

## ORIGINAL ARTICLE

# Estimation of heritability with genomic information by method R

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## Abstract

Estimating heritabilities with large genomic models by established methods such as restricted maximum likelihood (REML) or Bayesian via Gibbs sampling is computationally expensive. Alternatively, heritability can be estimated indirectly by method R and by maximum predictivity, referred to as MaxPred here, at a much lower computing cost. By method R, the heritability used for predictions with whole and partial data is considered the best estimate when the predictions based on partial data are unbiased relative to those with the complete data. By MaxPred, the heritability estimate is the one that maximizes predictivity. This study compared heritability estimation with genomic information using average information REML (AI-REML), method R and MaxPred. A simulated population was generated with ten generations of 5000 animals each and an effective population size of 80. Each animal had one record for a trait with a heritability of 0.3, a phenotypic variance of 10.0 and was genotyped at 50 k SNP. In method R, the heritability estimate is found when the expectation of a regression coefficient is equal to one. The regression is the EBV of selection candidates calculated with the whole dataset regressed on the EBV of candidates calculated from a partial dataset. In this study, we used the GBLUP framework and therefore, GEBV was calculated. The partial dataset was created by removing the last generation of phenotypes. Predictivity was defined as the correlation between the adjusted phenotypes of the selection candidates and their GEBV calculated from the partial data. We estimated the heritability for populations that included between three and 10 generations. In every scenario, predictivity increased as more data was used and was the highest at the simulated heritability. However, the predictivity for all data subsets and all heritabilities compared did not differ more than 0.01, suggesting MaxPred is not the best indication for heritability estimation. For the whole dataset, the heritability was estimated as  $0.30 \pm 0.01$ ,  $0.26 \pm 0.01$  and  $0.30 \pm 0.04$  for AI-REML without genomics, AI-REML with genomics and method R with genomics, respectively. Heritability estimation with genomics by method R reduced timing by 83%, implying a reduction in computing time from 9.5 to 1.6 h, on average, compared to AI-REML with genomics. Method R has the

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potential to estimate heritabilities with large genomic information at a low cost when many generations of animals are present; however, the standard error can be high when only a few iterations are used.

#### KEYWORDS

large data, linear regression, predictivity, variance components

## 1 | INTRODUCTION

Heritabilities change over time due to selection and the variance components used in the genetic evaluations need to be updated periodically. The magnitude of changes depends on the selection intensity and available genetic variation (Falconer, 1996; Walsh & Lynch, 2018). Additionally, some changes may be due to resource allocation constraints (Rauw, 2008) that are difficult to model. With the decrease in genotyping costs and, thus, the increase in the number of genotyped animals, traditional methods for variance component estimation (VCE) are becoming too costly or impossible (Misztal et al., 2021). Under genomic selection, the selection intensity is greater, possibly causing more rapid changes in genetic parameters compared to non-genomic selection. For example, Hidalgo et al. (2020) found large changes in heritability and genetic correlation for some traits in a swine population a few years after genomic selection was implemented. Therefore, with the rapid change in genetic parameters due to selection and the increase in data size, a feasible method to estimate heritabilities is needed.

The most popular methods for estimating variance components are REML (Patterson & Thompson, 1971) and Bayesian via Gibbs sampling (Gianola & Fernando, 1986). They have good theoretical properties (Gianola et al., 2009) and, with sparse matrix implementation (Misztal, 2008), could support large models. REML, by Monte Carlo sampling, could support models with a large number of parameters (Matilainen et al., 2013). However, with genomic information, mixed model equations are no longer sparse as the genomic component creates a dense subblock (Misztal et al., 2021). For smaller datasets, computations were much faster compared with larger datasets and were facilitated by using a sparse matrix package that recognizes dense blocks in a matrix and processes them using parallel computing (Masuda et al., 2015). Since the inverse of the genomic relationship matrix can be approximated by a sparse matrix for populations with a small effective population size using the algorithm for proven and young (Misztal, Legarra, et al., 2014; Misztal, Tsuruta, et al., 2014;  $\mathbf{G}_{\text{APY}}^{-1}$ ), Junqueira et al. (2022) attempted REML using  $\mathbf{G}_{\text{APY}}^{-1}$  in single-step GBLUP. However, no savings in computing resources were observed as the inverse of the

pedigree relationship matrix for genotyped animals was dense since sparse representations such as APY do not work for this matrix.

One way to reduce computing costs when doing VCE in large, genotyped populations is to use a subset of individuals with genotypes. However, this can introduce bias due to data preselection if the animals are not randomly chosen for genotyping or phenotyping (Bussiman et al., 2023; Patry & Ducrocq, 2011). Consequently, this bias propagates to GEBV. Therefore, using the entire dataset can help avoid biases. Before genomics, one method used for heritability estimation of complete populations was method R (Reverter et al., 1994b). Method R depends on the property of mixed models, where the expectation of the regression coefficient of breeding values obtained with the complete data on breeding values obtained with the partial data equals 1 when the correct variance ratio is used. Because estimates of mixed model equations do not depend on absolute variances but on variance ratios, method R is suitable for estimating heritabilities but not the actual variances. While models supported by method R were initially restricted to single trait with one additive effect, formulas exist for models with correlated effects (Druet et al., 2001).

Method R was used successfully to estimate additive and dominance variance ratios, which require large data sets for small standard errors (Misztal, 1997). Estimation of variance ratios without genomic information was successful with the complete dairy, beef and pig populations and for traits of low to high heritability (Culbertson et al., 1998; Gengler et al., 1998; Misztal et al., 1998). Because method R requires only an initial variance ratio value and the calculation of breeding values for partial and complete data sets, computations are manageable for any data size where the genetic evaluation is possible, including for the largest models. Likewise, method R should apply to genomic models. Some limitations of method R include its inability to estimate variances of the random effects separately from the other random effects, estimate genetic correlations between traits and its lack of theoretical properties (Misztal, 1997; Reverter et al., 1994a). Therefore, method R would not be suitable for models with multiple correlated traits or multiple random effects. However, Druet et al. (2001) showed that estimating

genetic covariances between direct and maternal effects is possible. Another method applicable to estimating heritabilities with large genomic datasets would be selecting variance components that maximize the predictivity, hereinafter denoted as MaxPred, where predictivity is the correlation between genomic estimated breeding values and adjusted phenotypes (Legarra et al., 2008). Finding such components would require a grid search and would be applicable to any data size. This study aimed to analyse heritability estimation by method R and MaxPred and compare the estimates to those obtained by average information REML (AI-REML) in the presence of genomic information.

## 2 | MATERIALS AND METHODS

### 2.1 | Data simulation

QMSim software (Sargolzaei & Schenkel, 2009) was used for data simulation. A historical population of 1000 generations with a constant size of 50,000 animals was generated with random mating, no selection and no migration. A bottleneck effect was simulated by reducing the population to 20,000 animals over 1800 generations. From the last generation of the historical population, 20 unrelated males and 5000 unrelated females were randomly selected as the breeding individuals for the first recent generation to create an effective population size equal to 80. A single phenotype was simulated for each animal for a trait with a QTL heritability of 0.3, no polygenic effect, an overall heritability of 0.3 and a phenotypic variance of 10. Ten generations were simulated with an effective population size constant at 80, litter size equal to one, equal probability of male or female progeny, random mating, replacement ratio of 0.9 for sires and 0.4 for dams and the selection and culling decisions were based on high and low GEBV, respectively. GEBV were calculated externally using blup90iod3 (Miszta, Tsuruta, et al., 2014) with a GBLUP model:

$$\mathbf{y} = \mathbf{u} + \mathbf{e}, \quad (1)$$

where  $\mathbf{y}$  is a vector of phenotypes,  $\mathbf{u}$  is a random vector of breeding values and  $\mathbf{e}$  is a random vector of residuals. The blup90iod3 program uses an iteration on data method with a convergence criterion of  $10^{-12}$ . The covariance matrices were assumed to be:

$$\text{Var} \begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}\sigma_a^2 & 0 \\ 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}, \quad (2)$$

where  $\sigma_a^2$  and  $\sigma_e^2$  are variances for the additive genetic and residual effects, respectively,  $\mathbf{I}$  is the identity matrix and  $\mathbf{G}$

is the genomic relationship matrix created using the first method of (VanRaden, 2008):

$$\mathbf{G} = \frac{\mathbf{W}\mathbf{W}'}{2 \sum p_j(1 - p_j)}, \quad (3)$$

where  $\mathbf{W} = \mathbf{M} - \mathbf{P}$ ,  $p_j$  is the allele frequency of marker  $j$ , calculated using observed allele frequencies,  $\mathbf{M}$  relates individuals to marker genotypes and  $\mathbf{P}$  is a matrix containing columns of  $2p_j$ . To avoid the singularity of  $\mathbf{G}$ ,  $\mathbf{G}$  was replaced with  $\mathbf{G}^*$ , where  $\mathbf{G}^* = 0.95\mathbf{G} + 0.05\mathbf{I}$ . For GEBV calculations for selection and culling purposes,  $\sigma_a^2$  and  $\sigma_e^2$  were assumed to be 3.0 and 7.0, respectively, as initialized in the simulation parameters.

All 50,020 animals in the population were genotyped and the genome consisted of 29 chromosomes, each of length 1 Morgan, 52,896 biallelic evenly spaced markers and 1247 biallelic randomly spaced QTL. The allelic effects were sampled from a gamma distribution with shape parameter 0.4, and the mutation rate was recurrent per generation and assumed to be  $2.5 \times 10^{-5}$  per locus for QTL and markers. The simulation was replicated 12 times, the two replicates that deviated the most from the average phenotype and average variance components were discarded and the remaining 10 replicates were analysed separately. Results are shown as an average of the 10 replicates with their respective standard deviations.

### 2.2 | Models and computations

To compare the heritability estimation by method R, variance components were estimated using the AI-REML algorithm implemented in blupf90+ (Miszta, Tsuruta, et al., 2014) with and without genomic information. Three to ten consecutive generations beginning with the first generation were analysed (i.e., 1–3, 1–4, ..., 1–10), as Hollifield et al. (2021) showed insufficient accuracies with intervals of less than three generations. For VCE by method R and AI-REML with genomic information (AIGREML), a GBLUP-based model was assumed and Henderson's mixed model equations were used to predict GEBV:

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \lambda\mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix}, \quad (4)$$

where  $\mathbf{y}$  and the covariance matrices are as mentioned above, the inverse of  $\mathbf{G}$  is as constructed in Equation 3,  $\hat{\beta}$  is a scalar of the mean,  $\hat{\mathbf{u}}$  is a random vector of additive genetic effects,  $\lambda$  is the variance ratio defined as  $\frac{\sigma_a^2}{\sigma_e^2}$  and  $\mathbf{X}$  and  $\mathbf{Z}$  are incidence matrices relating elements of  $\mathbf{y}$  to elements of  $\hat{\beta}$  and  $\hat{\mathbf{u}}$ , respectively (Henderson, 1949, 1950). Both  $\mathbf{G}$  and  $\mathbf{G}^{-1}$  were reconstructed for each data subset using observed

allele frequencies. For AI-REML without genomic information (AIREML), a similar model was used, but  $\mathbf{G}$  is replaced by  $\mathbf{A}$ , where  $\mathbf{A}$  is the numerator relationship matrix of the genotyped animals.

Whole and partial datasets were created for validation purposes (i.e., to obtain predictivity and statistics from method R) and their solutions are denoted as  $\hat{\mathbf{u}}_w$  and  $\hat{\mathbf{u}}_p$ , respectively. For every subset of data analysed, the partial dataset was created by removing the most recent generation of data and the validation animals were those that had their phenotypes removed in the partial dataset.

## 2.3 | Method R

Reverter et al. (1994b) propose a technique to estimate heritability by regressing the EBV of validation animals obtained using the whole dataset on EBV of validation animals obtained with a dataset where the phenotypes of the validation animals are removed. With the correct heritability, the expectation of the regression is 1. Previous studies have compared other heritability estimation methods; however, genomics was not included (Druet et al., 2001; Duangjinda et al., 2001; Misztal, 1997; Misztal et al., 1997). In this study, the regression of breeding values obtained with the whole on breeding values obtained with the partial data was calculated as (adapted from Reverter et al., 1994a):

$$b_{w,p} = \frac{\hat{\mathbf{u}}_w' \hat{\mathbf{u}}_p}{\hat{\mathbf{u}}_p' \hat{\mathbf{u}}_p}. \quad (5)$$

Note that equation (5) does not contain the relationship matrix as in Reverter et al. (1994a)  $\left( b_{w,p} = \frac{\hat{\mathbf{u}}_w' \mathbf{A}^{-1} \hat{\mathbf{u}}_p}{\hat{\mathbf{u}}_p' \mathbf{A}^{-1} \hat{\mathbf{u}}_p} \right)$ .

This is because relationship information is included in the calculation of  $\hat{\mathbf{u}}_w$  and  $\hat{\mathbf{u}}_p$  and is not needed for the regression. Leaving the relationship matrices out does not change the statistics. This was also observed by Legarra and Reverter (2018) who developed the LR validation method based on Method R. Additionally, unnecessarily including  $\mathbf{A}^{-1}$  or  $\mathbf{G}^{-1}$  matrix in the numerator and denominator products to obtain  $b_{w,p}$  increases computing time. Predictions  $\hat{\mathbf{u}}_w$  and  $\hat{\mathbf{u}}_p$  were calculated using blup90iod3 (Misztal, Tsuruta, et al., 2014).

For method R, the variance ratios compared had numerators of 1.5, 2.0, 2.5, 3.0, 3.5 and 4.0. The same heritability was used to calculate  $\hat{\mathbf{u}}_w$  and  $\hat{\mathbf{u}}_p$  and the same  $\mathbf{G}$  matrix as AIGREML was used. To keep the phenotypic variance constant for each variance ratio assessed, the variance ratio was calculated as  $\lambda = \frac{\sigma_e^2 + (\sigma_a^2 - x)}{x}$ , where  $\sigma_e^2$  and  $\sigma_a^2$  is the additive genetic and residual variances estimated by AIGREML by blupf90+ and  $x$  represents one of the values as mentioned above. Thus, the denominator of the variance ratio is one of

the six values mentioned above and the numerator is adjusted so that all variance ratio values maintain the same phenotypic variance as estimated by AIGREML. Using prior estimates from AIGREML to fix the phenotypic variance in the  $\lambda$  equation could create bias. Additional research should be conducted to compare method R with differing phenotypic variances. When two values of  $b_{w,p}$  were found closest to and marginally above and below 1.0, a line was fit between these two values and the estimated variance ratio was obtained when  $b_{w,p}$  equals 1.0. The variance ratios were on the x-axis and  $b_{w,p}$  values were on the y-axis. Then, the  $x$  value where  $y$  is equal to 1 was found and used as the variance ratio estimate for method R.

We compared six different heritabilities to analyse the behaviour of method R, where heritability was calculated as  $h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$ ; however, six heritabilities are not required. One only needs to find where  $b_{w,p}$  is marginally above and below 1. An algorithm could be implemented to iterate until a convergence criterion is met, potentially giving a more precise estimate. Method R without genomic information was not analysed in this study. The  $\sigma_e^2$  and  $\sigma_a^2$  values used as inputs in the formula for  $\lambda$  could be obtained from AIREML without genomics or from previous estimates. In this study, variances estimated by AIGREML were used because they were obtainable with the data size. Pedigree-based estimates could provide an initial baseline for traits where a reasonable heritability estimate is unknown. The heritability estimates by method R will not be affected by the initial values used; however, more iterations may be needed to find values where  $b_{w,p}$  is marginally above and below 1.

## 2.4 | Maximum predictivity (MaxPred)

Adjusted phenotypes ( $\mathbf{y}_c$ ) were used for predictivity and were calculated using the solution for the mean from the model [4] with the whole data as  $\mathbf{y}_c = \mathbf{y} - \mathbf{1}\hat{\mu}$ . Predictivity was calculated for all generation intervals using heritabilities equal to 0.15, 0.20, 0.25, 0.30, 0.35 and 0.40. For validation, the predictivity was calculated for the validation animals by  $r = \text{cor}(\mathbf{y}_c, \hat{\mathbf{u}}_p)$ . It was hypothesized that predictivity would be maximized with the best-fitting variance ratio and the heritability could be estimated by finding the values that maximized predictivity.

# 3 | RESULTS AND DISCUSSION

## 3.1 | Heritability estimation

Heritability estimates by AIREML, AIGREML and method R were compared using intervals with three to

ten generations of data. Figure 1 shows heritability estimates using the three methods for intervals with the base held constant at the first generation and increasing by one generation. The heritability estimates on average were  $0.30 \pm 0.01$ ,  $0.26 \pm 0.01$  and  $0.30 \pm 0.05$  for AIREML, AIGREML and method R, respectively. The AIREML and AIGREML estimates had smaller standard errors consistent with varying amounts of data. In contrast, the method R estimates had larger standard errors and were more variable with varying amounts of data, which aligns with the results in Duangjinda et al. (2001). Reverter et al. (1994a) compare subsequent evaluations to determine the heritability estimate; however, other studies create a partial dataset by removing a random percentage of animals from the whole dataset (Duangjinda et al., 2001; Misztal, 1997). The standard error could be decreased if the heritability estimation was repeated with various partial datasets, reducing the sampling variance (Misztal et al., 1997).

The lower heritability estimates from AIGREML compared to AIREML are consistent with recent studies comparing heritability with and without genomic information in populations undergoing genomic selection (Hidalgo et al., 2020; Richter et al., 2022). However, the variances in this study were not scaled against the same base, which could add bias to the estimations. In older studies where genomic preselection was not yet present, similar heritabilities but lower standard errors were estimated using genomic information in a pig population (Forni et al., 2011) and in a dairy cattle population (Veerkamp et al., 2011). As genomic selection was simulated in the study, the heritability estimates with AIREML may be biased as genomics were not considered and therefore, the information used for selection decisions was not included. However, the heritability parameter in the simulation was set to 0.3 and all data subsets begin with generation 1.

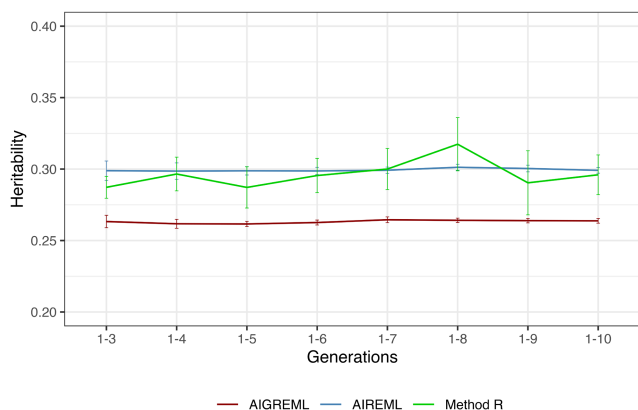


**FIGURE 1** Heritability estimates using AIGREML, AIREML, and method R with genomics for generation intervals with the base generation constant at generation 1.

As the properties of method R are based on finding unbiased breeding values, we analysed  $b_{w,p}$  of GEBV calculated with heritabilities estimated by AIGREML by regressing  $\hat{\mathbf{u}}_w$  on  $\hat{\mathbf{u}}_p$  for all generation intervals, as shown in Figure 2. The GEBV by AIGREML were slightly under-dispersed for all subsets of data. When more data was used, the distribution among replicates was smaller than for subsets with less data. This aligns with the results shown in Figure 1 and suggests that the heritability estimates by AIGREML were underestimated and thus the GEBV are under-dispersed. As stated in Misztal (1997), a  $b_{w,p}$  greater than one denotes an estimated additive variance that is too small and, thus, an estimated heritability that is lower than the correct value.

Elapsed wall-clock times in minutes for AIGREML and method R for various dataset sizes are shown in Figure 3. For each subset of data, the method R process included calculating and saving  $\mathbf{G}^{-1}$  once per subset of data and calculating  $\hat{\mathbf{u}}_w$  and  $\hat{\mathbf{u}}_p$  using iteration on data for the six variance ratios compared. The times presented in Figure 3 include the average computing time for all factors in the method R process per replicate. Method R was faster than AIGREML for all amounts of data and elapsed time increased as the amount of data increased. On average, for 10 generations of data (50,020 genotypes and phenotypes), method R took 1.6 h and AIGREML took 9.5 h. It is important to note that Method R, as implemented in this study, has a stopping criterion instead of a convergence criterion, which is based on grid search. However, an iterative algorithm could be implemented and possibly increase the resolution of the method R heritability estimates but a possible increase in computing time. Alternatively, convergence criteria could be implemented with an iterative algorithm instead of fitting a line to solve for the variance ratio estimates. This way, more precise estimates could be possible and research should be conducted for further testing.

Ultimately, the time savings by method R are due to its utilization of efficient methods to solve for breeding values as implemented in blup90iod3 (Misztal, Legarra, et al., 2014; Misztal, Tsuruta, et al., 2014) and the avoidance of costly variance component estimation methods. Method R can have a linear cost with the number of genotyped or phenotyped animals and it is feasible whenever a genetic evaluation is possible. Methods based on REML have quadratic memory requirements and have close to cubic costs with the number of genotyped animals. Methods based on Gibbs sampling have a quadratic cost but also a long computing time due to the high number of samples needed. Hence, method R can be applied to the datasets when the mixed model equations are not explicitly stored. In contrast, methods based on storing mixed model equations are inherently limited. Another option

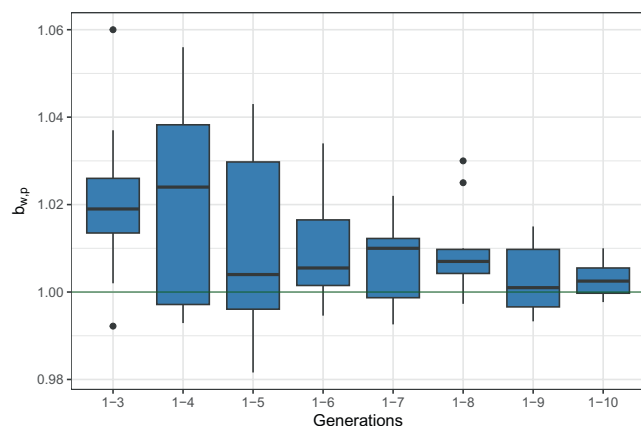


**FIGURE 2** The regression coefficient ( $b_{w,p}$ ) of GEBV from AIGREML with the whole dataset regressed on GEBV from AIGREML with the partial dataset for various subsets of data over 10 replicates.

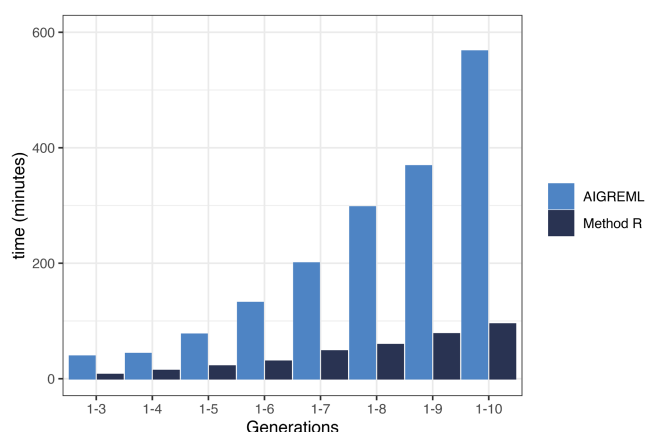


**FIGURE 3** Elapsed wall-clock time in minutes for heritability estimation using AIGREML and method R for various dataset sizes.

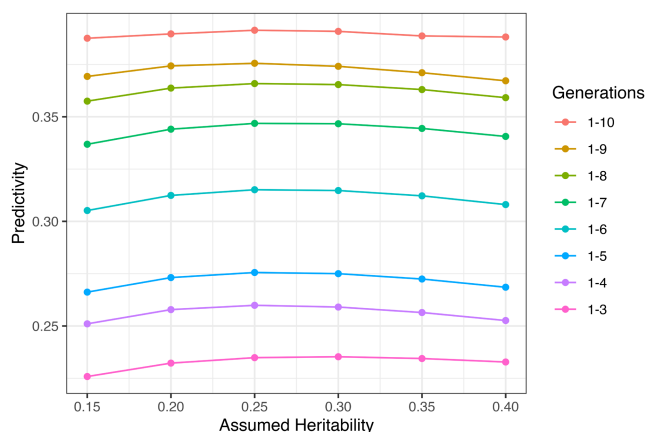


**FIGURE 4** Analysing the MaxPred method by calculating predictivity as  $\text{cor}(y_e, \hat{u}_p)$ , with  $\hat{u}_p$  from AIGREML with partial data for subsets of data with 3 to 10 generations of data and heritabilities equal to 0.15, 0.20, 0.25, 0.30, 0.35 and 0.40.

is to use SNPBLUP as an alternative to GBLUP, whereas efficient SNPBLUP-based software exists (Lee & van der Werf, 2016; Lidauer et al., 2011).

### 3.2 | MaxPred

Predictivities are shown in Figure 4. The values ranged from 0.23 to 0.39 and increased as the number of generations of data increased in the interval. The values for all subsets of data increased, peaked and decreased. However, the curves are relatively flat and there were minimal differences between the predictivity for all heritabilities compared. The curves were flatter when all data was used and a more substantial peak was present when fewer generations of data were used. In agreement with previous studies, predictivity is dependent on the amount of data used and the correctness of the model (Legarra et al., 2008). Specifically, in a sire model with all sires having the same number of daughters, the predictivity does not largely depend on heritability. A small numerical example using a sire model is presented in Appendix A to show the lack of major change in predictivity as the variance ratio substantially changes.

### 3.3 | Validation

TBV and GEBV calculated with heritability estimates from AIGREML and method R were compared. Correlations, regression coefficients ( $b_1$ ) and intercepts ( $b_0$ ) were calculated on linear regressions of combinations of TBV, GEBV by AIGREML and GEBV by method R. The correlation,  $b_1$  and  $b_0$  of the regressions using intervals of generations 1–10 and 1–3 are shown in Table 1. The whole dataset and a subset with the first three generations of data were used to compare the performance of method R with large and small datasets. Correlations were 1.0 between GEBV by AIGREML and GEBV by method R using all generations and for the first three generations. As the simulated population was under genomic selection, it is expected that the GEBV using variance components estimated with genomic information will be more similar compared to EBV calculated from non-genomic models. Correlations and  $b_1$  for TBV regressed on GEBV by AIGREML and TBV regressed on GEBV by method R were closer to 1.0 when all generations were used and deviated further from 1.0 when only the first three generations were used. This is as expected, as accuracies tend to be higher with more data. The intercept, however, was closer to the expected value of 0.0 when the first three generations were used compared to all generations. Because selection was simulated in this population, the phenotypes are changing

**TABLE 1** Correlation, regression coefficient ( $b_1$ ), and intercept ( $b_0$ ) of TBV regressed on GEBV by AIGREML, GEBV by method R, and GEBV by AIGREML on GEBV by method R.

| y, x              | Correlation |             | $b_1$       |             | $b_0$       |             |
|-------------------|-------------|-------------|-------------|-------------|-------------|-------------|
|                   | 1–10        | 1–3         | 1–10        | 1–3         | 1–10        | 1–3         |
| TBV, AIGREML      | 0.95 ± 0.00 | 0.73 ± 0.01 | 1.01 ± 0.00 | 1.04 ± 0.02 | 3.93 ± 0.19 | 0.41 ± 0.09 |
| TBV, Method R     | 0.95 ± 0.00 | 0.73 ± 0.01 | 1.01 ± 0.01 | 1.01 ± 0.03 | 3.93 ± 0.19 | 0.41 ± 0.09 |
| AIGREML, Method R | 1.00 ± 0.00 | 1.00 ± 0.00 | 1.00 ± 0.00 | 0.97 ± 0.02 | 0.00 ± 0.00 | 0.00 ± 0.00 |

Note: Results using data from generations 1–10 and generations 1–3 are shown.

directionally with each generation; therefore, bias is expected to increase with more generations of data. All validation comparisons between GEBV by AIGREML and TBV and GEBV by method R and TBV are identical or overlap when accounting for the standard error. This suggests that the GEBV calculated with heritabilities from either AIGREML or method R have negligible differences and it is promising that method R can be used as a fast alternative to REML or Bayesian methods for heritability estimation in single-trait GBLUP models.

## 4 | CONCLUSION

The main advantage of heritability estimation with genomics using method R is its ability to process any size model for which the genetic evaluation is possible. Although its heritability estimates do not have the theoretical properties of REML, method R is a quick way to compute the estimates. Additional VCE should be conducted prior to implementing the variance ratio obtained by method R into official evaluations. Further research on method R with genomics is needed for multiple trait models, complex models and real data.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no real or perceived conflicts of interest.

## DATA AVAILABILITY STATEMENT

Research data are not shared.

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## APPENDIX A

Numerical example of predictivity as heritability changes using a sire model:

$$y = \mu + s + e$$

$$\lambda = \frac{\sigma_e^2}{\sigma_s^2} = \frac{(4 - h^2)}{h^2}$$

Assuming that:

$$\lambda_1 = 7; \lambda_2 = 0.5; \lambda_3 = 50.$$

$$\mathbf{y} = [120 \ 176 \ 154 \ 138 \ 162]'$$

$$\mathbf{A} = \begin{bmatrix} 1 & 0 & 0 & 0.5 \\ 0 & 1 & 0.5 & 0 \\ 0 & 0.5 & 1 & 0 \\ 0.5 & 0 & 0 & 1 \end{bmatrix}$$

For  $\lambda_1 = 7$ ,

$$\lambda_1 \mathbf{A}^{-1} = \begin{bmatrix} 9.33 & 0 & 0 & -4.67 \\ 0 & 9.33 & -4.67 & 0 \\ 0 & -4.67 & 9.33 & 0 \\ -4.67 & 0 & 0 & 9.33 \end{bmatrix}$$

$$\begin{bmatrix} 5 & 2 & 1 & 1 & 1 \\ 2 & 11.33 & 0 & 0 & -4.67 \\ 1 & 0 & 10.33 & -4.67 & 0 \\ 1 & 0 & -4.67 & 10.33 & 0 \\ 1 & -4.67 & 0 & 0 & 10.33 \end{bmatrix} \begin{bmatrix} \hat{\mu} \\ \hat{s}_1 \\ \hat{s}_2 \\ \hat{s}_3 \\ \hat{s}_4 \end{bmatrix} = \begin{bmatrix} 750 \\ 282 \\ 176 \\ 154 \\ 138 \end{bmatrix}$$

$$\begin{bmatrix} \hat{\mu} \\ \hat{s}_1 \\ \hat{s}_2 \\ \hat{s}_3 \\ \hat{s}_4 \end{bmatrix} = \begin{bmatrix} 150.54 \\ -2.68 \\ 3.29 \\ 1.82 \\ -2.42 \end{bmatrix}$$

$$\mathbf{y}^* = (\mathbf{y} - \mathbf{XB})' \mathbf{Z}$$

$$\mathbf{y}^* = \begin{bmatrix} -19.07 & 25.46 & 3.46 & -12.53 \end{bmatrix}'$$

$$\text{cor}(\mathbf{y}^*, \hat{\mathbf{s}}) = 0.9 \quad (6)$$

| $\lambda$ | $\text{cor}(\mathbf{y}^*, \hat{\mathbf{s}})$ |
|-----------|----------------------------------------------|
| 0.5       | 0.96                                         |
| 7         | 0.96                                         |
| 50        | 0.95                                         |