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Sparse single-step genomic BLUP in crossbreeding schemes[1]

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We declare that we do not have any competing interest in the matter and results covered by this manuscript.

ABSTRACT

20 The algorithm for Proven and Young animals (**APY**) efficiently computes an approximated

21 inverse of the genomic relationship matrix, by dividing genotyped animals in so-called core

22 and non-core animals. The APY leads to computationally feasible single-step genomic Best

23 Linear Unbiased Prediction (**ssGBLUP**) with a large number of genotyped animals, and was

24 successfully applied to real single breed or line datasets. This study aimed to assess the

25 quality of genomic breeding values (**GEBV**) when using the APY (**GEBV$_{APY}$**), in comparison

26 to GEBV when using the directly inverted genomic relationship matrix (**GEBV$_{DIRECT}$**), for

27 situations based on crossbreeding schemes, including F1 and F2 crosses, such as the ones for

28 pigs and chickens. Based on simulations of a three-way crossbreeding program, we compared

29 different approximated inverses of a genomic relationship matrix, by varying the size and the

30 composition of the core group. We showed that GEBV$_{APY}$ were accurate approximations of

31 GEBV$_{DIRECT}$ for multivariate ssGBLUP involving different breeds and their crosses.

32 GEBV$_{APY}$ as accurate as GEBV$_{DIRECT}$ were obtained when the core groups included animals

33 from different breed compositions, and when the core groups had a size between the numbers

34 of the largest eigenvalues explaining 98% and 99% of the variation in the raw genomic

35 relationship matrix.

36

37 **Key words:** single-step, genomic evaluation, APY

38

INTRODUCTION

Single-step genomic Best Linear Unbiased Prediction (**ssGBLUP**) is currently the method of choice to predict genomic breeding values in many species (Legarra et al., 2014). The main reason is that ssGBLUP enables simultaneous use of phenotypes from genotyped and non-genotyped animals by combining genomic and pedigree relationship matrices. An inconvenience of ssGBLUP is that the inverse of a dense genomic relationship matrix ($\mathbf{G}$) is required, leading to a soft limit of approximately 100,000 genotyped animals for the currently available computers (Misztal et al., 2014).

Recently, Misztal et al. (2014, 2016) proposed the so-called Algorithm for Proven and Young animals (**APY**) to compute an approximated inverse of $\mathbf{G}$ ($\mathbf{G}_{APY}^{-1}$) for a large number of genotyped animals. The computation of $\mathbf{G}_{APY}^{-1}$ involves the inversion of a genomic relationship submatrix among a limited number of genotyped animals, called core animals, and the recursive computation of other coefficients for non-core animals. The APY was successfully applied on (large) real datasets with animals originating from a single breed or line (Fragomeni et al., 2015; Lourenco et al., 2015; Masuda et al., 2016; Ostersen et al., 2016; Pocrnic et al., 2016b; Strandén et al., 2017). However, several livestock production systems, such as the ones for pigs and chickens, are based on well-structured crossbreeding schemes, generating production animals with a specific breed composition. In these cases, the ssGBLUP may include non-genotyped and genotyped animals from different breeds, as well as their crossbred progeny. Using the APY with such datasets is desirable for implementing ssGBLUP in crossbreeding schemes efficiently.

The aim of this study was to assess the quality of genomic estimated breeding values (**GEBV**) when using $\mathbf{G}_{APY}^{-1}$, in comparison to GEBV when using the direct inversion of $\mathbf{G}$ ($\mathbf{G}_{direct}^{-1}$), for situations based on well-structured crossbreeding schemes that include genotyped animals

63   from a few different breeds and their F1 and F2 crosses. Influence of the selection strategy of

64   the core animals and of the number of core animals, were also investigated. All analyses were

65   based on simulated data.

66

67   **MATERIALS AND METHODS**

68   *Single-step genomic Best Linear Unbiased Prediction*

69   The ssGBLUP method replaces the inverse of the pedigree relationship matrix for all animals

70   ($\mathbf{A}^{-1}$) with the inverse of the combined pedigree-genomic relationship matrix ($\mathbf{H}^{-1}$), defined

71   as (Aguilar et al., 2010; Christensen and Lund, 2010):

72     $$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix} \qquad (1)$$

73   where $\mathbf{A}_{22}$ is the pedigree relationship matrix for the genotyped animals, $\mathbf{G} = (1 - w)\mathbf{G}_a +$

74     $w\mathbf{A}_{22}$ with $\mathbf{G}_a$ being a genomic relationship matrix adjusted to be on the same scale as $\mathbf{A}_{22}$,

75   and w being the weight on the pedigree relationship matrix. Several approaches for

76   computing $\mathbf{G}_a$ by adjusting a raw genomic relationship matrix $\mathbf{G}^*$ towards $\mathbf{A}_{22}$ were proposed

77   in the literature (Powell et al., 2010; Vitezica et al., 2011; Christensen, 2012; Lourenco et al.,

78   2016).

79   Highest computational costs for creating $\mathbf{H}^{-1}$ are the creation and the inversion of the dense

80   matrices $\mathbf{G}$ and $\mathbf{A}_{22}$. Additional computational costs also appear during solving of the mixed

81   model equations due to an increase of non-zero elements in $\mathbf{H}^{-1}$, increasing the number of

82   operations per iteration, e.g., of the preconditioned conjugate gradient used to solve the mixed

83   model equations (Ostersen et al., 2016).

84   *Sparse inversion of G*

85   The matrix $\mathbf{G}$ can be divided into four submatrices as:

86      $$\mathbf{G} = \begin{bmatrix} \mathbf{G}_{cc} & \mathbf{G}_{cn} \\ \mathbf{G}'_{cn} & \mathbf{G}_{nn} \end{bmatrix}$$

87   where the subscript c refers to a group of genotyped animals called hereafter "core animals",

88   and the subscript n refers to a second group of genotyped animals called hereafter "noncore

89   animals".

90   Following Misztal (Misztal et al., 2014; Misztal, 2016), the inverse of $\mathbf{G}$, $\mathbf{G}^{-1}$, can be

91   approximated using the APY as follows:

92      $$\mathbf{G}_{APY}^{-1} = \begin{bmatrix} \mathbf{G}_{cc}^{-1} + \mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}\mathbf{M}^{-1}\mathbf{G}'_{cn}\mathbf{G}_{cc}^{-1} & -\mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}\mathbf{M}^{-1} \\ -\mathbf{M}^{-1}\mathbf{G}'_{cn}\mathbf{G}_{cc}^{-1} & \mathbf{M}^{-1} \end{bmatrix}$$

93   where the matrix $\mathbf{M}$ is a diagonal matrix of size of the number of noncore animals and with a

94   diagonal element for the ith noncore animal equal to $\mathbf{M}_{ii} = diag\left(\mathbf{G}_{nn_{ii}} - \mathbf{G}'_{ci}\mathbf{G}_{cc}^{-1}\mathbf{G}_{ci}\right)$ with

95      $\mathbf{G}_{ci}$ being the ith column of $\mathbf{G}_{cn}$. It is worth noting that the matrix $\mathbf{M}$ is an approximation of the

96   Schur complement of $\mathbf{G}_{cc}$, i.e., $\mathbf{S} = \mathbf{G}_{nn} - \mathbf{G}'_{cn}\mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}$. Replacing $\mathbf{M}$ by $\mathbf{S}$ in the formula of

97      $\mathbf{G}_{APY}^{-1}$ would lead to the computation of the inverse of $\mathbf{G}$, $\mathbf{G}^{-1}$.

98   The APY only requires the computation of the submatrices $\mathbf{G}_{cc}$, $\mathbf{G}_{cn}$ and of the diagonal

99   elements of $\mathbf{G}_{nn}$, in addition to the inversion of the submatrix $\mathbf{G}_{cc}$. Thus, the computational

100   costs of the APY are reduced in comparison to the setting up and the direct inversion of $\mathbf{G}$.

101   Also, the memory costs of the APY are reduced because only submatrices, $\mathbf{G}_{cc}$ and $\mathbf{G}_{cn}$,

102   must be stored and the matrix $\mathbf{G}_{APY}^{-1}$ is sparse thanks to the diagonal matrix $\mathbf{M}^{-1}$.

Simulated data

Populations. The assessment of the quality of the genomic predictions from a sparse

ssGBLUP in crossbreeding schemes was achieved by simulating a three-way crossbreeding

program with random selection (Figure 1). Simulations of historic, purebred and crossbred

recent populations were performed using the QMSim software (Sargolzaei and Schenkel,

2009). For the historic population, 70 discrete random mating generations (i.e., generations 1

to 70) with a constant size of 18,840 individuals with equal number of individuals from each

sex were simulated, followed by 10 generations (i.e., generations 71 to 80) in which the

effective population size was gradually reduced to 390 individuals. The next 20 generations

(i.e. generations 81 to 100) were simulated to gradually expand the population size to 18,840.

The last generation (i.e. generation 100) included 90 males and 18,750 females. Matings for

all generations were based on the random union of gametes, which were randomly sampled

from the pools of male and female gametes. To simulate the three breed populations (hereafter

referred to as breeds A, B, and C), three random samples were drawn from the generation 100

of the historic population, each including 30 males and 6,250 females. Subsequently, within

each breed, 100 generations (i.e. generations 101 to 200) of random mating were simulated

before starting the three-way crossbreeding program (Figure 1). In each of the simulated 100

generations of random mating, each female had one male and one female offspring.

In the second step, a three-way crossbreeding program was simulated (Figure 1). Purebred

(i.e., A, B, and C) animals that were used as founders of the pedigree (i.e., the first generation

of the pedigree) were from generations 200. For each breed, A, B, and C, the next 9 discrete

generations (i.e. generations 201 to 209) of purebred animals were simulated by means of

random selection and matings while maintaining a constant size of 30 males and 6,250

females. For mimicking a three-way crossbreeding program, from the generation 205 until the

generation 208, B and C purebred animals were randomly crossed to produce four generations

(i.e. generations 206 to 209) of F1 animals, that is 30 BC crossbred males and 6,250 BC

crossbred females. These BC crossbred animals were then randomly mated to males from

breed A to produce four generations (i.e. generations 206 to 209) of F2 animals, called A(BC)

crossbred animals. For each generation, 6,280 A(BC) crossbred animals were simulated

(Figure 1). Purebred animals that were used as parents of crossbred animals could also be

parents of purebred animals in the next generation. A total of 5 replicates were simulated

using the QMSim software.

Genotypes. The genome was simulated using the QMSim software, simultaneously with the

simulation of the historic, purebred and crossbred recent populations. The genome consisted

of 18 chromosomes designed to resemble the Sus Scrofa genome with a SNP density that was

comparable to that of a 60k SNP chip. The SNP positions were randomized across the

genome and a recurrent mutation rate of 2.5×10^{-5}, as well as 1 mean crossover per 1 Morgan,

were assumed. All SNPs that segregated in the last historical generation (i.e., generation 100)

and with a minor allele frequency (MAF) higher than or equal to 0.05 were selected and used

to simulate the genotypes of the purebred and crossbred animals. In addition to the SNPs,

4,500 QTL were simulated, and their positions were also randomized across the genome.

Mutation rate and MAF of the QTL were the same as the ones for the simulated SNPs.

Phenotypes. For all purebred and crossbred animals, phenotypes for the breed composition to

which they belonged were simulated under additive gene action using a custom Fortran

program. This resulted in five traits: one trait for each of the purebred performances A, B and

C, and one trait for each of the crossbred performances BC and A(BC). Genetic correlations

between traits were randomly sampled in the range [0.2-0.8] from a uniform distribution.

Simulated genetic correlations between purebred and crossbred traits were in the lowest range

151   of reported values in the literature as reviewed by Wientjes and Calus (2017) (Table 1).

152   Heritabilities (h_i^2) were randomly sampled in the range of [0.2-0.4] from a uniform

153   distribution. Residual covariances were set to zero, as they would be in practice, because each

154   animal has a phenotype for one of the five traits only. The same genetic correlations and

155   heritabilities were used in all replicates, and are reported in Table 1.

156   For each animal and for each of the five traits, a true breeding value (TBV) was simulated by

157   summing a polygenic effect and the multiplication of the simulated allele substitution effects

158   with the genotypes of the 4,500 QTL coded as 0, 1 and 2. This genotype multiplication

159   allowed different genetic levels across breeds for the same trait because QTL allele

160   frequencies differ across breeds. For each trait, the polygenic effect of each individual was

161   equal to the sum of the average of polygenic effects of the parent and a Mendelian sampling

162   term. The Mendelian sampling terms for the five traits were sampled from a multinormal

163   distribution with means of 0 and variances equal to the Mendelian sampling variances

164   (Mrode, 2005). Correlations between the simulated Mendelian sampling terms were assumed

165   to be equal to the genetic correlations. The variance of the polygenic effect of each ith trait

166   was assumed to be equal to 5% of the total additive genetic variance (σ_{Ai}^2).

167   The allele substitution effects of QTLs were sampled from a multinormal distribution with

168   means of 0, and variances of 1. The correlations between allele substitution effects of the QTL

169   underlying the 5 traits were equal to the genetic correlations. For each trait, the genetic

170   variance explained by all QTLs was computed as the sum of the variances across all QTLs,

171   assuming no correlation between the QTLs. The simulated additive genetic variance of each

172   jth QTL was calculated as $\sigma_{gj}^2 = 2p_j(1 - p_j)a_j^2$, where p_j is the allele frequency and a_j is the

173   allele substitution effect of jth QTL. For each trait, the allele substitution effects were rescaled

174   to obtain an additive genetic variance explained by the QTLs (σ_g^2) equal to 1. The part of the

175   total additive genetic variance explained by the QTLs was assumed to be equal to 95% for

176   each ith trait. Finally, the phenotypes for each trait for each animal were generated by

177   summing the TBV and a residual error sampled from a normal distribution with a mean 0 and

178   a variance equal to $\left(\frac{1}{h_i^2} - 1\right) * \sigma_{Ai}^2$.

179   ***Datasets.*** For all the analyses, the pedigree included all the animals simulated for the creation

180   of the three-way crossbreeding program. The phenotype dataset included 126,000 records.

181   Among all records, 100,000 records were associated with purebred (i.e. A, B, and C) animals

182   randomly sampled among all purebred animals from generations 204 until 208. A total of

183   16,000 records were associated with A(BC) crossbred animals randomly sampled among all

184   A(BC) crossbred animals from generations 206 until 209. Finally, 10,000 records were

185   associated with BC crossbred dams. Average numbers of purebred and crossbred animals per

186   generation with a phenotype are given in the E-Supplements Table S1.

187   The genotype dataset included 89,000 genotypes. This included all 26,000 phenotyped BC

188   and A(BC) crossbred animals. A total of 48,000 genotypes were from purebred (i.e. A, B, and

189   C) animals randomly sampled among all purebred animals from the generations 205 until 208,

190   regardless whether they had a phenotype or not. A total of 15,000 genotypes were from

191   purebred (i.e. A, B, and C) animals randomly sampled among all purebred animals from

192   generation 209. These 15,000 animals did not have phenotypes and are hereafter considered

193   as selection candidates. Average numbers of purebred and crossbred animals per generation

194   with a phenotype and a genotype are given in the E-Supplements Table S2.

195

196   ***Model and scenarios evaluated***

197   Five-trait ssGBLUP was performed. The model for the ith trait ($i = A, B, C, BC, A(BC)$) was

198   as follows:

199    $\mathbf{y}_i = \mathbf{1}\mu_i + \mathbf{W}_i\mathbf{a}_i + \mathbf{e}_i$

200   where, for the ith trait, $\mathbf{y}_i$ is the vector of records, μ_i is the general mean, $\mathbf{a}_i$ is the vector of

201   additive genetic effects, $\mathbf{e}_i$ is the vector of residuals, the vector $\mathbf{1}$ is a vector of 1's relating the

202   records to the general mean, and $\mathbf{W}_i$ is an incidence matrix relating the records to the animals.

203   The variance components used for the simulations were used for the five-trait ssGBLUP. The

204   vector of additive genetic effects $\mathbf{a} = \begin{bmatrix} \mathbf{a}'_A & \mathbf{a}'_B & \mathbf{a}'_C & \mathbf{a}'_{BC} & \mathbf{a}'_{A(BC)} \end{bmatrix}'$ followed a multivariate

205   normal (MVN) distribution $MVN(\mathbf{0}, \mathbf{H^{-1}} \otimes \mathbf{\Gamma})$ where $\otimes$ is the Kronecker product, $\mathbf{\Gamma}$ is the

206   additive genetic (co)variance matrix, and the vector of residuals $\mathbf{e} =$

207    $\begin{bmatrix} \mathbf{e}'_A & \mathbf{e}'_B & \mathbf{e}'_C & \mathbf{e}'_{BC} & \mathbf{e}'_{A(BC)} \end{bmatrix}'$ followed a MVN distribution $MVN(\mathbf{0}, \mathbf{I} \otimes \mathbf{R})$ where $\mathbf{R}$ is the

208   residual (co)variance matrix.

209   Using all the 89,000 genotypes, the matrix $\mathbf{G}$ required for the computation of $\mathbf{H^{-1}}$ was

210   computed without breed-specific adjustments, as suggested by Lourenco et al. (2016). This

211   matrix was equal to $\mathbf{G} = 0.95\mathbf{G}_a + 0.05\mathbf{A}_{22}$ with the adjusted genomic relationship matrix $\mathbf{G}_a$

212   computed as follows:

213    $\mathbf{G}_a = \left(1 - \overline{f_p}\right)\mathbf{G}^* + 2\overline{f_p}\mathbf{J}$

214   where $\mathbf{G}^*$ is a raw genomic relationship matrix computed following the first method of

215   VanRaden (2008) using current allele frequencies computed from all genotyped animals, $\mathbf{J}$ is a

216   matrix of ones, and $\overline{f_p}$ is the average pedigree inbreeding coefficient across (core) genotyped

217   animals. The matrix $\mathbf{H^{-1}}$ was constructed in two different ways. First, the complete $\mathbf{G}$ was

218   directly inverted to obtain $\mathbf{G}^{-1}_{direct}$. Second, $\mathbf{G}^{-1}_{direct}$ was replaced by $\mathbf{G}^{-1}_{APY}$. Because the APY

219   relies on the size and the composition of the set of core animals (Misztal et al., 2014), we

220   investigated different numbers of core animals and different strategies to select the core

221   animals. For all the strategies, the selection candidates were allowed to be considered as core

222   animals. The number of core animals were 4,000, 6,000, 8,000, 10,000, and 13,000. For each

223   size, four different strategies were applied to select the core animals. The core animals were

224   randomly sampled 1) among all breed A genotyped animals (called "Breed A"), 2) among all

225   purebred genotyped animals (called "Purebred"), or 3) among all purebred and crossbred

226   genotyped animals (called "Purebred + Crossbred"). For the fourth strategy, a QR

227   decomposition with pivoting of the transposed genotype matrix was applied to the animals.

228   The QR decomposition with pivoting returns a permutation matrix such that the diagonal

229   elements of the upper triangular matrix $\mathbf{R}$ are decreasing (Golub and Van Loan, 1996). The

230   genotyped animals corresponding to the highest diagonal elements of the matrix $\mathbf{R}$ were

231   chosen as core animals (called "QR"). The aim of this fourth strategy was to select core

232   animals such that the conditioning of the mixed model equations was improved, resulting in

233   faster convergence, in comparison to the other three strategies (Fernando et al., 2016). All

234   computations and analyses were run using our own custom programs for QR decomposition

235   and statistical analyses, calc_grm (Calus and Vandenplas, 2016) for the computation of the

236   different relationship matrices (i.e., $\mathbf{G}_{direct}^{-1}$, $\mathbf{G}_{APY}^{-1}$, and $\mathbf{A}_{22}^{-1}$), and MiXBLUP (ten Napel et al.,

237   2016) for predicting the different GEBV. The matrices $\left(\mathbf{G}_{direct}^{-1} - \mathbf{A}_{22}^{-1} \right)$ and $\left(\mathbf{G}_{APY}^{-1} - \mathbf{A}_{22}^{-1} \right)$

238   were provided to MiXBLUP as external matrices.

239   *Criteria*

240   We evaluated the prediction of GEBV of genotyped selection candidates for the purebred A,

241   B, and C performances and the crossbred A(BC) performances, for each set of core animals

242   and each breed separately. Three criteria were computed from the GEBV of the selection

243   candidates. First, the ratios between the accuracies of $GEBV_{APY}$ from alternative core groups

244   and the accuracies of $GEBV_{DIRECT}$ (i.e., from $\mathbf{G}_{direct}^{-1}$), were computed. Accuracies were

245   computed as the Pearson correlation between GEBV and TBV. A ratio of accuracies smaller

246   than 1 means that $GEBV_{APY}$ is less accurate than $GEBV_{DIRECT}$. Second, regression

247   coefficients of TBV on $GEBV_{APY}$ and on $GEBV_{DIRECT}$ (hereafter called bias) were computed.

248   Third, ratios between mean squares errors (MSE) of $GEBV_{APY}$ and MSE of $GEBV_{DIRECT}$,

249   were computed. The MSE were computed as the mean of the squared differences between

250   GEBV and TBV. All results were averaged across five replicates. Tukey's honest significant

251   difference test (Tukey, 1949) was used to assess significance of differences between scenarios

252   at a 5% significance level.

253   For situations with single breeds, the number of required core animals that gives accurate

254   GEBV, can be determined as the number of largest eigenvalues explaining 98-99% of the

255   variation in $\mathbf{G}^*$ (Misztal, 2016; Pocrnic et al., 2016a; b). For investigating this relationship in

256   situations involving multiple breeds and their F1 and F2 crosses, we computed the numbers of

257   eigenvalues that explained 98% and 99% of the variation in $\mathbf{G}^*$ that included all the 89,000

258   genotyped purebred and crossbred animals. Computations were performed with calc_grm

259   (Calus and Vandenplas, 2016). For each scenario, the number of eigenvalues were compared

260   to the number of core animals needed such that the accuracies of $GEBV_{APY}$ were equal to or

261   higher than 99% of the accuracy for $GEBV_{DIRECT}$ for both purebred and crossbred

262   performance traits.

263

264   **RESULTS**

265   *Characteristics of simulated data*

12

266 The simulation yielded three breeds, A, B, and C, that were highly separated, as shown by the

267 projections of genomic relationships into the two first eigenvectors for the first replicate

268 (Figure 2). The estimated global Wright's F_{st} statistics, that is a measure to quantify the level

269 of genetic differentiation between the breeds, was equal to 0.35 on average across the five

270 replicates. The global Wright's F_{st} statistics were estimated from the genotypes of all purebred

271 animals of the generation 204 with the software Genepop (4.2) (Raymond and Rousset, 1995;

272 Rousset, 2008). The mean absolute difference in allele frequencies between breeds was about

273 0.34 on average across the five replicates. All these observations suggest three genetically

274 divergent populations. The average linkage disequilibrium, expressed as r^2 (Hill and

275 Robertson, 1968), between adjacent SNP pairs with MAF > 0.05 and across chromosomes,

276 was 0.25 for the three breeds on average across the five replicates. Genomic relationship

277 matrices required for the singular value decomposition and genomic predictions were based

278 on 52,518 SNPs on average across the five replicates.

Composition of the core groups

280 Four selection strategies were applied to compose the core groups: (1) the core animals were

281 randomly selected among only breed A animals, (2) the core animals were randomly selected

282 among purebred animals of breed A, B, and C, (3) the core animals were randomly selected

283 among purebred animals of breed A, B, and C, and crossbred BC and A(BC) animals, and (4)

284 the core animals were selected based on a QR decomposition of the genotype matrix. For the

285 four selection strategies, Figure 3 shows the proportions of core animals across the

286 generations and across the breed compositions of a randomly chosen replicate for the scenario

287 with 8,000 core animals. Similar results were obtained for the other replicates and sizes of

288 core groups. Proportions of core animals were similar across the generations, and across the

289 breed compositions for the first three selection strategies. For the selection strategy based on

290   QR decomposition, core animals were unequally spread across all generations and breed

291   compositions: the highest proportions of core animals selected within a generation and a breed

292   composition were observed among the crossbred A(BC) animals and the first generation of

293   genotyped purebred animals (Figure 3).

Quality of GEBV with G_{direct}^{-1}

295   On average 5,000 genotyped selection candidates per breed were considered for computing

296   accuracy, bias, and MSE (Table 2). For purebred performance, the accuracies were between

297   0.79 and 0.81. For crossbred performance, the accuracies were between 0.63 and 0.71. All

298   sets of GEBV were almost unbiased (i.e., values for bias were close to 1) and had values of

299   MSE close to 0 (Table 2).

Quality of GEBV with only breed A core animals

301   When the core groups included only breed A animals, $GEBV_{APY}$ were predicted as accurately

302   as $GEBV_{DIRECT}$ for the breed A selection candidates for both purebred and crossbred

303   performance traits, as shown by the ratios between the accuracies of $GEBV_{APY}$ and of

304    $GEBV_{DIRECT}$ (Figure 4). In addition, $GEBV_{APY}$ were unbiased, and MSE was close to 0

305   (Figure 4; Table 3; Table 4; E-Supplements Tables S3-S6). However, $GEBV_{APY}$ were less

306   accurate and more biased than $GEBV_{DIRECT}$ for the breed B and breed C selection candidates,

307   as shown by low ratios of accuracies, and high values for bias and ratios of MSE of

308    $GEBV_{APY}$ (Figure 4; Table 3; Table 4; E-Supplements Tables S3-S6). Across core groups,

309    $GEBV_{APY}$ were from 18% to 40% less accurate than $GEBV_{DIRECT}$, and MSE of $GEBV_{APY}$

310   were between 16 and 81% higher than the corresponding MSE of $GEBV_{DIRECT}$.

Quality of GEBV with core animals of different breed compositions

14

312   Based on the three performance criteria, ratios of accuracies, bias, and ratios of MSE, the

313   scenarios with core animals of different breed compositions outperformed the scenarios with

314   only breed A core animals for both purebred and crossbred performance traits. Use of core

315   groups with core animals of different breed compositions allowed the prediction of GEBV_{APY}

316   that were unbiased, and (almost) as accurate as $\text{GEBV}_{\text{DIRECT}}$, for all selection candidates and

317   performance traits. Indeed, the regression coefficients of TBV on GEBV_{APY} were close to 1

318   (Table 3); the ratios of accuracies were higher than 0.97 for the purebred performance trait,

319   and higher than 0.94 for the crossbred performance trait (Figure 5; Figure 6; E-Supplements

320   Table S3); and the MSE of GEBV_{APY} were similar to MSE of $\text{GEBV}_{\text{DIRECT}}$ (Table 4; E-

321   Supplements Table S6). Ratios of accuracies close to, or higher than, 0.99 were then obtained

322   for both traits when at least 8,000 core animals were used. The corresponding Pearson

323   correlations between GEBV_{APY} and $\text{GEBV}_{\text{DIRECT}}$, which is usually used as criteria in studies

324   on real datasets (e.g., Ostersen et al., 2016; Strandén et al., 2017), were about 0.995 (E-

325   Supplements). It is worth noting that the core size of 8,000 animals is between the numbers of

326   eigenvalues that explained 98% and 99% of the variation in $\mathbf{G}^*$, that is about 6,498 and 9,213

327   eigenvalues on average across the five replicates, respectively (Figure 4-Figure 6).

328   Comparison of the three performance criteria for the purebred performance trait showed no

329   difference among the three core selection strategies involving core animals of different breed

330   compositions (Figure 5;Table 3; Table 4; E-Supplements Tables S3-S6). For the crossbred

331   performance trait, the scenarios with purebred and crossbred core animals, either randomly

332   chosen or chosen based on a QR decomposition, slightly outperformed the scenarios with

333   only purebred core animals (Figure 6). However, these outperformances were not always

334   significant (E-Supplements).

335   ***Quality of GEBV for core and non-core selection animals***

15

336   Table 5 shows ratios of accuracies and of MSE, and the regression coefficients for the

337   scenario using 8000 core animals randomly selected among purebred and crossbred animals.

338   The regression coefficients and ratios of MSE for $GEBV_{APY}$ of core selection candidates and

339   of non-core selection candidates were similar. Ratios of accuracies for non-core selection

340   candidates were slightly lower than the corresponding ratios for the core selection candidates,

341   meaning that $GEBV_{APY}$ of non-core selection candidates were slightly less accurate than those

342   of core selection candidates, in comparison to $GEBV_{DIRECT}$. However, the differences

343   between accuracies of $GEBV_{APY}$ of core and of non-core selection candidates were not

344   significant following a Welch's t-test (Welch, 1947) with a 5% significance level.

345   ***Convergence of ssGBLUP with alternative core groups***

346   Convergence of ssGBLUP with alternative core groups of 8,000 animals were compared

347   against ssGBLUP using $\mathbf{G}_{direct}^{-1}$. Number of iterations of ssGBLUP using $\mathbf{G}_{APY}^{-1}$ were

348   expressed as the ratio to the number of iterations of ssGBLUP using $\mathbf{G}_{direct}^{-1}$. Average values

349   of this ratio across the 5 replicates (SD within brackets), were 0.85 (0.39) using breed A core

350   animals, 1.05 (0.33) using purebred core animals, 0.95 (0.31) using purebred and crossbred

351   animals, and 0.94 (0.30) using core animals selected based on a QR decomposition of the

352   genotype matrix. In comparison to ssGBLUP with $\mathbf{G}_{direct}^{-1}$, use of the APY led to similar

353   number of iterations to reach convergence. The selection strategy based on the QR

354   decomposition led to similar convergence as the other selection strategies.

355

356   **DISCUSSION**

357   In this study, we showed that $GEBV_{APY}$ were accurate approximations of $GEBV_{DIRECT}$ for

358   multivariate ssGBLUP involving multiple breeds and their crosses. $GEBV_{APY}$ as accurate as

359   GEBV$_{\text{DIRECT}}$ were obtained when the core groups included animals from different breed

360   compositions, and when the core groups had a size between the numbers of the largest

361   eigenvalues explaining 98% and 99% of the variation in the raw (i.e., before blending with the

362   pedigree relationship matrix) genomic relationship matrix ($\mathbf{G}^*$).

Composition of the core groups and selection strategies

364   The quality of the GEBV$_{\text{APY}}$ for both purebred and crossbred performance traits was close to

365   the GEBV$_{\text{DIRECT}}$ as long as all classes of purebred and crossbred animals were well

366   represented in the core group. This was not the case if not all breeds were included in the core

367   group. Such a situation where core animals are only from one breed, could be obtained with a

368   naive random selection strategy on a large genotype dataset that is dominated by one breed.

369   Due to the properties of the simulated datasets, e.g, similar numbers of genotyped animals per

370   breed and per generation, a random selection of core animals across the full dataset led to

371   similar proportions of core animas per breed composition and per generation. Based on a

372   study involving single breed ssGBLUP, Ostersen et al. (2016) advised that core groups should

373   represent all generations. Including animals from each generation in the core group was also

374   recommended by Bradford et al. (2017), especially when genotyped animals had incomplete

375   pedigree, such as unknown parents. Incomplete pedigree could be common in crossbreeding

376   schemes, because pedigree data for crossbred animals in field conditions is difficult to collect

377   (Ibánẽz-Escriche et al., 2009). From our results with the selection strategy based on QR

378   decomposition with pivoting, it seems that all generations, and all breed compositions, do not

379   have to be similarly represented in core groups. Indeed, in comparison to a random selection,

380   the selection strategy based on QR decomposition included higher proportions of crossbred

381   A(BC) animals and of the first generation of genotyped purebred animals selected as core

382   animals. One possible explanation is that genotypes of the crossbred A(BC) animals and of

383 the first generation of genotyped purebred animals include a large proportion of the

384 independent chromosome segments from all the genotyped purebred and crossbred animals.

385 However, core groups including animals that were randomly selected and that represented

386 similarly all generations and all breed composition gave results similar to the numerical

387 strategy based on QR decomposition, which is computationally expensive. Therefore, a

388 random selection of core animals by ensuring that core animals represent similarly all

389 generations and all breed compositions is advisable for the implementation of the APY in

390 well-structured crossbreeding schemes as investigated in this study. More complex situations,

391 such as multibreed (beef) cattle populations with a large variation in the observed breed

392 compositions, would probably benefit from more advanced APY core selection approaches

393 (Mäntysaari et al., 2017), such as the proposed numerical strategy based on QR

394 decomposition.

395 *Size of the core groups*

396 For single breed ssGBLUP, Pocrnic et al. (2016a; b) showed that the size of the core groups

397 required to predict GEBV$_{APY}$ at least as accurate as GEBV$_{DIRECT}$ was related to the

398 dimensionality of the genomic information. In their studies, the most accurate GEBV$_{APY}$ were

399 obtained when the core size was at least equal to the number of largest eigenvalues that

400 explained 98% of the variation in the raw genomic relationship matrix $\mathbf{G}^*$. In this study,

401 GEBV$_{APY}$ as accurate as GEBV$_{DIRECT}$ (i.e., with correlations between them ≥ 0.995) were

402 obtained when the core sizes were between the numbers of largest eigenvalues that explained

403 98% and 99% of the variation in the raw genomic relationship matrix $\mathbf{G}^*$, provided that the

404 composition of the core group represented the variation in all the breeds and crosses. Using a

405 multibreed beef cattle population, Mäntysaari et al. (2107) also showed that a core size larger

406 than the number of largest eigenvalues that explained 98% of the variation in $\mathbf{G}^*$ was needed

407 to get correlations between GEBV$_{APY}$ and GEBV$_{DIRECT}$ close to 1. Furthermore, Mäntysaari et

408 al. (2107) observed that the correlation between GEBV$_{APY}$ and GEBV$_{DIRECT}$ depended on the

409 composition of the core groups, even with a core size close to the number of largest

410 eigenvalues that explained 98% of the variation in $\mathbf{G}^*$. All these results suggest that the core

411 size involving multiple breeds and crosses can be also approximated based on the

412 dimensionality of the genomic information of all breeds and crosses together to ensure that

413 the core size is optimal. It should be noted, however, that in crossbreeding situations

414 relationships between the core size, the dimensionality of the genomic information, and some

415 population parameters (e.g., number of independent segments, effective population size) is not

416 as straightforward in as in single breed situations (Pocrnic et al., 2016a; b).

417

418 **CONCLUSIONS**

419 We showed that the APY algorithm gives results equivalent to those obtained with the direct

420 inversion of the genomic relationship matrix when genotyped animals belong to a few

421 different breeds and their F1 and F2 crosses, such as commonly observed in pig and poultry

422 breeding programs. For such situations, we suggest that core animals could be randomly

423 selected among all purebred and crossbred genotyped animals, while ensuring that they

424 represent all generations and all breed compositions. It was also shown that selecting a

425 number of core animals equal to the number of largest eigenvalues needed to explain 98-99%

426 of the variation on the raw genomic relationship matrix, is sufficient to achieve good quality

427 of GEBV in crossbreeding schemes.

428

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514

E-Supplements

Table S1 Number of purebred and crossbred animals with a phenotype per generation (average for the 5 replicates; SD within brackets).

Table S2 Number of purebred and crossbred animals with a phenotype and a genotype per generation (average for the 5 replicates; SD within brackets).

Table S3. Relative accuracies (average for the 5 replicates; SD within brackets) of GEBV from alternative core groups for the purebred (PB) and crossbred (CB) performance for genotyped selection candidates.

Table S4. Pearson correlations (average for the 5 replicates; SD within brackets) between GEBV for genotyped selection candidates from alternative core groups1 and GEBV from the direct inversion of **G**.

Table S5. Regression coefficients (average for the 5 replicates; SD within brackets) of TBV on GEBV from alternative core groups and the direct inversion of G for genotyped selection candidates.
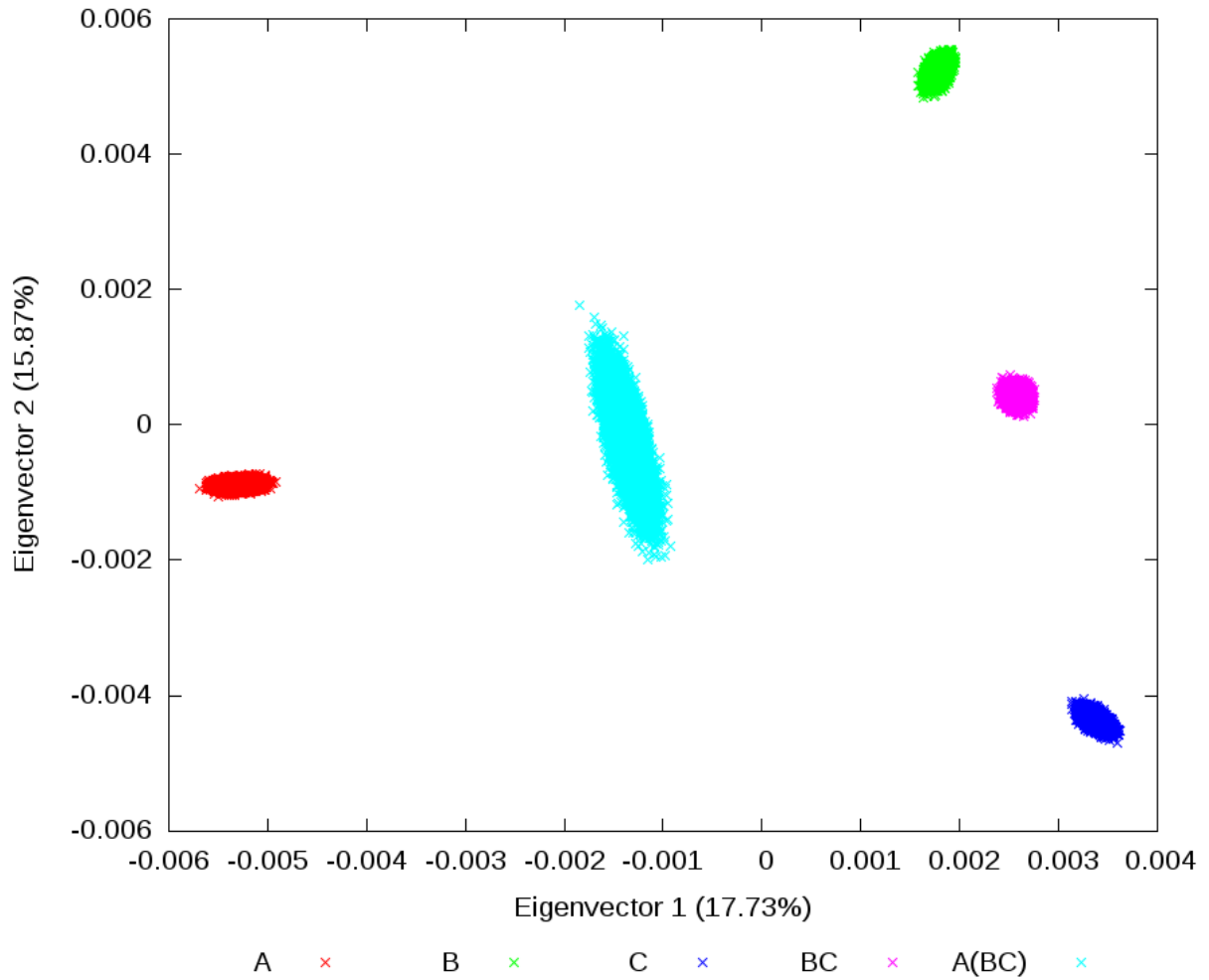
535 **Table S6.** Relative mean squares errors (average for the 5 replicates; SD within brackets) of

536 GEBV from alternative core groups for genotyped selection candidates.

537

Figures

Figure 2.

Strategy 1 (Breed A)

Animals	205	206	207	208	209
A	0.39	0.39	0.38	0.43	0.32
B	0.00	0.00	0.00	0.00	0.00
C	0.00	0.00	0.00	0.00	0.00
BC	0.00	0.00	0.00	0.00	0.00
A(BC)	0.00	0.00	0.00	0.00	0.00

Strategy 2 (PB)

Animals	205	206	207	208	209
A	0.13	0.13	0.13	0.12	0.13
B	0.13	0.13	0.13	0.13	0.13
C	0.13	0.13	0.13	0.13	0.12
BC	0.00	0.00	0.00	0.00	0.00
A(BC)	0.00	0.00	0.00	0.00	0.00

Strategy 3 (PB + CB)

Animals	205	206	207	208	209
A	0.09	0.09	0.09	0.09	0.09
B	0.09	0.09	0.09	0.09	0.09
C	0.09	0.09	0.09	0.09	0.06
BC	0.00	0.09	0.10	0.09	0.09
A(BC)	0.00	0.09	0.09	0.09	0.09

Generation

Strategy 4 (QR)

Animals	205	206	207	208	209
A	0.13	0.06	0.05	0.05	0.09
B	0.13	0.06	0.05	0.05	0.08
C	0.11	0.04	0.03	0.04	0.08
BC	0.00	0.07	0.05	0.05	0.06
A(BC)	0.00	0.19	0.19	0.17	0.20

Generation
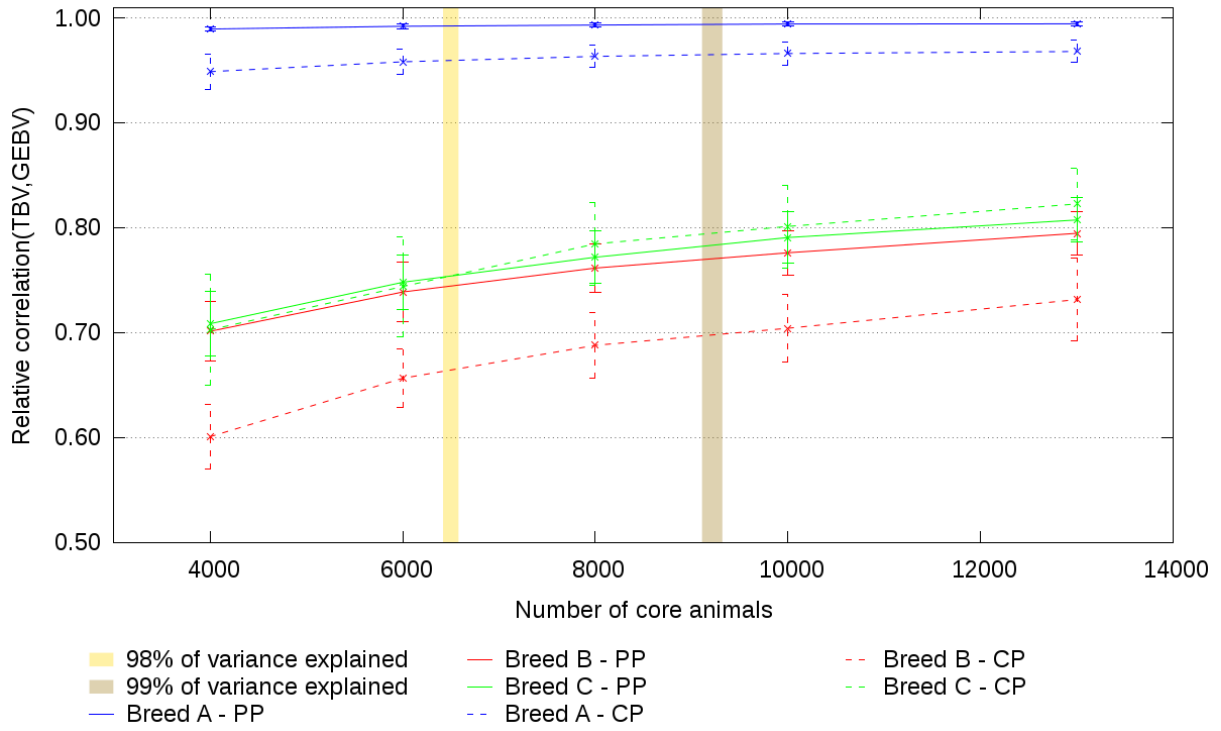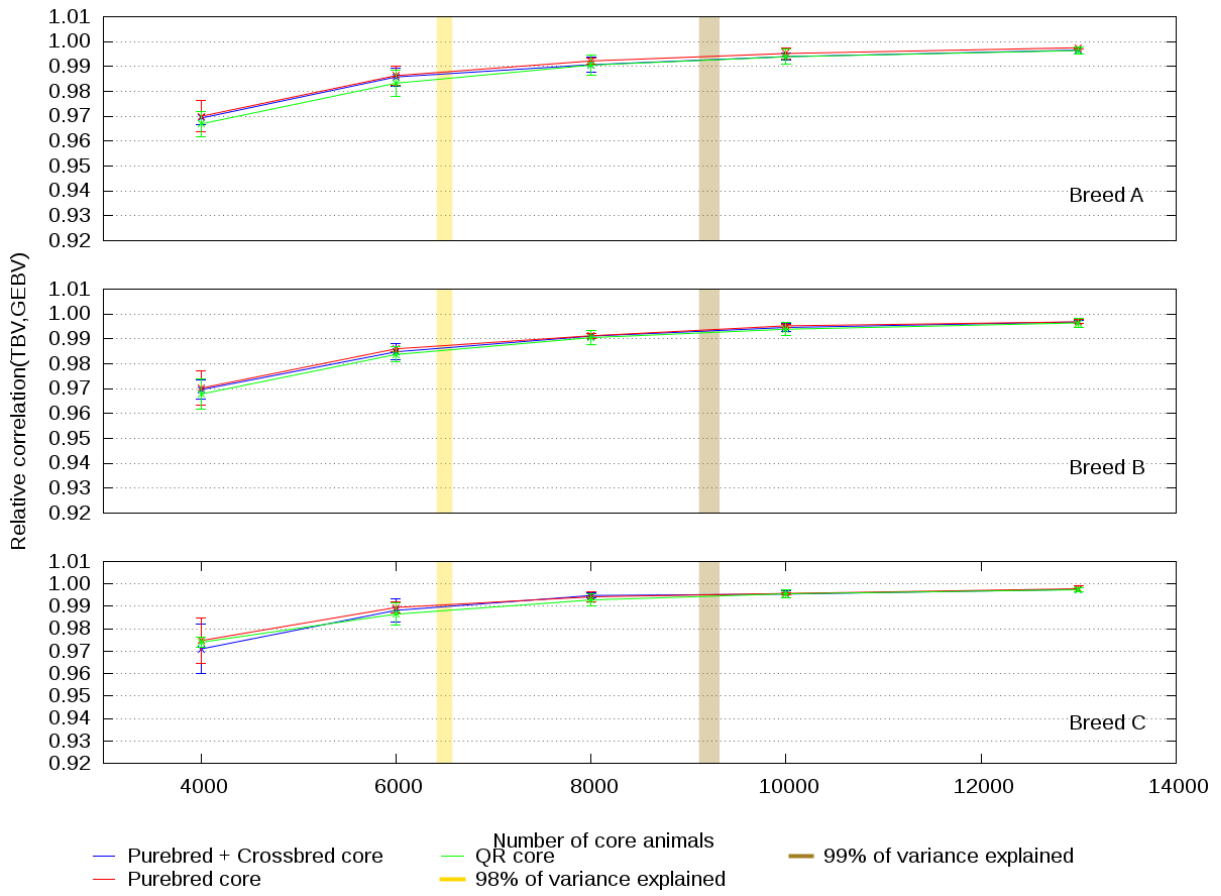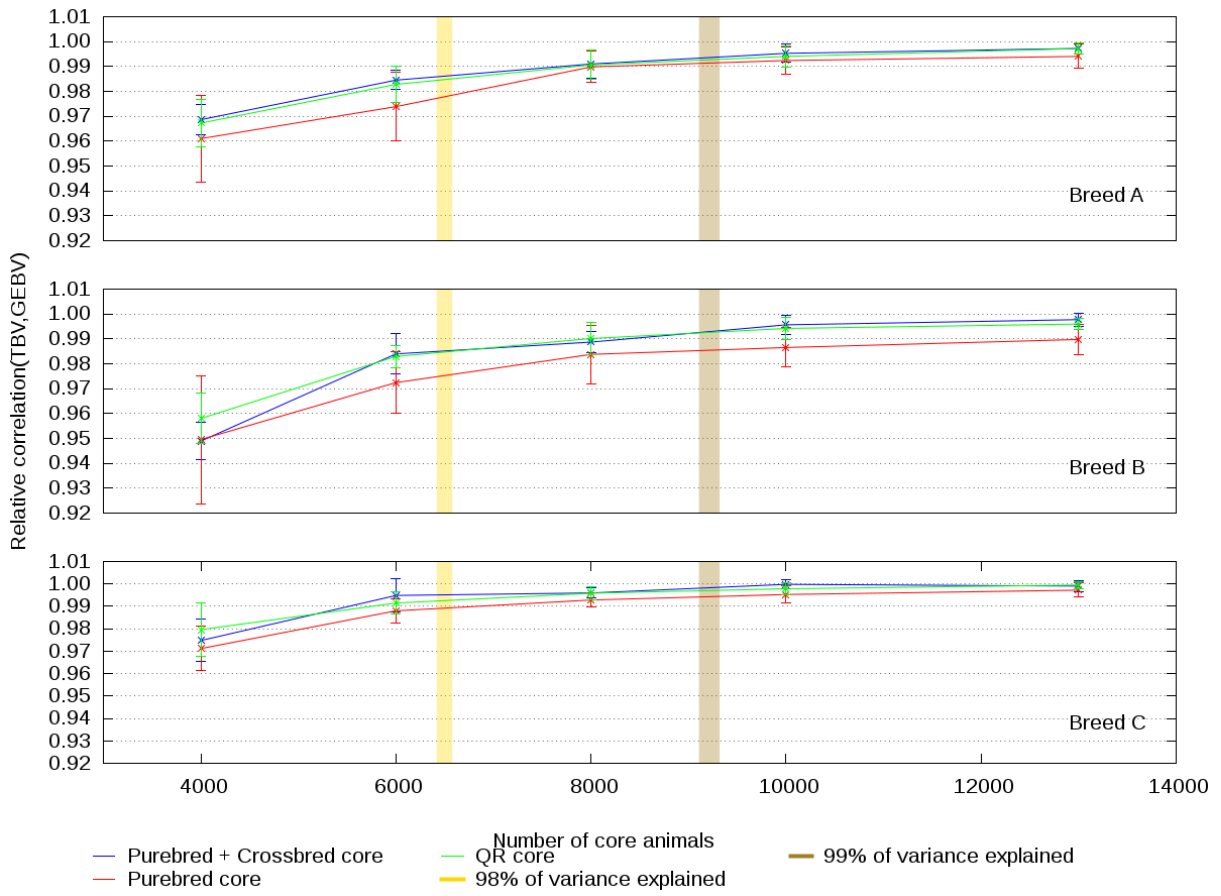
543

Figure 3.

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Figure 4.

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Figure 5.

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Figure 6.

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Figure 1. Schematic representation of the simulation. The crossbreeding program started at generation 200 (generation numbers in bold). The number of males (M) and females (F) per generation and per breed (A, B, and C), or per cross (BC, and A(BC)), are reported within brackets. Blue arrows denote the sires and dams of the next generation; red arrows denote the dams of the next generation; green arrows denote the sires of the next generation.

Figure 2. Projections of genomic relationships for purebred (A, B, and C) and crossbred (BC and A(BC)) genotyped animals into the two first eigenvectors for the first replicate.

Figure 3. Proportions of core animals per generation and breed composition of one replicate for the scenario using 8,000 core animals. Core animals were selected using four different strategies: 1) only from breed A animals (Breed A), 2) from purebred animals of breed A, B and C (PB), 3) from purebred animals of breed A, B and C, and crossbred BC and A(BC) animals (PB + CB), and (4) chosen based on a QR decomposition of the genotype matrix (QR). Darker colours represent higher proportions of core animals per generation and breed composition.

Figure 4. Relative correlations of GEBV from different sizes of core groups with only breed A animals. Relative correlations for the purebred performance (PP) and crossbred performance (CP) traits are defined as the ratio between the accuracies of GEBV from alternative core groups and the corresponding accuracies of GEBV from $\mathbf{G}_{direct}^{-1}$. Vertical columns depict the number of eigenvalues that explained 98% and 99% of the variation in $\mathbf{G}^*$. Results are averages for the 5 replicates.

578

579

580 **Figure 5**. Relative correlations of GEBV from alternative core groups for the purebred

581 performance traits. Core groups include randomly selected purebred and crossbred animals

582 (Purebred + Crossbred core), randomly selected purebred animals (Purebred core), and

583 animals selected based on a QR decomposition of the genotype matrix (QR core). Relative

584 correlations are defined as the ratio between the accuracies of GEBV from alternative core

585 groups and the corresponding accuracies of GEBV from $\mathbf{G}_{direct}^{-1}$. Vertical columns depict the

586 number of eigenvalues that explained 98% and 99% of the variation in $\mathbf{G}^*$. Results are

587 averages for the 5 replicates.

588

589 **Figure 6**. Relative correlations of GEBV from alternative core groups for the crossbred

590 performance trait. Core groups include randomly selected purebred and crossbred animals

591 (Purebred + Crossbred core), randomly selected purebred animals (Purebred core), and

592 animals selected based on a QR decomposition of the genotype matrix (QR core). Relative

593 correlations are defined as the ratio between the accuracies of GEBV from alternative core

594 groups and the corresponding accuracies of GEBV from $\mathbf{G}_{direct}^{-1}$. Vertical columns depict the

595 number of eigenvalues that explained 98% and 99% of the variation in $\mathbf{G}^*$. Results are

596 averages for the 5 replicates.

597

Tables

Table 1. Heritabilities (diagonal) and genetic correlations (off-diagonal) among the five simulated traits.

Trait	Purebred A	Purebred B	Purebred C	Crossbred BC	Crossbred A(BC)
Purebred A	0.28				
Purebred B	0.46	0.39			
Purebred C	0.27	0.80	0.22		
Crossbred BC	0.33	0.58	0.30	0.36	
Crossbred A(BC)	0.55	0.31	0.26	0.69	0.23

Table 2. Accuracies, bias, and mean square errors (MSE) of GEBV from the direct inversion of **G** (average for the 5 replicates; SD within brackets).

Selection candidates	Number	Purebred performance			Crossbred performance		
		Accuracy	Bias	MSE	Accuracy	Bias	MSE
Breed A	5010	0.81	1.04	1.11	0.68	0.98	0.68
	(24)	(0.02)	(0.05)	(0.69)	(0.04)	(0.08)	(0.51)
Breed B	4975	0.85	1.06	1.16	0.63	0.95	0.90
	(30)	(0.01)	(0.03)	(0.81)	(0.02)	(0.04)	(0.43)
Breed C	5016	0.79	1.04	1.42	0.71	1.04	1.35
	(45)	(0.04)	(0.03)	(0.74)	(0.04)	(0.07)	(1.18)

Table 3. Regression coefficients (average for the 5 replicates; SD within brackets) of TBV on GEBV from alternative core groups[1] for genotyped selection candidates.

Number of core animals	Purebred performance				Crossbred performance			
	Breed A	PB	PB+CB	QR	Breed A	PB	PB+CB	QR
Breed A selection candidates								
4000	1.04	1.05	1.06	1.06	0.90	0.96	0.99	0.99
	(0.06)	(0.06)	(0.06)	(0.06)	(0.08)	(0.08)	(0.09)	(0.08)
8000	1.04	1.05	1.05	1.05	0.92	0.97	0.99	0.99
	(0.05)	(0.06)	(0.06)	(0.06)	(0.08)	(0.08)	(0.08)	(0.08)
13000	1.04	1.05	1.05	1.05	0.93	0.97	0.98	0.98
	(0.05)	(0.05)	(0.05)	(0.05)	(0.08)	(0.08)	(0.08)	(0.08)
Breed B selection candidates								
4000	1.49	1.06	1.06	1.07	1.62	0.91	0.93	0.94
	(0.08)	(0.03)	(0.02)	(0.03)	(0.11)	(0.08)	(0.05)	(0.06)
8000	1.46	1.06	1.06	1.06	1.58	0.93	0.95	0.95
	(0.08)	(0.02)	(0.03)	(0.03)	(0.13)	(0.06)	(0.05)	(0.04)
13000	1.43	1.06	1.06	1.06	1.54	0.93	0.95	0.95
	(0.09)	(0.03)	(0.03)	(0.03)	(0.14)	(0.05)	(0.05)	(0.04)
Breed C selection candidates								
4000	1.69	1.05	1.06	1.05	2.41	1.07	1.09	1.08
	(0.15)	(0.04)	(0.04)	(0.03)	(0.30)	(0.08)	(0.07)	(0.07)
8000	1.62	1.04	1.05	1.04	2.27	1.06	1.06	1.06
	(0.12)	(0.04)	(0.04)	(0.03)	(0.19)	(0.07)	(0.07)	(0.07)
13000	1.58	1.04	1.04	1.04	2.14	1.06	1.05	1.05
	(0.11)	(0.03)	(0.04)	(0.03)	(0.14)	(0.07)	(0.07)	(0.07)

1 Core groups include 1) randomly selected breed A animals only (Breed A), 2) randomly selected purebred animals (PB), 3) randomly selected purebred and crossbred animals (PB+CB), and 4) animals selected based on a QR decomposition of the genotype matrix (QR).

Table 4. Relative mean squares errors[1] (average for the 5 replicates; SD within brackets) of GEBV from alternative core groups[2] for genotyped selection candidates.

Number of core animals	Purebred performance				Crossbred performance			
	Breed A	**PB**	**PB+CB**	**QR**	**Breed A**	**PB**	**PB+CB**	**QR**
Breed A selection candidates								
4000	1.09	1.05	1.05	1.04	1.14	1.14	1.04	1.03
	(0.33)	(0.08)	(0.04)	(0.06)	(0.29)	(0.20)	(0.04)	(0.04)
8000	1.11	0.98	0.98	0.99	1.20	1.11	1.11	1.11
	(0.34)	(0.05)	(0.06)	(0.07)	(0.28)	(0.22)	(0.23)	(0.22)
13000	1.12	1.04	0.98	0.98	1.20	1.11	1.12	1.10
	(0.33)	(0.19)	(0.06)	(0.06)	(0.28)	(0.22)	(0.22)	(0.23)
Breed B selection candidates								
4000	1.75	1.12	1.05	1.08	1.34	0.99	1.04	1.02
	(0.93)	(0.16)	(0.06)	(0.08)	(0.30)	(0.15)	(0.08)	(0.07)
8000	1.81	1.09	1.09	1.09	1.27	0.99	0.95	0.95
	(1.04)	(0.18)	(0.17)	(0.18)	(0.21)	(0.15)	(0.10)	(0.10)
13000	1.77	1.15	1.08	1.08	1.24	1.00	0.93	0.94
	(0.95)	(0.23)	(0.18)	(0.18)	(0.21)	(0.14)	(0.11)	(0.09)
Breed C selection candidates								
4000	1.29	0.97	1.02	1.00	1.20	1.00	1.00	1.02
	(0.43)	(0.08)	(0.05)	(0.05)	(0.44)	(0.16)	(0.08)	(0.07)
8000	1.28	0.96	0.97	0.96	1.19	0.99	0.94	0.95
	(0.37)	(0.08)	(0.09)	(0.09)	(0.38)	(0.16)	(0.09)	(0.09)
13000	1.24	0.88	0.96	0.96	1.16	1.00	0.95	0.95
	(0.34)	(0.16)	(0.08)	(0.09)	(0.35)	(0.16)	(0.09)	(0.08)

[1] Results are expressed as the ratio between MSE of GEBV from alternative core groups and MSE of GEBV from the direct inversion of **G**.

[2] Core groups include 1) randomly selected breed A animals only (Breed A), 2) randomly selected purebred animals (PB), 3) randomly selected purebred and crossbred animals (PB+CB), and 4) animals selected based on a QR decomposition of the genotype matrix (QR).

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Table 5. Quality of GEBV using APY for the core and non-core selection candidates. [1]

Selection candidates	Number	Purebred performance			Crossbred performance		
		Accuracy[2]	Reg. coef.	MSE[2]	Accuracy[2]	Reg. coef.	MSE[2]
A core	453 (19)	0.999	1.02	0.960	0.997	0.98	1.087
		(0.001)	(0.05)	(0.058)	(0.001)	(0.07)	(0.203)
A non-core	4557	0.990	1.06	0.980	0.990	0.99	1.112
	(32)	(0.003)	(0.06)	(0.066)	(0.006)	(0.08)	(0.232)
B core	456 (23)	0.998	1.02	1.076	0.995	0.88	0.946
		(0.002)	(0.06)	(0.169)	(0.004)	(0.09)	(0.091)
B non-core	4519	0.991	1.07	1.093	0.988	0.95	0.949
	(37)	(0.001)	(0.03)	(0.170)	(0.004)	(0.04)	(0.096)
C core	322 (43)	0.998	1.07	0.961	0.999	1.03	0.939
		(0.001)	(0.07)	(0.082)	(0.004)	(0.06)	(0.089)
C non-core	4694	0.994	1.04	0.966	0.996	1.06	0.942
	(27)	(0.001)	(0.04)	(0.087)	(0.003)	(0.07)	(0.093)

[1] Results (average for the 5 replicates; SD within brackets) are shown for the scenario using 8000 core animals randomly selected among purebred and crossbred animals.

[2] Results for accuracies and mean square errors (MSE) are expressed as the ratio between accuracies (MSE) of GEBV using APY and accuracies (MSE) of GEBV using the direct inversion of **G**.

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