# Reliability of Breeding Values in Selected Populations

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## Abstract

Selection reduces genetic variance in population. However, this is not taken into account when reliabilities are computed from prediction error variance (PEV) and base population additive genetic variance. Results of simulations confirmed that when selection is present PEV based reliabilities are too high and do not reflect the true uncertainty of EBV. The drop in reliability is substantial for the parent average based EBV, while the EBV for progeny tested or genomically evaluated animals is reduced only slightly. This implies that relative reliability of genomic EBV in comparison to parent average EBV is much higher than anticipated from the comparison of PEV based reliabilities.

**Key words:** accuracy, reliability, pedigree, genomic, selection

## Introduction

Modern breeding programs base genetic improvement on estimated breeding values (EBV). In the case of linear mixed models of type:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{e}, \qquad (1)$$

breeding values ($\boldsymbol{a}$) are inferred from the collected data ($\boldsymbol{y}$) by solving the mixed model equations to obtain estimates of $\boldsymbol{a}$ (EBV). In addition variances of prediction errors of EBV (PEV) are also routinely reported in order to provide a measure of the potential change of EBV in the future. In most breeding programs reliabilities are reported instead of the PEV, as computed by:

$$\mathrm{R}^2 = 1 - \frac{\mathrm{PEV}}{\mathrm{Var(a)}}, \qquad (2)$$

where $Var(a)$ is the additive genetic variance in the base population. Reliability of EBV is an important statistic as it describes the potential change of an EBV when more information becomes available and because it is one of the determining factors of a response to selection.

With the introduction of genomics, comparison of reliabilities has become a common way to compare different breeding programs, e.g., the reliability of EBV for progeny tested sires versus genomically tested young bulls. These comparisons often involve different types of reliabilities; some are based on the PEV from MME and others on some type of validation.

Bijma (2012) showed theoretically that PEV based reliabilities are too high when selection is present in the population, especially for the EBVs that rely to a great extent on the parent average information. The work presented in this paper complements previous theoretical derivations of Bijma (2012) by quantifying the effect of selection on PEV based reliability in genomic setting via simulation.

## Theoretical basis of the effect of selection on reliability

The effect of selection on reliability of parent average EBV (PA) ($a_o$) can be clearly demonstrated with an example of truncation

selection in parents ($a_s$ and $a_d$). Without selection the variance and reliability of PA is:

$$Var(\hat{a}_o) = \tfrac{1}{2}\left(\overline{Var(\hat{a}_s)+Var(\hat{a}_d)}\right),$$
$$R^2(\hat{a}_o) = \tfrac{1}{2}\left(\overline{R^2(\hat{a}_s)+R^2(\hat{a}_d)}\right), \quad (3)$$

The introduction of selection in the parents reduces the variability of EBV (only a part of parents are selected) which propagates to the reliability of the PA:

$$Var(\hat{a}_o) = \tfrac{1}{2}\left(\overline{Var(\hat{a}_s)+Var(\hat{a}_d)}\right)(1-k),$$
$$R^2(\hat{a}_o) = \tfrac{1}{2}\left(\overline{R^2(\hat{a}_s)+R^2(\hat{a}_d)}\right)(1-k), \quad (4)$$

The $k$ represents the reduction in $Var(\hat{a})$ due to selection (assuming equal intensity in both sexes). With 20% parents selected $k = i(i-x) \approx 0.78$, indicating a 78% reduction in variance and reliability.

The above equalities (3 and 4) hold only for one generation of truncation selection in parents. With a continuous selection, equilibrium is attained and the reliability of the PA when intensity and accuracy of selection is equal in both sexes is (Bijma, 2012):

$$R^2_\infty(\hat{a}_o) = \frac{R^2(\hat{a})}{2}\left(\frac{1-k}{1+k\left(1-R^2(\hat{a})\right)}\right), \quad (5)$$

while the reliability of the EBV obtained upon a progeny test is (Bijma, 2012):

$$R^2_\infty(\hat{a}) = R^2(\hat{a})\left(\frac{1}{1+k\left(1-R^2(\hat{a})\right)}\right). \quad (6)$$

The comparison of (5) and (6) over a range of selection intensities clearly shows that selection influences reliability, but to a much greater extent for PA than for progeny test based EBV (Figure 1). When selection intensity is different in males and females the equations (5) and (6) can be modified (Bijma, 2012).

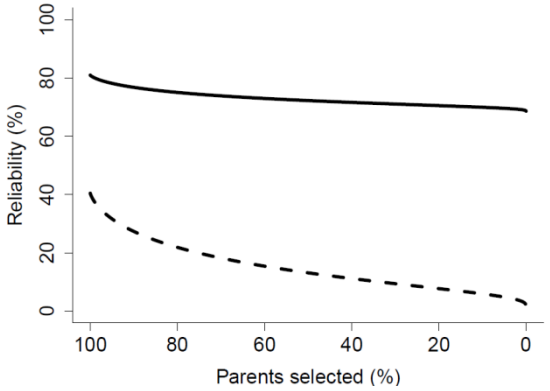


**Figure 1.** Effect of selection intensity on reliability of PA (dashed) and progeny test (solid) based EBV.

## Simulation

The simulation followed the workflow of Hickey and Gorjanc (2012) which involves a) coalescent simulation with mutation, recombination, and drop in historical effective population size (Ne) to obtain structured haplotypes for 30 chromosomes and b) haplotype dropping through pedigree. During the later phase mutations were assumed non-existent and Ne was constant. The pedigree consisted of 25 generations with each of the 50 sires mated with 10 dams having each 4 progeny per generation. Altogether, there were 2000=50×10×4 animals per generation. Phenotypes were assigned only to males. Heritability was high $(\boldsymbol{h^2 = 0.75})$ in order to keep the simulated data small but still mimic progeny testing. The simulation involved random selection of parents (no selection scenario) or the selection of parents on pedigree BLUP (ABLUP; selection scenario with 5% selected males and 50% selected females). In the first ten generations there was no selection in order to reach information equilibrium. At the end of simulation the available data consisted of pedigree, 60,000 SNP markers, true breeding values, and phenotypic values (5000 records from generations 16 to 20). Individuals in generations 21 through 25 had no phenotypes.

## Statistical Analysis

The obtained phenotype, pedigree, and genomic data were analysed with pedigree (ABLUP) and genomic (GBLUP) based linear mixed model (1). Analyses were performed for each generation successively to obtain PA ($\hat{a}_{A0}$) for each animal free of phenotypic information from descendants or collateral relatives. Squared correlations (validation reliabilities) between the obtained EBV from ABLUP ($\hat{a}_{A0}$ and $\hat{a}_A$) or GBLUP ($\hat{a}_G$) and the true values were compared with PEV based reliabilities (2).

## Results & Discussion

Irrespective of selection, reliabilities of $\hat{a}_{A0}$, $\hat{a}_A$, and $\hat{a}_G$ showed the expected pattern – higher reliabilities of $\hat{a}_A$ in males (due to progeny testing) than females; a drop in the reliabilities of PA with generations > 20 (due to segregation and recombination); higher reliabilities of $\hat{a}_G$ in comparison to $\hat{a}_A$; and higher and more stable reliabilities of $\hat{a}_G$ in generations >20 (Table 1).

In the scenario with no selection the reliabilities obtained from the PEV roughly matched validation-based reliabilities for both ABLUP and GBLUP (Table 1). This shows that in the case with no selection the PEV based reliabilities provide accurate information about the uncertainty of EBV. However, in the scenario with selection the validation reliabilities were consistently lower than PEV based reliabilities (Table 2). The difference was greater for $\hat{a}_{A0}$ and for $\hat{a}_A$ in females than for $\hat{a}_A$ in males, which is in agreement with developments of Bijma (2012) as shown in Figure 1. Validation reliability of the PA was only 14% of the PEV-based reliability of the PA (3% *vs.* 22%). The validation reliability of genomic EBV ($\hat{a}_G$) was also lower than the PEV based reliability; however the difference was much smaller than for the pedigree EBV (Table 2). The obtained validation reliabilities in the scenario with selection (Table 2) matched the expected equilibrium reliabilities with different selection intensity by sex (Bijma, 2012) - 50 sires and 500 dams selected from 2000 offspring (both sexes) each generation (Figure 2).

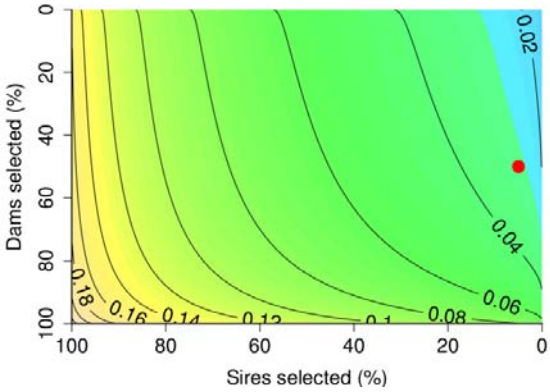


**Figure 2.** Expected (contours) and validation (point) reliability of PA according to selection intensity in sires and dams.

## Conclusions

In summary results of simulation corroborate the developments of Bijma (2012) who showed that selection reduces reliability of EBV and that PEV based reliabilities do not reflect this reduction. In addition results show that relative reliability of genomic EBV in comparison to PA is much higher than anticipated from the comparison of PEV based reliabilities.

## References

Bijma, P. 2012. Accuracies of estimated breeding values from ordinary genetic evaluations do not reflect the correlation between true and estimated breeding values in selected populations. *J. Anim. Breed. Genet. 129*, 345-358.

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**Table 1.** Prediction error variance and validation based reliabilities (%) by generation and source of information in the no selection scenario.

| | $R^2 = 1 - PEV/\mathrm{Var(a)}$ | | | $R^2 = \mathrm{Corr}(EBV, TBV)^2$ | | |
|---|---|---|---|---|---|---|
| Gen. | $\hat{a}_{A0}$ | $\hat{a}_A$ | $\hat{a}_G$ | $\hat{a}_{A0}$ | $\hat{a}_A$ | $\hat{a}_G$ |
| 20[a] | 24 ± 4 | 50 ± 2 | / | 29 ± 4 | 56 ± 3 | / |
| 20[s] | 24 ± 4 | 71 ± 3 | 83 ± 1 | 30 ± 5 | 78 ± 2 | 84 ± 1 |
| 20[d] | 24 ± 4 | 30 ± 1 | / | 28 ± 4 | 35 ± 4 | / |
| 21[a] | 24 ± 1 | | 64 ± 1 | 27 ± 4 | | 63 ± 3 |
| 22[a] | 10 ± 1 | | 57 ± 1 | 14 ± 4 | | 55 ± 5 |
| 23[a] | 4 ± 1 | | 54 ± 1 | 8 ± 4 | | 52 ± 4 |
| 24[a] | 0 ± 1 | | 52 ± 1 | 4 ± 3 | | 51 ± 6 |
| 25[a] | -2 ± 1 | | 50 ± 1 | 2 ± 2 | | 47 ± 4 |

a – all animals; s – sires; d – dams; no phenotypic information in generations > 20

**Table 2.** Prediction error variance and validation based reliabilities (%) by generation and source of information in the selection scenario.

| | $R^2 = 1 - PEV/\mathrm{Var(a)}$ | | | $R^2 = \mathrm{Corr}(EBV, TBV)^2$ | | |
|---|---|---|---|---|---|---|
| Gen. | $\hat{a}_{A0}$ | $\hat{a}_A$ | $\hat{a}_G$ | $\hat{a}_{A0}$ | $\hat{a}_A$ | $\hat{a}_G$ |
| 20[a] | 22 ± 3 | 47 ± 1 | / | 3 ± 1 | 39 ± 2 | / |
| 20[s] | 22 ± 3 | 66 ± 2 | 83 ± 1 | 3 ± 1 | 68 ± 1 | 78 ± 1 |
| 20[d] | 22 ± 3 | 28 ± 1 | / | 3 ± 2 | 11 ± 2 | / |
| 21[a] | 22 ± 1 | | 66 ± 1 | 3 ± 2 | | 53 ± 5 |
| 22[a] | 10 ± 1 | | 61 ± 1 | 0 ± 1 | | 48 ± 5 |
| 23[a] | 3 ± 1 | | 58 ± 1 | 0 ± 1 | | 45 ± 5 |
| 24[a] | 0 ± 1 | | 55 ± 1 | 0 ± 1 | | 41 ± 4 |
| 25[a] | -2 ± 1 | | 54 ± 1 | 0 ± 1 | | 41 ± 4 |

a – all animals; s – sires; d – dams; no phenotypic information in generations > 20