

1 **Interpretive Summary**

2 **Metafounder approach for single-step genomic evaluations of Red Dairy cattle.** By

3 Kudinov et al. Change from the multi-step to the single-step genomic prediction approach in
4 routine evaluations is complicated. In this study, we show the advantage of the metafounders
5 approach in the single-step prediction of milk performance in dairy cattle. In addition, we
6 also test the effect of markers selection on creating a metafounders relationship matrix.

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METAFOUNDERS IN RED DAIRY CATTLE EVALUATIONS

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10 **Metafounder approach for single-step genomic evaluations of Red Dairy cattle**

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12 A.A. Kudinov^{*,†}, E.A. Mäntysaari^{*}, G.P. Aamand[‡], P. Uimari[†], and I. Strandén^{*}

13 ^{*} Natural Resources Institute Finland (Luke), Jokioinen, Finland, FI-31600

14 [†] Department of Agricultural Science, University of Helsinki, Helsinki, Finland, FI-00014

15 [‡] Nordic Cattle Genetic Evaluation, Aarhus, Denmark, DK-8200

16

17 Corresponding author: Andrei Kudinov

18 e-mail: andrei.kudinov@luke.fi

ABSTRACT

20 Single-step genomic BLUP (**ssGBLUP**) is a powerful approach for breeding value prediction
 21 in populations with a limited number of genotyped animals. However, conflicting genomic
 22 (**G**) and pedigree (**A₂₂**) relationship matrices complicate the implementation of ssGBLUP
 23 into practice. The metafounder (**MF**) approach is a recently proposed solution for this
 24 problem and has been successfully used on simulated and real multi-breed pig data.
 25 Advantages of the method are easily seen across breed evaluations, where pedigrees are
 26 traced to several pure breeds, which are thereafter used as MF. Application of the MF method
 27 to ruminants is complicated due to multi-breed pedigree structures and the inability to
 28 transmit existing unknown parent groups (**UPG**) to MF. In this study, we apply the MF
 29 approach for ssGBLUP evaluation of Finnish Red Dairy cattle treated as a single breed.
 30 Relationships among MF were accounted for by a (co)variance matrix (**Γ**) computed using
 31 estimated base population allele frequencies. The attained **Γ** was used to calculate a
 32 relationship matrix **A₂₂^Γ** for the genotyped animals. We tested the influence of SNP selection
 33 on the **Γ** matrix by applying a minor allele frequency (**MAF**) threshold (**Γ_{MAF}**) where
 34 accepted markers had an $MAF \geq 0.05$. Elements in the **Γ_{MAF}** matrix were slightly lower than
 35 in the **Γ** matrix. Correlation between diagonal elements of the genomic and pedigree
 36 relationship matrices increased from 0.53 (**A₂₂**) to 0.76 (**A₂₂^Γ** and **A₂₂^{Γ_{MAF}}**). Average diagonal
 37 elements of **A₂₂^Γ** and **A₂₂^{Γ_{MAF}}** matrices increased to the same level as in the **G** matrix. ssGBLUP
 38 breeding values (**GEBV**) were solved using either the original 236 or redefined 8 UPG, or 8
 39 MF computed with or without the MAF threshold. For bulls, the GEBV validation test results
 40 for the 8 UPG and 8 MF gave the same adjusted R^2 (0.31) and over-dispersion (0.73,
 41 measured by regression coefficient b_1). No significant R^2 increase was observed in cows.
 42 Thus, the MF greatly influenced the pedigree relationship matrices but not the GEBV.

43 Selection of SNPs according to MAF had a notable effect on the Γ matrix and made the \mathbf{A}_{22}
44 and \mathbf{G} matrices more similar.

45

46 ***Key Words***

47 Genetic groups, single-step genomic BLUP, metafounders, base population.

48

INTRODUCTION

49 Single-step genomic BLUP (**ssGBLUP**) is an elegant approach for estimating
50 genomic breeding values (**GBV**) that uses pedigree (**A**) and genomic (**G**) relationship
51 matrices (Aguilar et al., 2010; Christensen and Lund, 2010). The approach has two important
52 theoretical assumptions concerning the **A** and **G** matrices: the same scale and equal base
53 population (Christensen, 2012). These assumptions complicate the application of ssGBLUP
54 in dairy cattle breeding. In order to meet the assumptions, several methods have been
55 proposed that make **G** to be like **A**. For example, base population allele frequencies (**AF**) are
56 used (VanRaden, 2008), and elements of **G** are scaled and centered to have on average the
57 same diagonal and off-diagonal elements as in **A** (Vitezica et al., 2011; Christensen et al.,
58 2012). In practice, base population AF are unknown and the **G** matrix is often constructed
59 using AF observed in the genotyped population.

60 Commercial dairy cattle pedigree can seldom be traced to a genetically homogeneous base
61 population because the pedigree often has a complicated breed structure with unknown parent
62 information (VanRaden, 1992; Sponenberg and Bixby, 2007). To solve the problem of
63 incomplete pedigree, Thompson (1979) and Quaas (1988) developed the concept of phantom
64 parents or unknown parent groups (**UPG**), for animals with unknown parent(s). UPG are
65 typically assigned according to selection pathways and share the same genetics allowing

66 more accurate estimation of genetic trend in traditional genetic evaluation (Theron et al.,
67 2002). In ssGBLUP, Misztal et al. (2013) observed bias in UPG solutions. The bias increased
68 with an increase in the number of genotyped animals.

69 The metafounder (**MF**) approach was proposed by Legarra et al. (2015) to achieve
70 compatibility in the pedigree and genomic relationship matrices. The MF approach combines
71 the idea of using AF equal to 0.5 for all markers when calculating the **G** matrix (Christensen,
72 2012) and assigning unknown parents to MF or pseudo-individuals with self-relationships in
73 the **A** matrix. MF are similar to UPG, but allow a related base population with non-zero
74 inbreeding coefficients. The relationships within and between the MF are modeled by a
75 gamma matrix (Γ), which is used in forming the relationship matrix (\mathbf{A}^Γ). The Γ matrix may
76 be constructed using an estimated base or observed genotyped population AF (e.g. Legarra et
77 al., 2015; Garcia-Bacciano et al., 2017). However, the Γ matrix may be poorly estimated
78 when certain AF are estimated inaccurately due to the low number of rare alleles. The large
79 number of UPG increases chances that an UPG is associated with a low number of rare allele
80 genotypes.

81 Legarra et al. (2015) and Garcia-Bacciano et al. (2017) showed the advantage of the MF
82 approach in GEBV estimation using simulated data. Xiang et al. (2017) used the MF method
83 for ssGBLUP evaluation in the crossbreed performance in pigs. According to their results, the
84 MF approach successfully combined two breeds in a GEBV evaluation. Pig evaluations
85 clearly focus on the youngest generation and, thus, fewer UPG are needed than in dairy cattle
86 (Arnold et al., 1992). MF approach studies have mostly focused on crossbred and admixture
87 populations (Bradford et al., 2019; van Grevenhof et al., 2019) because the approach may
88 help with implementing ssGBLUP for complicated pedigree populations such as in pigs and
89 poultry. However, implementing the MF approach for dairy cattle may be challenging

90 because of the frequently large number of UPG. The few published studies have used
91 simulated dairy cattle data to estimate the $\mathbf{\Gamma}$ matrix and its influence on ssGBLUP (Garcia-
92 Bacciano et al., 2017; Bradford et al., 2019), but had only a few MF.

93 We used the MF approach in the ssGBLUP evaluation of 305-d milk production in Finnish
94 Red dairy cattle. We present two approaches to estimate the $\mathbf{\Gamma}$ matrix, using different
95 numbers of markers. We compared values in the two $\mathbf{\Gamma}$ matrices. The effect of various $\mathbf{\Gamma}$
96 matrices is shown using model validation statistics from ssGBLUP evaluations having either
97 UPG or MF.

98 MATERIALS AND METHODS

99 *ssGBLUP models*

100 The joint relationship matrix of genotyped and non-genotyped animals in ssGBLUP is
101 commonly denoted as \mathbf{H} (Aguilar et al., 2010; Christensen and Lund, 2010). The \mathbf{H}^{-1} matrix
102 needed in the mixed model equations of ssGBLUP is

$$103 \quad \mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{pmatrix},$$

104 where \mathbf{A} is the full pedigree relationship matrix, \mathbf{G} is the genomic relationship matrix, and
105 \mathbf{A}_{22} is a pedigree relationship matrix of the genotyped animals.

106 *Single step with UPG in A.* Mean genetic levels of animals with missing parental information
107 were modeled using pedigree-based UPG proposed by Quaas and Pollack (1981). In the UPG
108 model, unknown parents are assumed to be unrelated and completely outbred. UPG effects in
109 the model only account for possible non-zero expectations in the breeding values of parent
110 groups. There are alternative ways to account for UPG in forming \mathbf{H}^{-1} . The standard way is
111 to replace the original \mathbf{H}^{-1} matrix with an augmented one, where the UPG are included as

112 “phantom parents” (Westell et al., 1988). Matilainen et al. (2018), following Miszta et al.
 113 (2013), formed the \mathbf{H}^{-1} matrix without groups, and, thereafter, included the UPG via so-
 114 called QP transformation (Quaas and Pollack, 1981) into the final augmented \mathbf{H}^{-1} . However,
 115 Masuda et al. (2019) recommended omitting the terms involving \mathbf{G}^{-1} in the UPG coefficient
 116 part of the augmented \mathbf{H}^{-1} matrix. In our UPG models, the genomic relationship matrix was
 117 constructed using VanRaden (2008) method 1 ($\mathbf{G}_{\mathbf{PVR1}}$), where base population AF were used
 118 to center and scale the marker data. Base population AF were estimated with the GLS model
 119 (McPeck et al., 2004) using the Bpop v. 0.30 program (Strandén and Mäntysaari, 2019),
 120 which is based on the computational approach described in Strandén et al. (2017). The
 121 genomic information was assumed to account for 90% of the variation in breeding values, i.e.
 122 the polygenic proportion was 10%. This was attained using a modified \mathbf{G} matrix obtained by
 123 averaging original \mathbf{G} and \mathbf{A}_{22} matrices with weights of 0.9 and 0.1, respectively.

124 *Single step with metafounders.* In the MF approach, the \mathbf{H}^{-1} matrix is replaced by a
 125 modified $(\mathbf{H}^\Gamma)^{-1}$ matrix described by Legarra et al. (2015) and Christensen et al. (2015) as

$$126 \quad (\mathbf{H}^\Gamma)^{-1} = (\mathbf{A}^\Gamma)^{-1} + \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_w^{-1} - (\mathbf{A}_{22}^\Gamma)^{-1} \end{pmatrix},$$

127 where $\mathbf{G}_w = (1 - w)\mathbf{G}_{05} + w\mathbf{A}_{22}^\Gamma$, w is the proportion of genetic variance not explained by
 128 the markers, $\mathbf{G}_{05} = (\mathbf{Z}_{101}\mathbf{Z}'_{101})\frac{2}{m}$, \mathbf{Z}_{101} is an n by m marker matrix with genotypes coded by
 129 $\{-1,0,1\}$, m is the number of SNP markers, n is the number of genotyped animals, \mathbf{A}^Γ is
 130 pedigree relationship matrix formed with a $\mathbf{\Gamma}$ matrix, and \mathbf{A}_{22}^Γ is a submatrix of \mathbf{A}^Γ for the
 131 genotyped animals. We used a 10% polygenic proportion, i.e. $w = 0.1$, as in Garcia-Baccino
 132 et al. (2017). The variance covariance structure of the MF can be estimated by $\mathbf{\Gamma} = 8 \text{Cov}(\mathbf{P})$,
 133 as presented in the Appendix of Christensen et al. (2015), where \mathbf{P} is an m by r matrix of AF
 134 and r is the number of MF.

135 ***Test data and model validation***

136 We used Red Dairy Cattle (**RDC**) milk production data provided by Nordic Cattle Genetic
137 Evaluations (**NAV**). The data sample was extracted from the NAV production evaluation
138 database by including all cows from 426 Finnish herds with at least 10 genotyped cows. This
139 gave 112,479 cows with first-lactation 305-d milk production records produced during 1988–
140 2018. The pedigree included 226,012 animals born in 1960–2016 consisting of 86% RDC,
141 12% Holstein (**HOL**), 2% Finn cattle (**FIN**, an indigenous Finnish cattle population), and a
142 total of 1% of other breeds (Red Holstein, Jersey, Brown Swiss etc.). There were 236 UPG
143 which were based on selection path, birth year, and population of origin. These UPG
144 definitions were the same as those used in the Nordic TD evaluations in November 2018
145 (Lidauer et al., 2015) and were provided by NAV.

146 Genotypes were available for 19,757 animals (3,571 bulls and 16,186 cows), which either
147 had observations or were in the pedigree of the animals with observations. Bulls were
148 genotyped using Illumina Bovine SNP50 Bead Chip (Illumina, San Diego, USA) and the
149 cows using a lower-density EuroG 10k chip (<http://www.eurogenomics.com/>) that had been
150 imputed to the 50K density by NAV. There were 46,914 markers from the 29 bovine
151 autosomes available for the analysis.

152 Cow and bull validation data sets were created by removing milk production records for
153 either the last year or for four of the previous production years, respectively, as in Gao et al.
154 (2018) and Mäntysaari et al. (2010). We included 101 and 3,551 genotyped test bulls and
155 cows, respectively. Daughter yield deviations (**DYD**) and yield deviations (**YD**) were attained
156 using the full data and an animal model by the MiX99 software (Strandén and Lidauer,
157 1999), as in Gao et al. (2018). The calculated DYD and YD were used for bulls and cows,
158 respectively, in validation regression models $(D)YD = b_0 + b_1 * GEV$, with weights for

159 the DYD observations. The weight for DYD was $EDC/(EDC + \lambda)$, where λ is $(4 - h^2) / h^2$,
160 h^2 is heritability, and EDC is the bull's effective daughter contributions
161 (https://interbull.org/ib/cop_appendix4) in evaluation with the full data set. To attain adjusted
162 validation reliability, we divided the model coefficient of determination (R^2) by the average
163 weight. The regression coefficient b_1 for the bulls was multiplied by two because DYD only
164 represents the sire effect. All the analyses used h^2 of 0.44, which is a parameter derived from
165 the NAV milk production test day model for 305-d milk yield.

166 *Unknown parents and metafounders*

167 Eight groups were defined according to the full pedigree structure and replaced the original
168 236 UPG. We included six groups for RDC (birth years <1971, 1971–1980, 1981–1990,
169 1991–2000, 2001–2010, 2011–2016), a HOL group, and a group for the other breeds. These
170 eight groups were treated as UPG or MF. In the MF approach, the base population AF, used
171 to calculate the Γ matrix, were estimated using a GLS approach. The GLS model was $\mathbf{m}_i =$
172 $\mathbf{Q}\boldsymbol{\mu}_i + \mathbf{e}_i$, where \mathbf{m}_i is an n by 1 vector of marker i genotypes, \mathbf{Q} is an n by 8 matrix, the rows
173 of which sum up to 1, and that assigns individuals to fractions of MF, $\boldsymbol{\mu}_i$ is an 8 by 1 vector
174 of group means, and $\mathbf{e}_i \sim (\mathbf{0}, \mathbf{A}_{22}^* \sigma^2)$ where \mathbf{A}_{22}^* was the pedigree relationship matrix for the
175 genotyped animals and σ^2 is the common variance. In allele frequency estimation, the
176 common variance need not be known (e.g. Garcia-Baccino et al., 2017). Estimated base
177 population AF for the MF are $\hat{\mathbf{p}}_i = \frac{1}{2} \hat{\boldsymbol{\mu}}_i$ for each marker $i = 1, \dots, m$.

178 To estimate AF for the MF in the GLS model, the \mathbf{A}_{22}^* matrix was based on a truncated
179 pedigree, where one parent generation at most was accepted to the genotyped animals. The
180 pedigree truncation guaranteed that the young genotyped animals would contribute to the
181 recent birth year MF and not to the old birth year MF. In addition, the truncation used more
182 genomic information than the full pedigree because genotyped animals had less genotyped

183 ancestors but instead a young birth year MF. It can be proven that the GLS method will
184 ignore genotype of an animal whose both parents are genotyped and the animal is not an
185 ancestor to a genotyped animal.

186 The eight columns of base population AF in the \mathbf{P} matrix were used to estimate the variance
187 covariance structure of the eight MF or the $\mathbf{\Gamma}$ matrix, $\mathbf{\Gamma} = 8 \text{Cov}(\mathbf{P})$. The effect of minor
188 allele frequencies (\mathbf{MAF}) on the MF covariances were tested by creating two alternative $\mathbf{\Gamma}$
189 matrices. In the first scenario, the full \mathbf{P} matrix was used to calculate the $\mathbf{\Gamma}$ matrix, denoted
190 $\mathbf{\Gamma}_8$. In the other scenario, denoted $\mathbf{\Gamma}_{8\text{MAF}}$, only those markers with MAF greater or equal to
191 0.05 in all RDC cattle MF were included in the \mathbf{P} matrix. The MAF requirement eliminated
192 3,783 markers and left 43,131 markers that were used to calculate the $\mathbf{\Gamma}_{8\text{MAF}}$ matrix.

193 *ssGBLUP computation*

194 All ssGBLUP calculations used the full pedigree with 226,012 animals and genomic
195 relationship matrices (\mathbf{G}_{PvR1} or \mathbf{G}_{05}) for the 19,757 animals. For the ssGBLUP with MF, the
196 augmented additive relationship matrix of genotyped animals ($\mathbf{A}_{22}^{\mathbf{\Gamma}}$) was calculated using the
197 modified Relax2 v. 1.83 program (Strandén and Vuori, 2006). The
198 $(\mathbf{G}_{\text{PvR1}}^{-1} - \mathbf{A}_{22}^{-1})$ and $(\mathbf{G}_w^{-1} - (\mathbf{A}_{22}^{\mathbf{\Gamma}})^{-1})$ matrices were calculated using the HGinv v. 0.87
199 program (Strandén and Mäntysaari, 2018). The latest MiX99 v. 17.1107 (Strandén and
200 Lidauer, 1999) was used to solve the GEBV using the four ssGBLUP models. Two of the
201 evaluations were UPG models with either 236 UPG (ssGBLUP_{236UPG}) or 8 UPG
202 (ssGBLUP_{8UPG}) in \mathbf{A} . UPG were treated as random by adding the inverse of genetic variance
203 to the diagonal of group equations in the mixed model equations. The other two ssGBLUP
204 evaluations were MF models that had eight MF, and the pedigree relationship matrices were
205 based on $\mathbf{\Gamma}_8$ (ssGBLUP $_{\mathbf{\Gamma}_8}$) or $\mathbf{\Gamma}_{8\text{MAF}}$ (ssGBLUP $_{\mathbf{\Gamma}_{8\text{MAF}}}$). Genetic variance parameters from the
206 model with unrelated founders were used to estimate corresponding parameters for the model

207 with MF. The variance of breeding values in base population descending from MF ($\sigma_{a,k}^2$) in
208 ssGBLUP $_{\Gamma_8}$ and ssGBLUP $_{\Gamma_{8MAF}}$ models were calculated using the scaling parameter k , i.e.,
209 $\sigma_{a,k}^2 = \sigma_a^2/k$, where $k = (1 + \text{tr}(\Gamma)/(2n) - \mathbf{1}'\Gamma\mathbf{1}/n^2)$ and $\text{tr}(\Gamma)$ is the sum of diagonal
210 elements of the Γ matrix (Legarra et al. 2015).

211 *Comparisons*

212 Two traditional ssGBLUP evaluations were computed using different numbers of UPG, and
213 two MF-based ssGBLUP evaluations were computed using different Γ matrices and
214 inbreeding coefficients. We present the two Γ matrices such that the direct effect of the MAF
215 threshold marker selection is seen in elements of the Γ matrices. The MF approach is
216 expected to give more similar pedigree and genomic relationship matrices than the traditional
217 pedigree and genomic relationship matrices. In addition, the off-diagonal elements in the
218 pedigree relationship matrix by the MF approach are expected to be higher than in the
219 traditional pedigree relationship matrix. We assessed differences in the diagonal elements
220 (related to the definition of inbreeding) and off-diagonals (related to relatedness) of \mathbf{A}_{22}^{Γ} ,
221 \mathbf{A}_{22} , \mathbf{G}_{05} , and \mathbf{G}_{PvR1} by correlations and mean differences between these matrices. To
222 identify differences in trends of diagonals to the pedigree and genomic matrices (that are
223 related to breeding selection and changes in inbreeding), average diagonal elements of \mathbf{A}_{22}^{Γ}
224 \mathbf{G}_{05} , \mathbf{G}_{PvR1} , and \mathbf{A}_{22} were plotted by birth year.

225 The two UPG definitions and two MF Γ matrices gave four sets of ssGBLUP predictions.
226 Validation tests used GEBV from the ssGBLUP evaluations separately from the groups of
227 genotyped bulls and cows. Approximately 80% of bulls born in 1990 to 2014 were
228 genotyped. Thus, differences between the ssGBLUP models may be largest in the genetic
229 trends of the bulls. Averages and standard deviation of selected bull GEBVs by birth year
230 were plotted for comparison purposes. The bulls selected for plotting had at least 10

231 daughters each. Average cow GEBVs by birth year were plotted using GEBVs from all cows
232 to illustrate the genetic trend in the general population.

233 **RESULTS AND DISCUSSION**

234 *Elements of Γ , A_{22} , G_{05} , G_{PvR1} , and A_{22}^{Γ}*

235 Table 1 has elements of the Γ_8 and Γ_{8MAF} matrices. Elements of the Γ_{8MAF} matrix were
236 slightly lower than corresponding elements in the Γ_8 matrix. All diagonal elements in the Γ
237 matrices were less than one, which corresponds to negative inbreeding of MF (Table 2)
238 calculated as $F = \gamma - 1$, where γ is the relationship across gametes (diagonal element of Γ).
239 All elements in the calculated Γ_8 and Γ_{8MAF} matrices were from 0.452 to 0.797.

240 Because the MF were partially formed by breed, the greater than zero off-diagonal elements
241 suggest shared genetics between breeds. Average mean relationship between the RDC and
242 HOL metafounders was 0.564 and 0.473 in Γ_8 and Γ_{8MAF} , respectively. Off-diagonal
243 elements of the Γ matrix between Holstein and Jersey cattle in Legarra et al. (2015) was 0.48,
244 which is close to the value we obtained in Γ_{8MAF} . They calculated the Γ matrix using
245 published statistics in VanRaden et al. (2011), which included only SNP markers with MAF
246 ≥ 0.05 (Wiggans et al., 2009). The self-relationships in the HOL and RDC metafounders in
247 our study were also comparable to 0.55 presented for the HOL and Jersey breeds in Legarra
248 et al. (2015). In our study, an exception to this was the RDC < 1970 group, which had a
249 diagonal value of 0.618 and 0.719 in Γ_{8MAF} and Γ_8 , respectively. The larger diagonal value in
250 the oldest RDC group may be due to changes in the Finnish RDC breeding program. Before
251 1970, breeding in the RDC group was mostly limited to Ayrshire cattle with only a low
252 number of imported animals. After 1970, importation began changing the population to more
253 resemble a mixed Nordic RDC breed. Diagonal elements in the group of other breeds were

254 high in both of the $\mathbf{\Gamma}$ matrices (0.740 and 0.797). This may be due to the influence of Finn
255 Cattle having only a small number of animals, which may produce unreliable AF estimates.

256 Table 3 shows correlations between (off-)diagonal elements of \mathbf{A}_{22} , \mathbf{G}_{05} , \mathbf{G}_{PvR1} , $\mathbf{A}_{22}^{\Gamma_8}$, and
257 $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ matrices. Constructing \mathbf{A}_{22} using $\mathbf{\Gamma}_8$ and $\mathbf{\Gamma}_{8MAF}$ increased the correlation between the
258 diagonal elements of \mathbf{G}_{05} and \mathbf{A}_{22} from 0.66 to 0.76. The diagonal element correlation
259 between elements of $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ and \mathbf{A}_{22} was higher (0.84) than between $\mathbf{A}_{22}^{\Gamma_8}$ and \mathbf{A}_{22} (0.81).
260 The correlation between diagonal elements of \mathbf{G}_{PvR1} and \mathbf{A}_{22} decreased from 0.53 to 0.33 and
261 0.37 for $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ and \mathbf{A}_{22} , respectively. Despite the high correlation of 0.99 between the
262 diagonal elements of $\mathbf{A}_{22}^{\Gamma_8}$ and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$, average diagonal elements by the birth year of an
263 animal (Figure 1) were at a higher level for $\mathbf{A}_{22}^{\Gamma_8}$ than for $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ or \mathbf{G}_{05} . Average diagonal
264 elements for both augmented matrices ($\mathbf{A}_{22}^{\Gamma_8}$ and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$) were at the same level as \mathbf{G}_{05} , i.e.,
265 from 1.30 to 1.38, while the average diagonals of \mathbf{A}_{22} and \mathbf{G}_{PvR1} were in range from 0.98 to
266 1.08. According to the summary statistics in Table 4, values for the off-diagonal elements of
267 the pedigree relationship matrix \mathbf{A}_{22} increased when using $\mathbf{\Gamma}$ to make \mathbf{A}_{22}^{Γ} . Hence, all
268 elements in the \mathbf{G}_{05} , $\mathbf{A}_{22}^{\Gamma_8}$, and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ matrices were higher on average than those in the \mathbf{A}_{22}
269 and \mathbf{G}_{PvR1} matrices. Interestingly, both the diagonal and off-diagonal element mean,
270 minimum, and maximum values of \mathbf{G}_{05} and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ agreed very well.

271 Average inbreeding coefficients in the \mathbf{A}_{22} and \mathbf{G}_{05} matrices were 0.02 and 0.31,
272 respectively. This difference of 0.29 was close to the 0.272 reported in VanRaden et al.
273 (2011) for HOL cattle (0.056 for \mathbf{A}_{22} and 0.328 for \mathbf{G}_{05}). The average inbreeding coefficient
274 increased from 0.02 in \mathbf{A}_{22} to 0.34 and 0.29 in $\mathbf{A}_{22}^{\Gamma_8}$ and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$, respectively. Following
275 Legarra et al. (2015), a diagonal element value less than one in the $\mathbf{\Gamma}$ matrix means a negative
276 individual inbreeding coefficient for MF. In all RDC MF, all elements of $\text{diag}(\mathbf{\Gamma})-1$ ranged

277 from -0.38 to -0.43. We observed the highest self-relationships and corresponding MF
278 inbreeding coefficients in the other breed group, which could be explained by the relatively
279 closed small-scale selection program for FinnCattle.

280 Use of the Γ matrix to make the pedigree-based relationship matrix $\mathbf{A}_{22}^{\Gamma_8}$ or $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ increased
281 the correlation between elements of the pedigree and genomic relationship matrices when
282 compared to the correlation between traditionally formed matrices (\mathbf{G}_{PvR1} and \mathbf{A}_{22}).
283 Correlation between diagonal elements of $\mathbf{A}_{22}^{\Gamma_8}$ and \mathbf{G}_{05} , as well as between $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ and \mathbf{G}_{05} ,
284 was 0.76, which is higher than the correlation of 0.53 between the diagonal elements of
285 \mathbf{G}_{PvR1} and \mathbf{A}_{22} . Correlation between the off-diagonal elements of $\mathbf{A}_{22}^{\Gamma_8}$ ($\mathbf{A}_{22}^{\Gamma_{8MAF}}$) and \mathbf{G}_{05} was
286 0.91, which is a bit higher than the same correlation (0.89) between \mathbf{G}_{PvR1} and \mathbf{A}_{22} . Thus,
287 using the Γ matrix to form the relationship matrix lifted the diagonal elements of \mathbf{A}_{22}^{Γ} matrix
288 to the same level as in the \mathbf{G}_{05} matrix (Figure 1).

289 The average diagonal of the $\mathbf{A}_{22}^{\Gamma_8}$ matrix was at a higher level than the average diagonal of
290 the \mathbf{G}_{05} matrix (Figure 1). Use of the MAF threshold to make Γ_{8MAF} for $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ gave lower
291 average diagonal values than those in \mathbf{G}_{05} . In constructing the Γ_{8MAF} matrix, we deleted the
292 low MAF markers to omit markers with highly uncertain or erroneous AF estimates. This,
293 however, may lead to deleting nearby markers and accepting more markers from certain
294 regions of the genome, particularly if a MAF threshold value higher than 5% is used.
295 Consequently, AF from various MF may become more similar. For example, two breeds may
296 differ due to more intense selection in one of the breeds, leading to the MAF criterion
297 favoring unselected or highly polymorphic markers clustered in certain regions of the
298 genome. Consequently, the Γ matrix may show inflated covariances between the MF of these
299 breeds. Linkage Disequilibrium (**LD**) criteria, in which markers are chosen to minimize LD,
300 is an alternative approach to SNP pruning (Hill and Robertson, 1968). Patterns of LD are

301 widely used in marker data quality control and in the analysis of population history for
302 various species (Porto-Neto et al., 2014; Makina et al., 2015; Cañas-Álvarez et al., 2016).
303 Multiple studies have shown persistence in LD levels of various breeds and populations (de
304 Roos, 2008; Xu et al., 2019), making LD a potential tool for marker selection.

305 *ssGBLUP estimation & validation results*

306 The correction factor k used to calculate the variance of breeding values in base population
307 descending from metafounders ($\sigma_{a,k}^2$) in the GEBV calculations for $ssGBLUP_{\Gamma_8}$ and
308 $ssGBLUP_{\Gamma_{8MAF}}$ was 0.72 and 0.77, respectively. Averages and standard deviations of bull
309 GEBV by birth year are shown in Figures 2 and 3 and the average cow GEBV are shown in
310 Figure 4. We centered the average GEBV trends of cows and bulls, so that the mean GEBV
311 of animals born in 2009 equaled zero. Average bull GEBV in Figure 2 had a similar shape in
312 all the models. The SD level in Figure 3 for bulls born in 2012–2014 was 20 kg (3%) higher
313 in the MF models than in the UPG models. Average cow GEBV by birth year had a similar
314 shape in all models (Figure 4).

315 Validation test statistics for the approaches are shown in Table 5. Regression coefficients (\mathbf{b}_1)
316 were generally slightly higher using MF than UPG. In the bull validation set, we obtained
317 similar adjusted model reliability by $ssGBLUP_{8UPG}$, $ssGBLUP_{\Gamma_8}$, and $ssGBLUP_{\Gamma_{8MAF}}$, and the
318 gain was 0.04 in comparison to $ssGBLUP_{236UPG}$. In the cow validation set, the validation
319 reliabilities using MF were 0.01 higher than achieved by the UPG models. To exclude pre-
320 selection bias, we conducted the validation tests for bulls also using DYD computed from
321 $ssGBLUP_{236UPG}$. The adjusted model reliabilities did not change from those in Table 5.

322 Genetic trends in GEBV from the UPG and MF models had a similar shape, showing no
323 effect of the alternative group or founder definitions. We assumed that the inadequate

324 definition of groups would reduce the genetic trend estimate (Tsuruta et al., 2014) but this
325 was not observed. Each of the bulls included in the yearly means in Figures 2 and 3 had at
326 least 10 daughters and, therefore, may be less affected by MF. Perhaps ssGBLUP predictions
327 where most of the sires are genotyped are robust against the definition of UPG or MF. Meyer
328 and Tier (2018) reported a slightly higher estimated genetic trend with the MF approach
329 compared to ssGBLUP without groups. However, females were the most often genotyped
330 group in their data. Also, the SDs of the GEBV were fairly similar between all evaluations
331 (Figure 3). The unstandardized genetic levels in the MF models were at a higher level
332 compared to the UPG models. This difference did not affect the animal rankings by GEBV
333 but indicate that the models defined base populations differently. We observed a high
334 correlation of bull GEBVs between the MF model and the original 236 UPG model (0.972),
335 while correlation of GEBVs between the MF model and the 8 UPG model was much lower
336 (0.931; correlations not given in Tables).

337 We used pedigree-based UPG in the ssGBLUP model via incomplete QP transformation
338 (Quaas and Pollak, 1981), i.e. QP transformation for \mathbf{A}^{-1} instead of \mathbf{H}^{-1} . In case of a multi-
339 breed structure, i.e. for the joint Nordic (Denmark, Finland, Sweden) RDC genetic
340 evaluation, Matilainen et al. (2018) proposed to use QP transformation in \mathbf{H}^{-1} (Misztal et al.,
341 2013). Bradford et al. (2019) observed that the incomplete QP transformation in ssGBLUP
342 may be applied successfully by accounting for \mathbf{A}^{-1} only, when a purebred population is
343 analyzed. The MF approach used in this study could be a smooth way to implement the
344 ssGBLUP model for the joint Nordic evaluation.

345 *Estimation of allele frequencies*

346 Defining the base population is the greatest challenge in the MF approach. We focused on
347 two issues: the number of MF and the genetic change in time. Simply replacing current UPG

348 by MF is often impossible in genetic evaluations of large commercial populations, which
349 have many UPG and animals with missing parents. We combined all UPG by breed and split
350 the RDC-based UPG by decade to form eight MF. For the HOL and OTHER breeds, the
351 limited number of animals and absence of phenotypic data were the key reasons for using
352 only one MF per breed. By using multiple MF in RDC, we could account for a possible
353 change in AF with time.

354 Base population AF for the MF are needed to calculate the Γ matrix. Garcia-Baccino et al.
355 (2017) presented three approaches for estimating base population AF to be used for
356 populations with crossbred animals. All of these methods use genotypes and a pedigree
357 relationship matrix or matrices. We used the genetics group model utilizing GLS. An
358 alternative GLS approach allows differences between gene content variances across breeds
359 and relies on a multi-breed model presented in Garcia-Cortes et al. (2006). All the pedigree-
360 based approaches only need the pedigree of ancestors to the genotyped animals, and the base
361 population groups are defined by MF through pedigree information. However, the
362 unbalanced distribution of genotyped animals to UPG or MF in the full pedigree affects all
363 base population AF estimation methods that rely on the pedigree relationship matrix.

364 In our study, a major part of the genotyped animals (75%) contributed to the oldest RDC
365 group (RDC < 1971) when the full pedigree was used, although most of the genotyped
366 animals (90.6%) were born after 2000. Thus, the contribution gained from genotypes of
367 animals born in 2000–2016 to the recent year groups would be small and would depend on
368 pedigree incompleteness. Consequently, the base population AF of the oldest RDC groups
369 would be well estimated with, possibly, a small influence from young animal genotypes. To
370 solve these issues in the base population AF estimation for the MF, we limited the length of

371 the pedigree of genotyped animals by only accepting ungenotyped animals with genotyped
372 offspring.

373 In our study, we calculated the base population AF of HOL and the other breeds group using
374 the ancestor structure of genotyped RDC animals only. We tested the applicability of the
375 chosen GLS approach by estimating an additional $\mathbf{\Gamma}$ matrix ($\mathbf{\Gamma}_{RDC\&HOL}$, Table 6). The matrix
376 was calculated using HOL AF (Koivula 2019, personal communication). We estimated these
377 AF with HOL breed genotypes and the pedigree used in Koivula et al. (2018). The estimated
378 $\mathbf{\Gamma}_{RDC\&HOL}$ was compared with the presented $\mathbf{\Gamma}_8$ and $\mathbf{\Gamma}_{8MAF}$ matrices (Table 1), which were
379 only based on genotyped RDC animals. The closeness of the average diagonal values in the
380 HOL MF of $\mathbf{\Gamma}_{RDC\&HOL}$ (0.615), $\mathbf{\Gamma}_8$ (0.661), and $\mathbf{\Gamma}_{8MAF}$ (0.593) suggest that we were able to
381 estimate the $\mathbf{\Gamma}$ matrices fairly well without including the pure HOL population genotypes. In
382 addition, the MAF-based marker selection gave the closest value to the HOL genotypes-
383 derived value. Using the truncated pedigree is one possible reason for the good estimation of
384 HOL AF using RDC data. The aim of the pedigree truncation was to distribute available
385 genotypes evenly across MF. Pruning the pedigree appeared to solve two important
386 problems: unequal distribution of genotyped animals across MF and the mixture of AF breed
387 groups.

388 Off-diagonal elements of the $\mathbf{\Gamma}$ matrix suggested fairly high similarity between all founder
389 groups. We tested a $\mathbf{\Gamma}$ matrix where the off-diagonal elements were half of those in the
390 estimated $\mathbf{\Gamma}$ matrix (results not shown). This half-reduced off-diagonal element $\mathbf{\Gamma}$ matrix
391 nearly gave the same GEBVs solutions, with a correlation of 0.998. Thus, for this data set,
392 the MF-based ssGBLUP evaluation does not seem to be very sensitive to the off-diagonal
393 element values in the $\mathbf{\Gamma}$ matrix. Further work is needed to ascertain that this can be
394 generalized to data sets with more genotyped animals and different population structure.

395 We observed differences in the Γ matrix depending on the set of markers used to estimate the
396 Γ matrix. When markers were required to have an MAF above a certain limit, values in the Γ
397 matrix were lower than when all the markers were used. This is to be expected because the Γ
398 matrix is estimated by the variance of AF and the MAF threshold reduced range of marker
399 AF is used to calculate the variance. The case is similar to that in Chen et al. (2011) where
400 increasing the MAF threshold in the marker selection decreased the values of (off-)diagonal
401 elements in the genomic relationship matrix. The Γ matrix is a function of the chosen MAF
402 threshold as a consequence of the marker selection. We must therefore be careful when
403 making interpretations of values in the estimated Γ matrix. For example, the MAF threshold
404 was applied to all of the RDC-based MF, but the set of selected markers will change if the
405 HOL animals have genotypes.

406 The pedigree pruning approach allowed estimation of base population AF for the breed
407 groups despite all the genotyped animals being from the RDC breeding program. Still, it is
408 impossible to model AF changes in base populations and MF before the first genotyped
409 parent generations. One possibility is to assume that the AF changes have continuity and that
410 the changes can also be extrapolated to early years before the genotyping began. Then the
411 variance structures of Γ in the observed base populations, i.e. parents of genotyped animals,
412 could be extended to describe variances of unobservable MF using covariance functions
413 (Kirkpatrick et al. 1994) with appropriate breeds and birth years.

414

415 **CONCLUSIONS**

416 We tested the metafounder approach on RDC data with a complicated multi-breed structure.
417 The original 236 UPG were replaced by eight MF and tested in ssGBLUP evaluation. Use of
418 MF increased correlation between elements of the pedigree and genomic relationship

419 matrices. Introduction of MAF-based marker selection before computing the Γ matrix for the
420 MF gave $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ an advantage over the original $\mathbf{A}_{22}^{\Gamma_8}$ in correlations with elements of the
421 genomic relationship matrix. The reduction of UPG groups from 236 to eight reduced the
422 inflation in the predictions and increased validation accuracy. The GEBVs from models with
423 eight MF gave almost the same validation results and genetic trends as the eight UPG. Future
424 development should focus on ways to increase the number of MF closer to the number of
425 UPG.

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615 **Table 1.** Estimated Γ_8 (lower) and Γ_{8MAF} (upper) triangle for the metafounders. The diagonal
 616 includes diagonals (i.e. self-relationships of metafounders) of Γ_8 (in brackets) and Γ_{8MAF} .

	RDC ¹ <1970	RDC ¹ 1971– 1980	RDC ¹ 1981– 1990	RDC ¹ 1991– 2000	RDC ¹ 2001– 2010	RDC ¹ 2011– 2016	HOL ¹	OTHER ¹
RDC ¹ <1970	0.618 (0.719)	0.555	0.563	0.563	0.566	0.566	0.471	0.453
RDC ¹ 1971– 1980	0.659	0.569 (0.670)	0.566	0.561	0.564	0.562	0.473	0.454
RDC ¹ 1981– 1990	0.668	0.670	0.609 (0.710)	0.588	0.589	0.585	0.473	0.452
RDC ¹ 1991– 2000	0.667	0.664	0.690	0.587 (0.689)	0.585	0.583	0.473	0.455
RDC ¹ 2001– 2010	0.671	0.667	0.692	0.688	0.598 (0.701)	0.597	0.474	0.452
RDC ¹ 2011– 2016	0.671	0.666	0.688	0.686	0.699	0.603 (0.705)	0.474	0.453
HOL ¹	0.563	0.564	0.564	0.564	0.566	0.566	0.593 (0.661)	0.479
OTHER ¹	0.544	0.544	0.544	0.545	0.544	0.545	0.552	0.740 (0.797)

617 ¹Red dairy cattle (RDC) has been divided into metafounders by birth year, Holstein (HOL)
 618 cattle has one metafounder, and the other breeds (OTHER) have been combined into one
 619 metafounder.

620

621

622 **Table 2.** Inbreeding coefficients of metafounders calculated using Γ_8 and Γ_{8MAF} .

Groups ¹	Γ_8	Γ_{8MAF}
RDC <1970	-0.28	-0.38
RDC 1971–1980	-0.33	-0.43
RDC 1981–1990	-0.29	-0.39
RDC 1991–2000	-0.31	-0.41
RDC 2001–2010	-0.29	-0.40
RDC 2011–2016	-0.29	-0.39
HOL	-0.34	-0.40
OTHER	-0.34	-0.26

623 ¹Red dairy cattle (RDC) has been divided into metafounders by birth year, Holstein (HOL)
624 cattle has one metafounder, and the other breeds (OTHER) have been combined into one
625 metafounder.

626

627 **Table 3.** Correlation of diagonal (upper triangle) and off-diagonal (lower triangle) elements
 628 of \mathbf{A}_{22} , \mathbf{G}_{05} , \mathbf{G}_{PvR1} , $\mathbf{A}_{22}^{\Gamma_8}$, and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$.

	\mathbf{A}_{22}	$\mathbf{A}_{22}^{\Gamma_8}$	$\mathbf{A}_{22}^{\Gamma_{8MAF}}$	\mathbf{G}_{05}	\mathbf{G}_{PvR1}
\mathbf{A}_{22}	1	0.81	0.84	0.66	0.53
$\mathbf{A}_{22}^{\Gamma_8}$	0.89	1	0.99	0.76	0.33
$\mathbf{A}_{22}^{\Gamma_{8MAF}}$	0.92	0.99	1	0.76	0.37
\mathbf{G}_{05}	0.83	0.91	0.91	1	0.70
\mathbf{G}_{PvR1}	0.89	0.86	0.88	0.88	1

629

630 **Table 4.** Mean, minimum (Min), and maximum (Max) element values of \mathbf{A}_{22} , \mathbf{G}_{05} ,
 631 \mathbf{G}_{PvR1} , $\mathbf{A}_{22}^{\Gamma_8}$, and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ from diagonal and off-diagonal.

Elements	Matrix	Mean	Min	Max
Diagonal	\mathbf{A}_{22}	1.02	1.00	1.29
	\mathbf{G}_{05}	1.31	1.24	1.48
	\mathbf{G}_{PvR1}	1.01	0.91	1.30
	$\mathbf{A}_{22}^{\Gamma_8}$	1.35	1.27	1.51
	$\mathbf{A}_{22}^{\Gamma_{8MAF}}$	1.31	1.23	1.50
Off-diagonal	\mathbf{A}_{22}	0.07	0.06	0.81
	\mathbf{G}_{05}	0.63	0.47	1.29
	\mathbf{G}_{PvR1}	0.05	-0.11	0.99
	$\mathbf{A}_{22}^{\Gamma_8}$	0.72	0.54	1.22
	$\mathbf{A}_{22}^{\Gamma_{8MAF}}$	0.62	0.45	1.16

632

633 **Table 5.** GEBV validation test regression coefficients and validation reliabilities of single-
634 step GBLUP GEBVs for genotyped bulls and cows.

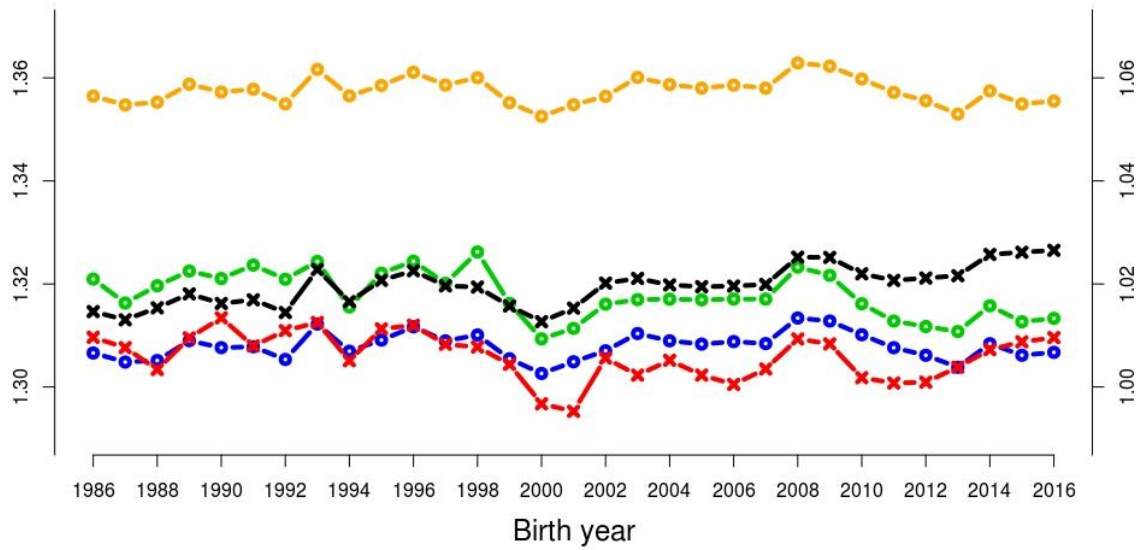
Validation set	Model ¹	b_0	SE	b_1 ²	SE	R^2 ³	R_{EDC}^2 ³
Bulls	ssGBLUP _{236UPG}	70	16	0.61	0.06	0.23	0.27
	ssGBLUP _{8UPG}	18	16	0.73	0.06	0.26	0.31
	ssGBLUP _{Γ_8}	-22	22	0.72	0.06	0.26	0.31
	ssGBLUP _{Γ_{8MAF}}	-27	23	0.73	0.06	0.26	0.31
Cows	ssGBLUP _{236UPG}	118	9	0.89	0.03	0.16	0.36
	ssGBLUP _{8UPG}	150	8	0.89	0.03	0.16	0.36
	ssGBLUP _{Γ_8}	12	13	0.90	0.03	0.16	0.37
	ssGBLUP _{Γ_{8MAF}}	-0.2	13	0.93	0.04	0.16	0.37

635 ¹Model ssGBLUP_{236UPG} (ssGBLUP_{8UPG}) had 236 (8) unknown parent groups; ssGBLUP _{Γ_8} had 8
636 metafounders with the metafounder Γ matrix calculated using all markers; ssGBLUP _{Γ_{8MAF}} used
637 markers with a minor allele frequency ≥ 0.05 in the metafounder Γ matrix calculation.

638 ²Regression coefficient b_1 in equation $DYD = b_0 + b_1 * GEBV$ for the bulls has been multiplied by
639 2.

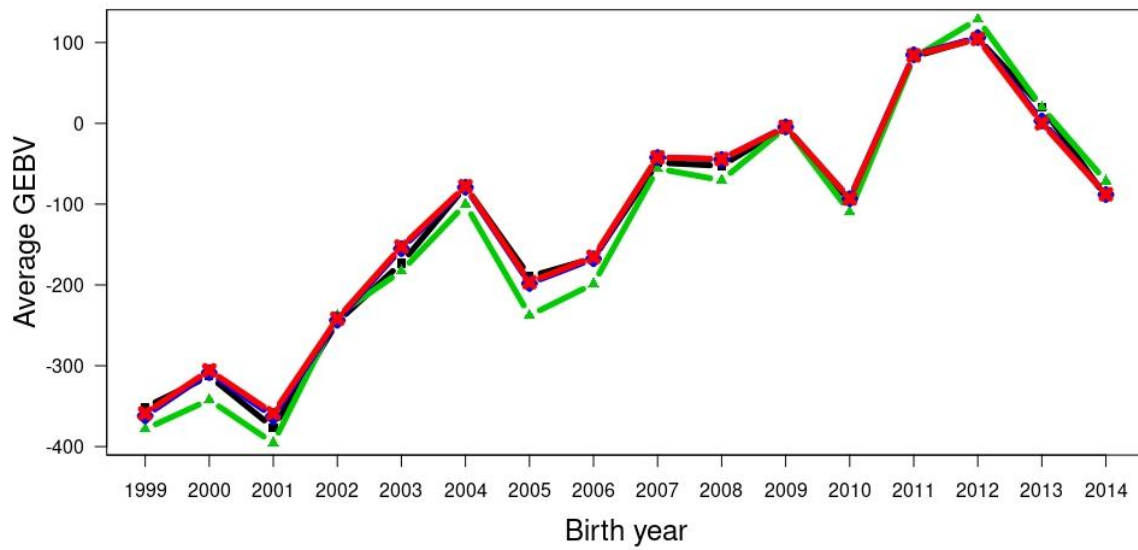
640 ³ R^2 is the coefficient of determination from the validation regression, R_{EDC}^2 is adjusted by the average
641 reliability of phenotypes in the validation group.

642



643

644 **Figure 1.** Average diagonal elements of \mathbf{A}_{22} (black cross), \mathbf{G}_{PvR1} (red cross), \mathbf{G}_{05} (green
645 circles), $\mathbf{A}_{22}^{\Gamma_8}$ (orange circles), and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ (blue circles) by the birth year of an animal. The
646 left side of the y-axis has a scale for \mathbf{G}_{05} , $\mathbf{A}_{22}^{\Gamma_8}$ and $\mathbf{A}_{22}^{\Gamma_{8MAF}}$ and the right side has a scale for
647 \mathbf{A}_{22} and \mathbf{G}_{PvR1} .



648

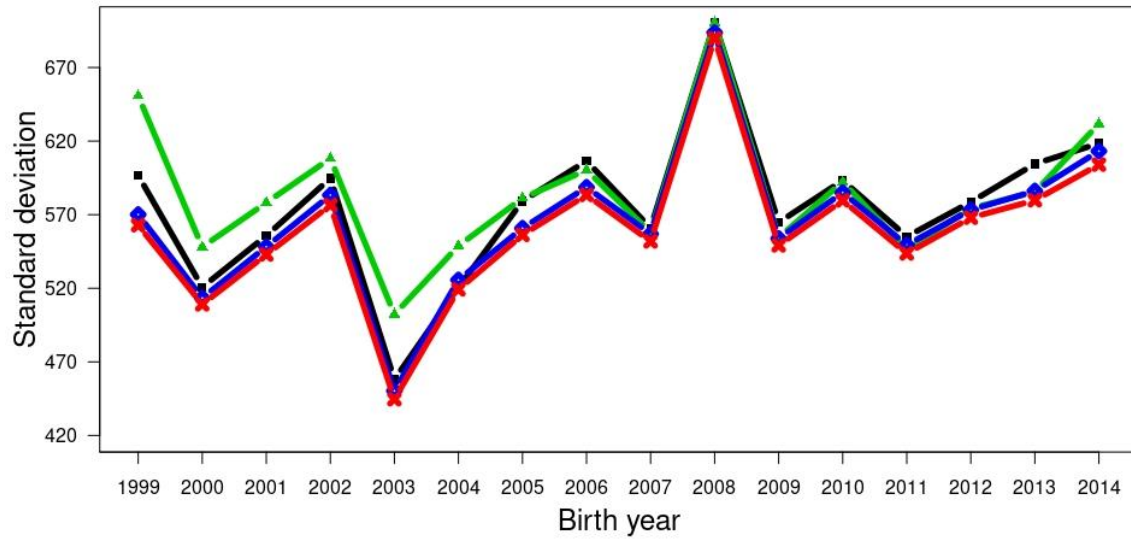
649 **Figure 2.** Average genomic breeding value of bulls by birth year in 305-d milk yield (kg).

650 Each bulls had at least 10 daughters. The lines above each other are from the unknown parent

651 group models ssGBLUP_{236UPG} (black square) and ssGBLUP_{8UPG}, (green triangle) and from the

652 metafounders models ssGBLUP_{T8} (blue diamond) and ssGBLUP_{T8MAF} (red cross).

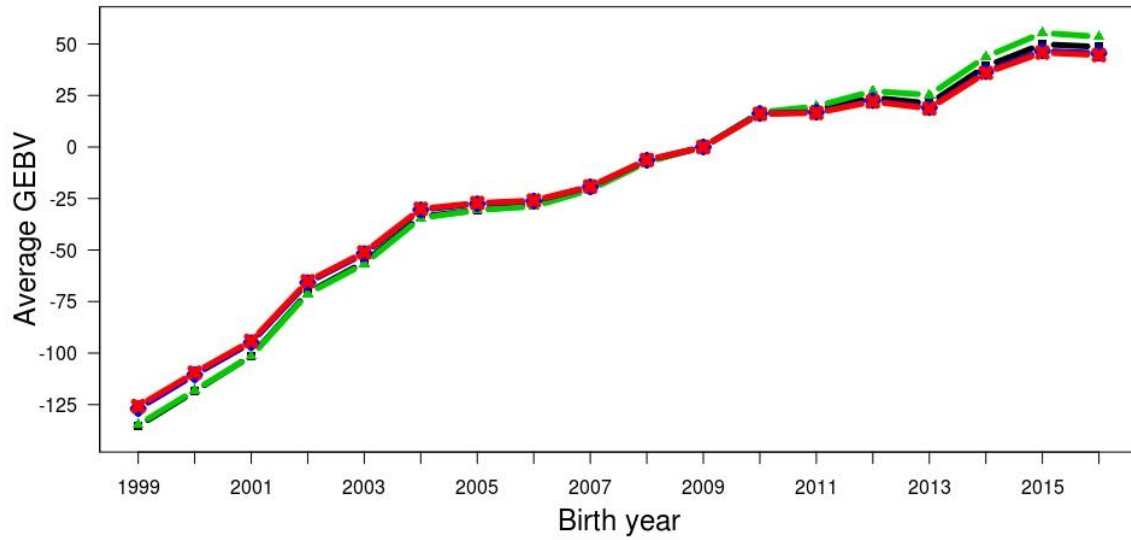
653



654

655 **Figure 3.** Standard deviation of bull genomic breeding values by birth year in 305-d milk
 656 yield, kg. Each bull had at least 10 daughters. Trends are from the unknown parent group
 657 models ssGBLUP_{236UPG} (black square) and ssGBLUP_{8UPG}, (green triangle) and from the
 658 metafounders models ssGBLUP_{T8} (blue diamond) and ssGBLUP_{T8MAF} (red cross).

659



660

661 **Figure 4.** Average genomic breeding value of cows by birth year in 305-d milk yield (kg).

662 The lines above each other are from the unknown parent group models ssGBLUP_{236UPG}

663 (black square) and ssGBLUP_{8UPG}, (green triangle) and from the metafounders models

664 ssGBLUP_{T8} (blue diamond) and ssGBLUP_{T8MAF} (red cross).

665

666

667 Table 6. Gamma matrix created using base population allele frequencies calculated from Red
 668 Dairy Cattle (RDC) and Holstein (HOL) cattle genotypes.

	RDC ¹ <1970	RDC ¹ 1971– 1980	RDC ¹ 1981– 1990	RDC ¹ 1991– 2000	RDC ¹ 2001– 2010	RDC ¹ 2011– 2016	OTHER ¹	HOL ¹ <1970	HOL ¹ 1970– 1980	HOL ¹ 1981– 1990	HOL ¹ 1991– 2000	HOL ¹ 2001– 2010	HOL ¹ 2011– 2016
RDC ¹ <1970	0.825	0.613	0.602	0.604	0.604	0.603	0.536	0.521	0.533	0.524	0.516	0.515	0.512
RDC ¹ 1971– 1980		0.638	0.629	0.629	0.627	0.622	0.539	0.521	0.539	0.526	0.516	0.515	0.512
RDC ¹ 1981– 1990			0.665	0.665	0.657	0.648	0.543	0.520	0.538	0.525	0.515	0.514	0.512
RDC ¹ 1991– 2000				0.670	0.664	0.654	0.543	0.520	0.538	0.525	0.516	0.515	0.512
RDC ¹ 2001– 2010					0.676	0.668	0.542	0.520	0.538	0.525	0.515	0.515	0.512
RDC ¹ 2011– 2016						0.666	0.547	0.521	0.539	0.526	0.517	0.516	0.514
OTHER ¹							0.813	0.511	0.525	0.518	0.509	0.507	0.503
HOL ¹ <1970								0.581	0.559	0.579	0.586	0.587	0.589
HOL ¹ 1970– 1980									0.574	0.567	0.562	0.561	0.560
HOL ¹ 1981– 1990										0.595	0.594	0.595	0.598
HOL ¹ 1991– 2000											0.613	0.615	0.621
HOL ¹ 2001– 2010												0.628	0.638
HOL ¹ 2011– 2016													0.690

669 ¹RDC and HOL cattle have been divided into metafounders by birth year, while the other
 670 breeds (OTHER) have been combined into one metafounder.

671