{IP_i} is the reliability of IP for the i th focal

animal; b_0 is the intercept; b_1 is the slope; and e_i is a random residual term. It is worth noting that when the analyses are done using the MB model, REL_{GEBV_i} refers to REL_{GEBV,MB_i} and REL_{IP_i} to REL_{IP,MB_i} . In contrast, in the SB model, REL_{GEBV_i} refers to REL_{GEBV,SB_i} and REL_{IP_i} to REL_{IP,SB_i} . Provided that REL_{GEBV} and REL_{IP} are on the same scale, we expect an intercept close to zero and a slope close to one. Additionally, we calculated the Pearson correlation between REL_{GEBV} and REL_{IP} and their means.

RESULTS AND DISCUSSION

Multibreed ssGBLUP Evaluation

Regression coefficients for males and females indicate that $REL_{IP,MB}$ matched well with $REL_{GEBV,MB}$ for males ($b_1 = 0.98$) and for females ($b_1 = 0.96$) in HO (Figure 1). The intercept was zero for males and 0.02 for females. The 2 reliabilities were equal for HO when the calculation included inbreeding and the blending and tuning parameters. Some HO animals exhibited larger differences between $REL_{GEBV,MB}$ and $REL_{IP,MB}$. However, these cases involved crossbred females classified as pure HO in the pedigree. This misclassification caused these deviations, as the animals originated from populations with allele frequencies different from those of a pure HO population. Consequently, their outcome resembled those of non-HO populations rather than the pure HO. For JE and BS, calculating $REL_{IP,MB}$ based on PEC_{cc} from the MB evaluation did not yield accurate results (Figure 2). The $REL_{IP,MB}$ were overdispersed and overestimated in both sexes and breeds. In JE, b_1 was 0.60 (males) and 0.78 (females), whereas in BS, it was 0.88 (males) and 0.82 (females). The scale of $REL_{IP,MB}$ differed in both breeds, with a lesser effect on BS with b_0 of 0.03 (males) and 0.08 (females) but higher intercepts for JE with 0.32 (males) and 0.15 (females).

In the MB evaluation, genetic differences among breeds were not explicitly modeled. Typically, this is addressed by incorporating genetic groups (i.e., unknown parent groups [UPG] or metafounders [MF]) to assign different breeds to different genetic groups and constructing a breed-specific genomic relationship matrix where allele frequencies are calculated separately for each breed. In this study, however, the inverse of the genomic relationship matrix was built based on all breeds in the population with a core set representing all of them. This decision was made because the computation of $REL_{GEBV,MB}$ did not include UPG or MF, and to enable a fair comparison between both reliabilities, genetic groups were not included in our model.

Given the differences in the results of smaller breeds, it is possible that breed differences in allele frequencies influenced the approximation of the PEC in the multi-breed evaluations. Smaller breeds may be more sensitive to such assumptions, particularly when the largest breed dominates the population structure. Cesarani et al. (2022) analyzed GEBV predictive ability across 5 dairy breeds with almost 4 million genotyped animals, finding similar results in SB and MB evaluations. This was attributed to a representative set of core animals from all 5 breeds and the use of UPG to model breed differences. In our case, these differences may reflect different population structures and modeling choices, and assuming uniform allele frequencies across all breeds may not be proper if reliabilities of IP must come from MB evaluations. The $REL_{IP,MB}$ could differ largely when uniform allele frequencies are assumed across all breeds, even if GEBV differences are negligible from a prediction standpoint.

Table 3 presents the correlations between $REL_{GEBV,MB}$ and $REL_{IP,MB}$ from the MB evaluation. For HO, correlations were 0.99 (males) and 0.96 (females), indicating consistency in both reliabilities. For JE, correlations were 0.79 (males) and 0.69 (females), whereas for BS, they were 0.99 (males) and 0.97 (females). These results were expected, as Figure 2 illustrates that reliabilities did not perfectly align, even when their correlations were high (i.e., BS). Previous studies (Lourenco et al., 2018;

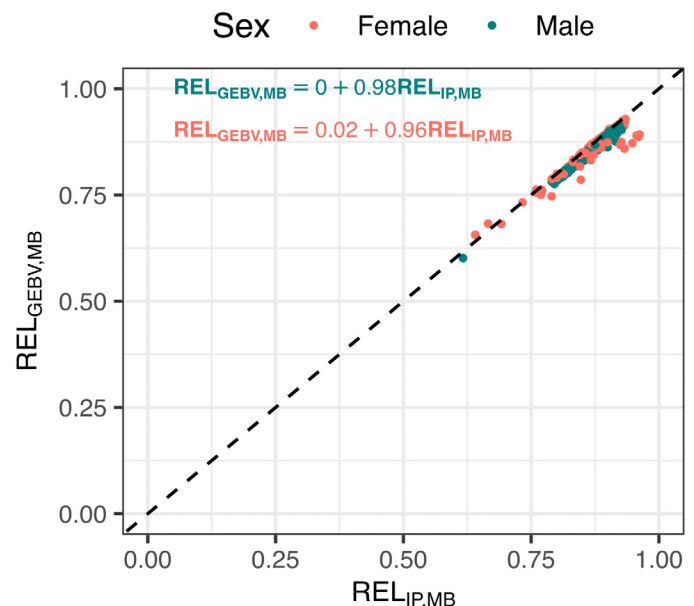


Figure 1. Multibreed reliability for Holstein focal animals with 5% residual polygenic effect. Abbreviations: $REL_{GEBV,MB}$ = reliability of genomic predicted breeding value; $REL_{IP,MB}$ = reliability of indirect prediction.

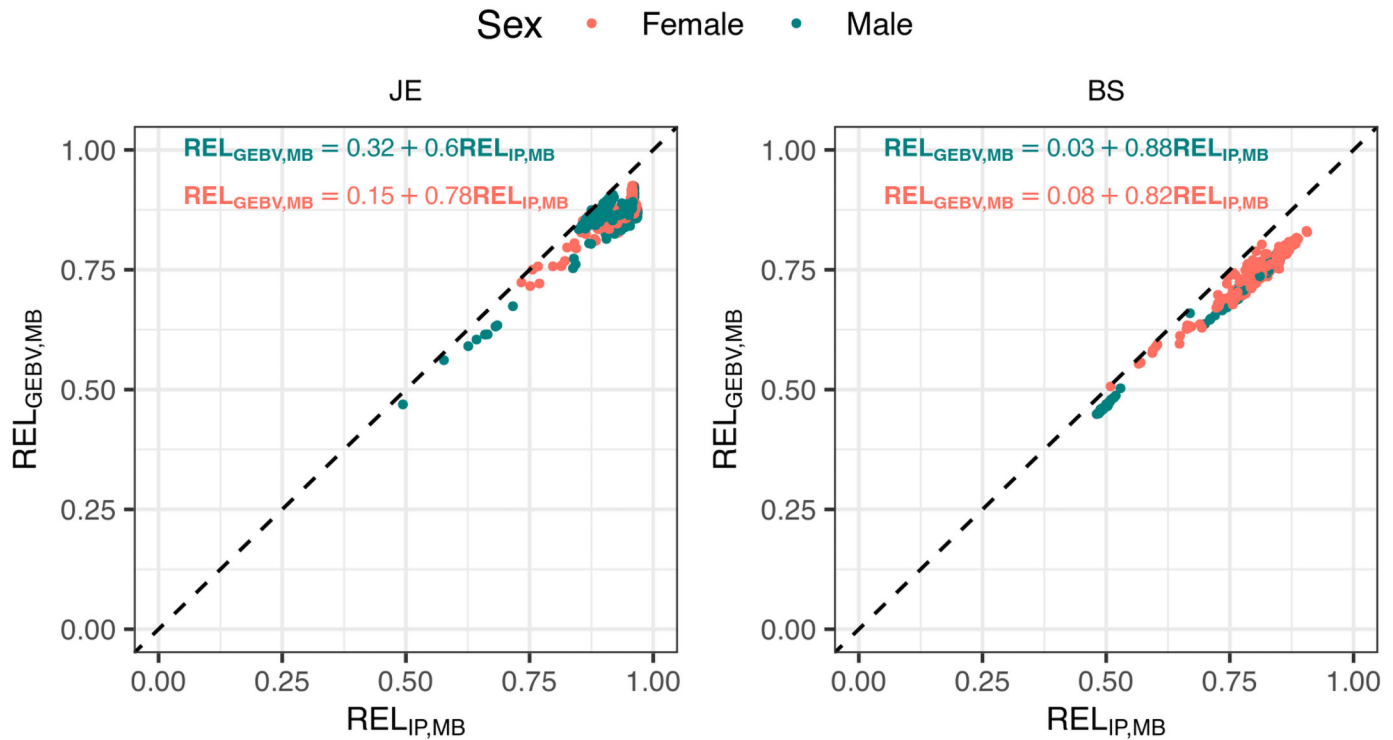


Figure 2. Multibreed reliability for Jersey (JE) and Brown Swiss (BS) focal animals with 5% residual polygenic effect. Abbreviations: $REL_{GEBV,MB}$ = reliability of genomic predicted breeding value; $REL_{IP,MB}$ = reliability of indirect prediction.

Garcia et al., 2020) reported high correlations (~ 0.99) between GEBV and IP estimations based on core animals. However, no direct comparison of their reliabilities was done. Garcia et al. (2022) showed that IP accuracies could be derived from the variance of estimated SNP effects based on the exact PEC of core animals using $\mathbf{G}_{APY}^{-1}$.

For smaller breeds, our findings suggest that approximating $Var(\hat{\mathbf{a}})$ based on $\mathbf{PEC}_{cc}$ from the MB evaluation may be affected by several factors, for example, the population structure driven by the breed with the highest number of genotypes, in this case, HO. This could, in turn, overestimate reliabilities of less-represented breeds.

Single-breed ssGBLUP Evaluations

For JE, REL_{IP} changed from MB ($REL_{IP,MB}$) to SB evaluations ($REL_{IP,SB}$; Figure 3). Dispersion issues were resolved ($b_1 = 0.99$ for males and $b_1 = 1.00$ for females), and $b_0 = 0.01$ in both sexes. Correlations also improved for both sexes (from 0.79 to 0.99 in males and from 0.69 to 0.99 in females). This indicates that reliability approximations align well when variances of estimated SNP effects are breed-specific. Additionally, the reliability overestimation was mitigated in the SB analysis. Table 4 shows the mean reliabilities of $REL_{IP,SB}$ and $REL_{GEBV,SB}$ were equal to 0.77 (males) and 0.82 (females) in the JE

SB evaluation. In contrast, in the MB analysis, reliability means differed between the 2 methods, with an overestimation in both (> 0.88) compared to the SB analysis.

For BS, the approximation of $REL_{IP,SB}$ improved after removing genotypes from other breeds (Figure 4), demonstrating that the $\mathbf{PEC}_{cc}$ (SB evaluation) was effectively approximated. Reliabilities were slightly underdispersed ($b_1 = 1.14$ for males and $b_1 = 1.08$ for females), with intercepts close to zero. Correlations for BS were already high in the MB evaluation and remained above 0.98 in the SB analysis (Table 3). The overestimation of $REL_{GEBV,SB}$ and $REL_{IP,SB}$ was also mitigated, as shown in Table 4, where the means of both reliabilities were

Table 3. Pearson correlations between genomic reliabilities (REL_{GEBV}) and reliability of indirect predictions (REL_{IP}) for Holstein (HO), Jersey (JE), and Brown Swiss (BS) from multibreed and single-breed evaluations

Sex	HO	JE	BS
		Multibreed	
Male	0.99	0.79	0.99
Female	0.96	0.69	0.97
		Single-breed	
Male		0.99	0.99
Female		0.99	0.98

Table 4. Mean (and SD) genomic reliabilities (REL_{GEBV}) and reliabilities of indirect predictions (REL_{IP}) for Jersey (JE) and Brown Swiss (BS) from multibreed ($REL_{GEBV,MB}$, $REL_{IP,MB}$) and single-breed evaluations ($REL_{GEBV,SB}$, $REL_{IP,SB}$)

Reliability	JE		BS	
	Male	Female	Male	Female
$REL_{GEBV,MB}$	0.88 (0.03)	0.89 (0.01)	0.70 (0.10)	0.74 (0.04)
$REL_{IP,MB}$	0.94 (0.04)	0.95 (0.01)	0.76 (0.10)	0.81 (0.04)
$REL_{GEBV,SB}$	0.77 (0.08)	0.82 (0.04)	0.37 (0.10)	0.44 (0.05)
$REL_{IP,SB}$	0.77 (0.08)	0.82 (0.04)	0.37 (0.09)	0.43 (0.05)

equal in the SB evaluation (0.37 for males and 0.44 for females) compared to the MB evaluation.

VanRaden et al. (2009) emphasized the importance of accounting for breed differences when performing MB evaluations by noting that estimating SNP effects across breeds without considering these differences can lead to allele frequency shifts, especially for rare alleles. Our findings suggest that accounting for breed differences may be important not only for improving breeding value prediction but also for obtaining better estimates of both approximated reliabilities. Correct reliability estimation may require accounting for breed differences when constructing $\mathbf{G}_{cc}^{-1}$ and calculating variances of estimated SNP effects, especially when allele frequencies vary across breeds, potentially leading to deviations in reliability estimates. In the MB evaluation, allele frequencies were predominantly influenced by the HO breed, which represents most genotyped animals. This affected

the reliability approximation of smaller breeds. In addition, the genomic relationships among core animals may change as we shift from an MB to an SB evaluation, which could affect the variances of estimated SNP effects and, consequently, the derived reliabilities. Fixed effects common to all breeds may contribute to the observed discrepancies, as datasets are different between MB and SB. Another factor worth considering is the tuning applied to $\mathbf{G}$, which can influence its scale and properties. The tuning may be different from MB to SB evaluations, leading to differences in reliabilities (IP vs. GEBV) estimation. A potential solution is using MF (Legarra et al., 2015), although this requires further investigation. Bermann et al. (2023) developed a method to approximate reliabilities using MF that accounts for base population differences, showing that reliabilities match those obtained from single-population models without MF.

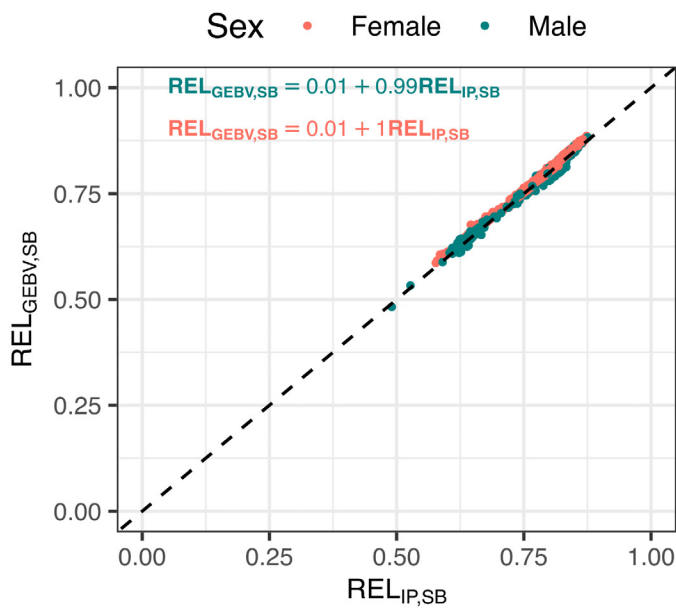


Figure 3. Single-breed reliability for Jersey focal animals with 5% residual polygenic effect. Abbreviations: $REL_{GEBV,SB}$ = reliability of genomic predicted breeding value; $REL_{IP,SB}$ = reliability of indirect prediction.

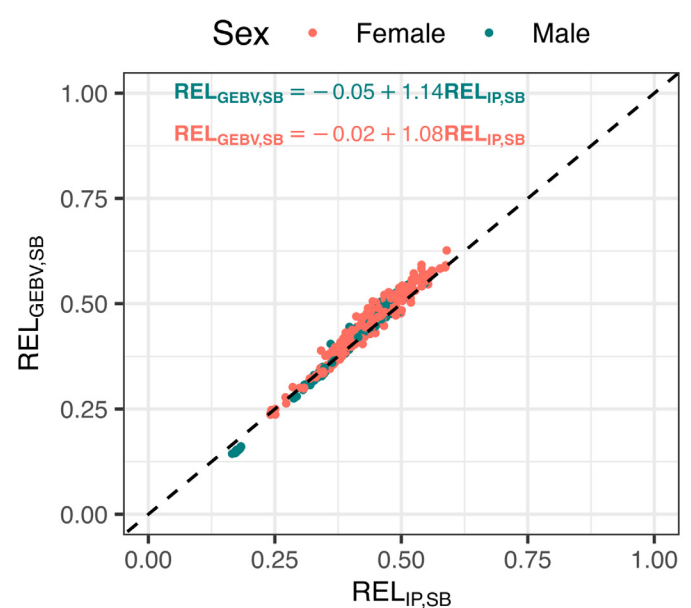


Figure 4. Single-breed reliability for Brown Swiss focal animals with 5% residual polygenic effect. Abbreviations: $REL_{GEBV,SB}$ = reliability of genomic predicted breeding value; $REL_{IP,SB}$ = reliability of indirect prediction.

CONCLUSIONS

Our results showed that it is feasible to use the approximated PEC of GEBV of core animals to obtain the variance of estimated SNP effects and then compute the reliability of IP. These approximated REL_{IP} are consistent with the genomic reliability typically obtained from official genetic evaluations. In the multibreed analysis, reliability estimates of smaller breeds are likely influenced by population structure, where the dominant breed affects SNP effect estimation and variance. Factors such as breed-specific allele frequencies, tuning of the genomic relationship matrix, and shared fixed effects across breeds may contribute to these differences and warrant further investigation. At the moment, these animals can rely on their interim reliabilities obtained from SB evaluations.

NOTES

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Nonstandard abbreviations used: APY = algorithm for proven and young; AY = Ayrshire; BS = Brown Swiss; C = core; CDCB = Council of Dairy Cattle Breeding; GU = Guernsey; HO = Holstein; IP = indirect predictions; JE = Jersey; MB = multibreed; MF = metafounders; MME = mixed model equations; MS = Milking Shorthorn; MY = milk yield; n = noncore; PEC = prediction error covariance; PEC_{cc} = prediction error covariance matrix; PEV = prediction error variance; REL_{IP} = reliabilities of indirect predictions; SB = single-breed; ssGBLUP = single-step GBLUP; UPG = unknown parent groups; XX = cross-breeds.

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