

Genomic selection for any dairy breeding program via optimised investment in phenotyping and genotyping

Jana Obšteter^{1*}, Janez Jenko², John M. Hickey³, and Gregor Gorjanc^{3,4}

¹Department of Animal Science, Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000 Ljubljana, Slovenia

²Geno Breeding and A.I. Association, Storhamargata 44, 2317 Hamar, Norway

³The Roslin Institute and Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter Bush, Midlothian, EH259RG, United Kingdom

⁴Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, 1000 Ljubljana, Slovenia

*Jana Obšteter, Agricultural Institute of Slovenia, Department of Animal Science, Hacquetova ulica 17, 1000 Ljubljana, Slovenia

E-mail addresses:

J. O.: jana.obsteter@kis.si

J. J.: janez.jenko@geno.no

J. M. H.: john.hickey@roslin.ed.ac.uk

G. G.: gregor.gorjanc@roslin.ed.ac.uk

19 Abstract

20 **Background:** This paper evaluates the potential of maximizing genetic gain in dairy cattle breeding
21 programmes by optimizing investment into phenotyping and genotyping. Conventional dairy
22 breeding programmes focus on phenotyping selection candidates or their close relatives to increase
23 selection accuracy, since this is the main driver of genetic gain and quality assurance for producers.
24 Genomic selection decoupled phenotyping and selection and through this enabled increased genetic
25 gain per year compared to the conventional selection. However, genomic selection requires a large
26 initial investment, which limits the adoption of genomic selection for some breeding programmes.
27 The aim of this study was to evaluate the potential of maximizing genetic gain by optimizing
28 investment into phenotyping and genotyping in in a case-study and to provide suggestions for other
29 dairy breeding programmes.

30 **Methods:** We simulated a case-study of a small dairy population with a number of scenarios under
31 equal available resources. The conventional progeny testing scenario had 11 phenotype records per
32 lactation. In genomic scenarios, we reduced phenotyping to collect between 10 and 1 record per
33 lactation and invested the saved resources into genotyping. We tested these scenarios in settings
34 with or without initial training population for genomic selection.

35 **Results:** Reallocating a part of phenotyping resources to genotyping increased genetic gain
36 compared to the conventional scenario regardless of the amount and relative cost of phenotyping,
37 and the availability of initial training population. We further increased the genetic gain by
38 increasing investment in genotyping, despite reduced phenotyping, with high-genotyping scenarios
39 not even using the total available resources. Compared to the conventional scenario, genomic
40 scenarios also increased accuracy for young non-phenotyped male and female candidates, and cows.

41 **Conclusions:** This study shows that breeding programmes should optimise investment into
42 phenotyping and genotyping to maximise return on investment. We argue that phenotyped animals

43 should be extensively genotyped to increase the impact of phenotyping investments. These
44 conclusions suggest that any dairy breeding programme can implement genomic selection without
45 increasing the level of investment.

46 Background

47 This paper evaluates the potential of maximizing genetic gain in dairy cattle breeding programmes
48 by optimizing investment into phenotyping and genotyping. All breeding programmes strive to
49 maximize genetic gain, which is a function of selection intensity, accuracy of selection, genetic
50 variation, and generation interval. The conventional dairy breeding programme uses a long and
51 expensive progeny testing, which limits selection intensity. This programme allocates the majority
52 of resources into phenotyping to increase the accuracy of sire selection, since this is the main driver
53 of genetic gain. Genomic selection [1, 2] (Meuwissen et al., 2001; Schaeffer, 2006), on the other
54 hand, achieves genetic gain mainly through substantially reduced generation interval, increased
55 selection intensity on the male side, and increased accuracy of selection for young animals [2, 3]
56 (Schaeffer, 2006; Obšteter et al., 2019). Despite lower accuracy of sire selection compared to the
57 conventional progeny testing, genomic selection doubles the rate of genetic gain per year in dairy
58 cattle [4] (Wiggans et al., 2017).

59 All breeding programmes operate with a certain amount of resources allocated between breeding
60 activities with the aim to maximise return on investment. Genomic selection is now a de-facto
61 standard in well-resourced breeding programmes, but is still challenging to implement for some
62 breeding programmes. The major hurdle is the large initial investment in genotyping to establish a
63 training population, though updating this population can also be challenging. These breeding
64 programs need to evaluate priorities and could optimise phenotyping and genotyping to maximise
65 return on investment.

66 The accuracy of conventional pedigree-based estimates of breeding values increases with increasing
67 heritability and increasing number of phenotype records per animal or its closest relatives (e.g.,
68 [5] Mrode, 2005). To illustrate, assume a female-expressed trait with the heritability of 0.25 and
69 progeny testing in a population with 100 sires each tested on 100 daughters (10,000 cows in total).
70 Collecting 10 phenotype records per daughter gives the accuracy of 0.98 for progeny tested sires,

0.86 for cows, and 0.66 for non-phenotyped progeny. If we decrease the number of phenotype records per daughter to five, two, or one, the accuracy respectively decreases to 0.97, 0.96, or 0.93 for sires; to 0.81, 0.70, or 0.62 for cows; and to 0.64, 0.59, or 0.56 for non-phenotyped progeny. This example shows diminishing returns with repeated phenotype records and a scope for optimizing return on investment. Namely, at the extreme we reduced phenotyping 10x, which reduced accuracy only for 0.04 in sires and 0.10 in non-phenotyped progeny.

We could invest the resources saved from reducing the number of phenotype records per daughter into phenotyping more daughters. Assuming resources for 100,000 phenotypes and decreasing the number of phenotype records per daughter to five, two, or one respectively enables phenotyping 200, 500, or 1,000 daughters per sire (100 sires). This change increases accuracy for sires to 0.99 in all cases, barely increases accuracy for cows, and respectively increases accuracy for non-phenotyped progeny to 0.64, 0.61, or 0.59.

The accuracy of genome-based estimates of breeding values also increases with increasing heritability and increasing number of phenotype records per genotyped animal, but also with increasing training population of phenotyped and genotyped animals, decreasing genetic distance between training and prediction individuals, and decreasing number of effective genome segments [6–10] (Daetwyler et al. 2008; Goddard, 2009; Habier et al., 2010; Clark et al, 2011; Goddard et al., 2011). The latter dictates linkage-disequilibrium between markers and causal loci, which drives accuracy of genomic evaluation and prediction. Recombination, mutation, migration, drift, and selection change linkage-disequilibrium and decrease the accuracy of genomic prediction across generations, particularly when the training population is not continually updated [1, 8, 11, 12] (Meuwissen et al., 2001; Calus, 2010; Habier et al., 2010; Wolc et al., 2011).

Following the previous example, assume 10,000 effective genome segments, trait heritability of 0.25, and a training population of 10,000 cows. Recording 10 phenotype values per cow gives the heritability of phenotype for training population of 0.78 and genomic prediction accuracy of 0.68

96 for non-phenotyped progeny [6](Daetwyler et al, 2008). Reducing the number of phenotype records
97 per cow to five, two, or one respectively reduces the heritability of phenotype for training
98 population to 0.66, 0.50, or 0.40, and genomic prediction accuracy to 0.64, 0.58, or 0.53. This
99 example again shows diminishing returns with replicated phenotyping and a scope for optimizing
100 return on investment also with genomic breeding programmes. Namely, at the extreme we reduced
101 phenotyping 10x, which reduced genomic prediction accuracy only for 0.11. Previous studies also
102 explored the value of adding a record to the training population when a number of records is already
103 available [13, 14] (Bijma, Recio). They concluded, that accuracy has a diminishing return
104 relationship with increasing the number of records in the training population, hence additional
105 phenotype is most valuable when the training population is small.

106 We could invest the resources saved from reducing the number of phenotype records per daughter
107 into genotyping. If we could increase the number of genotyped and phenotyped cows from 10,000
108 to 20,000, 50,000, or 100,000, each respectively phenotyped with five, two, or one record, we
109 would respectively increase the genomic prediction accuracy to 0.77, 0.86, or 0.91. While these
110 genomic prediction accuracies are lower than with progeny testing, shorter generation interval
111 enables larger genetic gain per unit of time [2](Schaeffer, 2006).

112 However, the above calculations assume we have resources to genotype and phenotype large
113 numbers of cows. In reality, breeding programmes consist of individuals with only phenotype,
114 genotype, or both types of information. To handle this, we can use single-step genomic prediction
115 that combines all phenotypic, pedigree, and genomic information and in turn increases prediction
116 accuracy even further [15–17](Gao et al., 2012, Gray et al., 2012; Lourenco et al., 2015).

117 The above examples indicate that repeated phenotyping could be an internal financial reserve that
118 enables any dairy breeding programme to implement genomic selection. In dairy breeding the most
119 repeatedly and extensively recorded phenotypes are milk production traits. There are different milk
120 recording methods that differ in the recording responsibility, sampling scheme, recording and

121 sampling frequency, and the number of milkings per day [18](ICAR, 2017). The recording interval
122 ranges from daily recording to recording every nine weeks, which translates to between 310 and 5
123 records per lactation. The different recording methods have different costs, which also vary
124 considerably between recording systems, countries, and even their regions. For example, some
125 organizations require payment of a participation fee plus the cost per sample, while others include
126 the fee in the sample cost, or cover the costs in other ways.

127 The aim of this study was to evaluate the potential of maximizing genetic gain by optimizing
128 investment into phenotyping and genotyping in dairy breeding programmes. Since milk recording is
129 an example of a repeated phenotype with diminishing returns, we aimed to optimize investment into
130 milk recording and genotyping. To this end we have compared a dairy breeding programme with
131 conventional progeny testing and genomic testing under equal available resources. To implement
132 genomic selection we reduced the number of milk records per cow per lactation and invested the
133 saved resources into genotyping. We compared these strategies in case-study with a small cattle
134 breeding programme where implementing genomic selection is challenging. The results show that
135 reallocating a part of phenotyping resources to genotyping increases genetic gain regardless of the
136 cost and amount of genotyping, and the availability of initial training population. The genetic gain
137 also increases with increasing investment into genotyping, despite reduced phenotyping.

138 **Methods**

139 The study aimed to evaluate the effect of different investment into phenotyping and genotyping
140 with a simulation of a case-study of a small dairy breeding programme. The simulation mimicked a
141 real dairy cattle population of ~30,000 animals analysed in our previous study [3] Obšteter et al.
142 (2019). We evaluated 36 genomic scenarios against the conventional scenario, all with equal
143 amount of available resources, but varying extent of phenotyping and genotyping. The conventional
144 scenario implemented progeny testing and collected 11 phenotype records per lactation, while
145 genomic scenarios reduced phenotyping and invested saved resources to genotyping. The genomic
146 scenarios differed in i) the number of phenotype records per cow per lactation; ii) the relative cost
147 of phenotyping and genotyping; and iii) the availability of an initial training population. All tested
148 scenarios were compared based on their genetic gain and accuracy of selection.

149 **Simulation of the base population, phenotype and historical breeding**

150 The simulation mimicked a small dairy cattle breeding programme of ~30,000 animals with
151 ~10,500 cows, where introduction of effective genomic selection is challenging. We use this
152 population as a case-study to optimize investment into phenotyping and genotyping. The breeding
153 programme aimed to improve dairy performance, which we simulated as a single polygenic trait.
154 For this we used a coalescent process to simulate whole-genome comprised of 10 cattle-like
155 chromosomes, each with 10^8 base pairs, 1,000 randomly chosen causal loci, and 2,000 randomly
156 chosen marker loci. We sampled the effects of causal loci from a normal distribution and calculated
157 animal's breeding value (a_i) for dairy performance (y_{ijkl}). We assigned permanent environment (p_i),
158 herd (h_j), herd-year (hy_{jk}), herd-test-day (htd_{jkl}), and residual environment (e_{ijkl}) effects to the trait:

$$159 \quad y_{ijkl} = a_i + p_i + h_j + hy_{jk} + htd_{jkl} + e_{ijkl}.$$

160 We sampled the permanent environment effects from a normal distribution with zero mean and
161 variance equal to the additive genetic variance (σ^2_A). We sampled herd, herd-year, and herd-test-day

162 effects each from a normal distribution with zero mean and variance of $1/3 \sigma_A^2$. Finally, we sampled
163 residual environment effects from a normal distribution with zero mean and variance of σ_A^2 . This
164 sampling scheme gave a trait with heritability 0.25 and repeatability of 0.50. With the simulated
165 genome and phenotype architecture we have initiated the dairy cattle breeding programme and ran it
166 for 20 years of conventional selection with progeny-testing based on 11 cow phenotype records per
167 lactation. The detailed parameters of the simulation are described in [3]Obšteter et al. (2019). In
168 summary, in the breeding programme we selected 3,849 out of 4,320 new-born females as cows and
169 139 as bull dams over their second, third, and fourth lactation. We generated 45 male calves from
170 elite matings and out of these chose 8 for progeny testing of which 4 were eventually selected as
171 elite sires. We made all selection decisions based on pedigree-based estimates of breeding values.
172 The 20 years represented historical breeding and provided a starting point for evaluating future
173 breeding scenarios, which we ran for additional 20 years.

174 Scenarios

175 We evaluated 36 genomic scenarios with varying the extent of phenotyping and genotyping against
176 the conventional scenario. All scenarios had equal amount of available resources. The conventional
177 scenario continued the breeding scheme from historical breeding. It used progeny testing and 11
178 phenotype records per lactation (named C11), corresponding to the standard ICAR recording
179 interval of 4 weeks [18]ICAR, 2017). We assumed that this scenario represented the total amount
180 of resources available for obtaining the data. We then created genomic scenarios that distributed the
181 total resources between phenotyping and genotyping - we reduced phenotyping and invested the
182 saved resources into genotyping. In the genomic scenarios we selected females as in the
183 conventional scenario and males based on genomic prediction. We varied the number of
184 genomically tested male candidates depending on the resources and always selected the best 5 as
185 elite sires solely on genomic prediction. We evaluated the genomic scenarios under a range of
186 factors: number of phenotype records per lactation, cost of genotyping, and the availability of an
187 initial training population.

188 Genomic scenarios reduced phenotyping of the conventional scenario and varied the number of
189 phenotype records per lactation between 10 and 1. The scenarios followed ICAR standards of 9, 8,
190 and 5 records per lactation, corresponding to recording intervals of 5, 6, and 9 weeks. Additionally,
191 we created three non-standard recording systems collecting 10, 2, and 1 records per lactation. We
192 named the scenarios as “GX” with X being the number of records per lactation. The reduction in
193 phenotyping and the relative cost of phenotyping to genotyping dictated the amount of saved
194 resources and therefore the number of genotyped animals (Table 1). We invested the saved
195 resources into genotyping females and males in ratio 7:1 based on our previous work [3] Obšteter et
196 al. (2019). We genotyped first parity cows. This maximized the accuracy of genomic prediction,
197 since it reduced the genetic distance between training and prediction population, prevented the loss
198 of information due to culled heifers, and minimized the time to obtain a phenotype. If the available
199 resources for genotyping females were larger than the cost of genotyping all first parity cows, we
200 did not reallocate the excess of resources to male genotyping. To maximise the genetic gain, we
201 genotyped male calves from elite matings and other high parent average matings.

202 Genomic scenarios next varied the relative cost of phenotyping (\$P) to genotyping (\$G). We
203 compared the cost of one genotype to the cost of 11 phenotype records per lactation. Based on a
204 survey of several breeding programmes, milk recording organizations, and genotyping providers we
205 have considered three cost ratios of \$P:\$G: 2:1, 1:1, and 1:2. Following the survey, we also
206 decreased the price of every additional milk recording, hence the first recording was the most
207 expensive and the cost of each subsequent control was 95% of the preceding control.

208 Lastly, we created scenarios with and without an initial training population for genomic prediction.
209 When we assumed an initial training population was available, we genotyped all active cows
210 (10,653) and progeny tested sires (100) before the first genomic evaluation. When initial training
211 population was not available, we yearly genotyped a designated number of first parity cows until
212 the training population reached 2,000 cows. Once we reached this goal, we started to genotype both
213 females and males as specified in Table 1. At that point we started genomic selection of males.

214 Estimation of breeding values

215 We selected the animals based on their estimated breeding values that we estimated with a pedigree
 216 or single-step genomic (Legarra et al., 2009) repeatability model with breeding value, permanent
 217 environment, and herd-year as random effects. We did not fit the herd-test-day effect as data
 218 structure of this small population did not enable its accurate estimation. We estimated breeding
 219 values once a year with blupf90 [19](Misztal et al, 2002) with default settings. In the estimation we
 220 included all available phenotype and pedigree records for all active, phenotyped, or genotyped
 221 animals and additional three generations of their ancestors. However, we used at most 25,000
 222 genotyped animals due to a maximum number of animals allowed in the non-commercial software
 223 version. When we accumulated more than 25,000 genotyped animals, we removed the oldest
 224 animals in favour of the latest genotyped cows and male selection candidates.

225 **Table 1. Number of genotyped animals per year by scenario and relative cost of phenotyping**
 226 **to genotyping.**

Relative cost	Scenario					
	G10	G9	G8	G5	G2	G1
\$P:\$G = 1:2	160 F	350 F	590 F	1610 F	3230 F	3850 F
	22 M	50 M	85 M	235 M	465 M	565 M
\$P:\$G = 1:1	310 F	700 F	1180 F	3230 F	3850 F	3850 F
	45 M	100 M	165 M	465 M	925 M	1125 M
\$P:\$G = 2:1	620 F	1400 F	2360 F	3850 F	3850 F	3850 F
	90 M	295 M	335 M	925 M	1845 M	2245 M

227 Scenarios are named “G” for genomic, followed by the number of phenotype records per lactation.
 228 The number of phenotype records and the relative cost of phenotyping to genotyping (\$P:\$G)
 229 dictated the number of genotyped animals. We genotyped females (F) and males (M) in 7:1 ratio.

230 Analysis of scenarios

231 All scenarios had equal amount of available resources. We compared the scenarios based on their
 232 final genetic gain, which indicated return on investment, and accuracy of selection. We measured

233 the genetic gain as an average true breeding value by year of birth and standardized it to have zero
234 mean and unit standard genetic deviation in the first year of comparison. We measured the accuracy
235 of breeding values as the mean correlation between true and estimated breeding values of the
236 evaluation years. We measured the accuracy separately for four groups of animals: i) male
237 candidates (genotyped and non-phenotyped); ii) sires (currently used in artificial insemination); iii)
238 females candidates (non-genotyped non-phenotyped); and iv) cows (all active phenotyped cows and
239 bull dams). We repeated simulation of the base population and each scenario 10 times and
240 summarised them with mean and standard deviation across the replicates. We used Tukey's multiple
241 comparison test to test the significance of the difference between means.

242 **Results**

243 Genomic scenarios increased the genetic gain compared to the conventional scenario regardless of
244 the number of phenotype records per lactation, relative cost of phenotyping to genotyping, and the
245 availability of an initial training population. Genomic scenarios with an existing initial training
246 population increased the genetic gain of the conventional scenario by up to 143%, despite reduced
247 phenotyping. The genetic gain further increased with increasing investment into genotyping, hence
248 more animals genotyped. Compared to the conventional scenario, implementing genomic selection
249 also increased the accuracy for non-phenotyped male and female candidates, and cows. Scenarios
250 without an initial training population showed the same trends for genetic gain and accuracy.
251 Although these scenarios had a slightly smaller genetic gain due to delayed implementation of
252 genomic selection, they still increased the genetic gain of the conventional scenario by up to 134%.

253 **Genetic gain with an initial training population**

254 **Table S1. Genetic gain by scenario, relative cost of phenotyping to genotyping, and availability**
255 **of initial training population.**

		Relative cost of phenotyping (\$P) to genotyping (\$G)		
Scenario *		\$P:\$G = 1:2	\$P:\$G = 1:1	\$P:\$G = 2:1
With initial TP	C11	3.01 _{0.22} ^{a,A}	3.01 _{0.22} ^{a,A}	3.01 _{0.22} ^{a,A}
	G10	5.43 _{0.20} ^{b, A}	5.41 _{0.29} ^{b, A}	6.50 _{0.20} ^{b, B}
	G9	5.58 _{0.26} ^{b, A}	6.30 _{0.17} ^{c, B}	7.02 _{0.24} ^{c, C}
	G8	6.35 _{0.25} ^{c, A}	6.62 _{0.25} ^{d, B}	7.02 _{0.17} ^{c, C}
	G5	6.78 _{0.21} ^{d, A}	7.07 _{0.20} ^{e, B}	7.26 _{0.19} ^{c, B}
	G2	7.13 _{0.29} ^{e, A}	7.33 _{0.26} ^{e, A}	7.28 _{0.17} ^{c, A}
	G1	7.11 _{0.16} ^{e, A}	7.27 _{0.28} ^{e, A}	7.24 _{0.22} ^{c, A}
Without initial TP	G10	3.93 _{0.22} ^{b, A}	4.54 _{0.14} ^{b, B}	5.61 _{0.25} ^{b, C}
	G9	4.64 _{0.18} ^{c, A}	5.75 _{0.28} ^{c, B}	6.52 _{0.17} ^{c, C}
	G8	5.61 _{0.28} ^{d, A}	6.24 _{0.19} ^{d B}	6.70 _{0.25} ^{cd, C}
	G5	6.43 _{0.21} ^{e, A}	6.90 _{0.22} ^{e, B}	7.05 _{0.27} ^{de, B}

G2	6.81 _{0.28} ^{f, A}	6.96 _{0.17} ^{e, A}	7.00 _{0.30} ^{de, A}
G1	6.78 _{0.29} ^{f, A}	6.92 _{0.26} ^{e, A}	7.01 _{0.23} ^{e, A}

*The table presents the means and standard deviations (subscript) across 10 replicates for the conventional (C) and genomic (G) scenarios, with numbers indicating the number of phenotype records per lactation. The scenarios in bold cells did not spend all the available resources. The table presents the results within three relative costs of phenotyping to genotyping (\$P:\$G). The genomic scenarios differ in the availability of the initial training population (TP). Lower-case letters denote statistically significant differences between scenarios within the same \$P:\$G and upper-case letters between different \$P:\$G within the same scenario.

Table S2. Intensity of sire selection by scenario and relative cost of phenotyping to genotyping.

Scenario	Relative cost of phenotyping (\$P) to genotyping (\$G)		
	\$P:\$G = 1:2	\$P:\$G = 1:1	\$P:\$G = 2:1
C11	0.80	0.80	0.80
G10	1.32	1.71	2.02
G9	1.76	2.06	2.48
G8	1.99	2.27	2.52
G5	2.40	2.63	2.85
G2	2.63	2.86	3.11
G1	2.70	2.93	3.14

The scenarios are named C/G for conventional/genomic with numbers indicating the number of phenotype records per lactation.

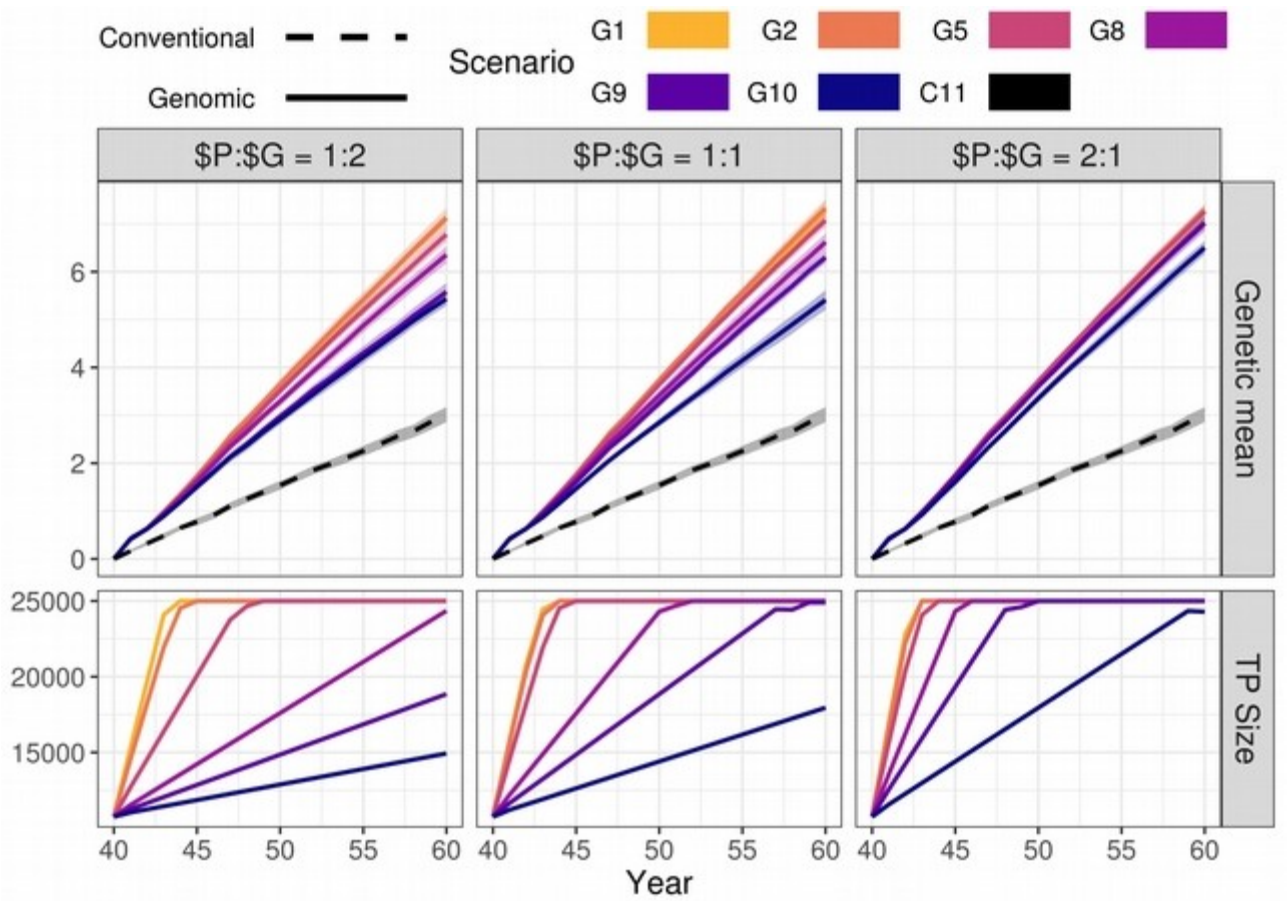
With the same amount of available resources, genomic scenarios with an initial training population increased the genetic gain of the conventional scenario between 79% and 143%. The genetic gain increased with the increasing investment in genotyping, despite reduced phenotyping. We show this in Figure 1 and Table S1 with genetic gain by scenario and by relative cost of phenotyping to genotyping with an initial training population. We show the intensities of sire selection in Table S2. When the cost of phenotyping was the same as the cost of genotyping (\$P:\$G = 1:1), the genomic scenarios increased the genetic gain of the conventional scenario between 79% and 143%. By reducing the number of phenotype records from 11 (C11) to 10 per lactation (G10), we saved

resources for genotyping 355 animals per year (310 cows and 45 male candidates). This small change increased the male selection intensity from 0.80 to 1.71 and increased the genetic gain by 79% (from 3.01 to 5.41). By reducing the phenotype records to nine or eight per lactation (G9 or G8), we respectively saved resources to genotype 800 or 1,345 animals per year, of which 100 or 165 were male candidates. This respectively increased the males selection intensity to 2.06 or 2.27, and genetic gain by 109% or 120% (from 3.01 to 6.30 or 6.62). We achieved the highest genetic gain, between 135% and 143% of the conventional scenario (between 7.07 and 7.33), when we collected five, two, or one phenotype records per lactation. In these three scenarios we saved resources for genotyping between 3,230 and 3,850 (all) cows and between 465 and 1,125 male candidates per year, and achieved the males selection intensity between 2.63 and 2.93.

We observed a similar trend for genetic gain when the cost of phenotyping was half or twice the cost of genotyping. Changing the relative cost of phenotyping to genotyping had the largest effect in the scenario with the smallest amount of genotyping (G10). In this scenario, when phenotyping was twice or half the cost of genotyping, we respectively saved resources for genotyping 182 or 710 animals, of which 22 or 90 were males, and increased the genetic gain for 80% (from 3.01 to 5.43) or 116% (from 3.01 to 6.50). When we maximized the investment into genotyping (G1), we genotyped all females at all three price ratios and between 565 and 2,245 male candidates. Correspondingly, we achieved a comparable genetic gain, between 136% and 143% of the conventional scenario, regardless of the relative cost of phenotyping to genotyping and different male selection intensities.

The high-genotyping scenarios achieved the observed genetic gain without using all the available resources (marked bold in Table S1). In these scenarios the resources designated to genotyping females exceeded the cost of genotyping all females. This made additional savings of between 85 (42) and 11,900 (23,800) genotypes (phenotypes).

298 In Figure 1 we also show the growth of the training population for genomic prediction. The training
299 population started with a ~10,000 individuals and grew until reaching 25,000 individuals. However,
300 the increase was not linear throughout generations, since the procedure for choosing the training
301 animal changed when the size was to exceed 25,000 (only latest females and male candidates
302 included).



304 **Figure 1 Genetic gain and training population size by scenario and relative cost of genotyping**
305 **with initial training population (TP).** The figure presents the means (lines) and 95% confidence
306 intervals (polygons) across 10 replicates for the conventional (C) and genomic (G) scenarios, with
307 numbers indicating the number of phenotype records per lactation. The figure presents the results
308 within three relative costs of phenotyping to genotyping (\$P:\$G).

309 **Accuracy with an initial training population**

310 **Table S3 Selection accuracy by scenario, relative cost of genotyping, and the availability of**
311 **initial training population (TP).**

Scenario	With initial training population			Without initial training population		
	Relative cost of phenotyping (\$P) to genotyping (\$G)					
	\$P:\$G = 1:2	\$P:\$G = 1:1	\$P:\$G = 2:1	\$P:\$G = 1:2	\$P:\$G = 1:1	\$P:\$G = 2:1
Male candidates						
C11, S1	0.37 _{0.04} ^{a,A}	0.37 _{0.04} ^{a,A}	0.37 _{0.04} ^{a,A}	0.37 _{0.04} ^{a,A}	0.37 _{0.04} ^{a,A}	0.37 _{0.04} ^{a,A}
C11, S2	0.94 _{0.01} ^{b,A}	0.94 _{0.01} ^{b,A}	0.94 _{0.01} ^{b,A}	0.94 _{0.01} ^{b,A}	0.94 _{0.01} ^{b,A}	0.94 _{0.01} ^{b,A}
G10	0.89 _{0.03} ^{c,A}	0.90 _{0.02} ^{bc,AB}	0.91 _{0.01} ^{bc,B}	0.81 _{0.03} ^{b,A *}	0.84 _{0.01} ^{b,B *}	0.87 _{0.01} ^{b,C *}
G9	0.90 _{0.03} ^{bc,A}	0.91 _{0.02} ^{bc,A}	0.91 _{0.01} ^{bc,A}	0.85 _{0.02} ^{c,A *}	0.87 _{0.01} ^{bc,B *}	0.90 _{0.01} ^{bc,C *}
G8	0.91 _{0.01} ^{bc,A}	0.91 _{0.01} ^{bc,A}	0.91 _{0.01} ^{bc,A}	0.86 _{0.01} ^{cd,A *}	0.89 _{0.01} ^{c,B *}	0.90 _{0.01} ^{bc,B}
G5	0.91 _{0.01} ^{bc,A}	0.91 _{0.00} ^{bc,A}	0.91 _{0.01} ^{bc,A}	0.90 _{0.01} ^{d,A}	0.91 _{0.01} ^{c,A}	0.91 _{0.01} ^{c,A}
G2	0.91 _{0.01} ^{bc,A}	0.91 _{0.00} ^{bc,A}	0.90 _{0.01} ^{bc,A}	0.90 _{0.01} ^{d,A}	0.90 _{0.01} ^{c,A}	0.90 _{0.01} ^{bc,A}
G1	0.89 _{0.01} ^{c,A}	0.90 _{0.01} ^{c,A}	0.89 _{0.01} ^{c,A}	0.89 _{0.01} ^{cd,A}	0.89 _{0.01} ^{c,A}	0.89 _{0.01} ^{bc,A}
Sires						
C11	0.86 _{0.05} ^{a,A}	0.86 _{0.05} ^{a,A}	0.86 _{0.05} ^{a,A}	0.86 _{0.05} ^{a,A}	0.86 _{0.05} ^{a,A}	0.86 _{0.05} ^{a,A}
G10	0.75 _{0.04} ^{b,A}	0.75 _{0.03} ^{b,A}	0.73 _{0.05} ^{b,A}	0.67 _{0.08} ^{bc,A *}	0.68 _{0.05} ^{cde,A *}	0.67 _{0.06} ^{b,A *}
G9	0.76 _{0.04} ^{b,A}	0.72 _{0.06} ^{bc,AB}	0.69 _{0.05} ^{c,A}	0.70 _{0.05} ^{b,A *}	0.72 _{0.05} ^{bc,A}	0.71 _{0.05} ^{b,A}
G8	0.76 _{0.03} ^{b,A}	0.69 _{0.05} ^{cd,B}	0.68 _{0.06} ^{c,B}	0.71 _{0.05} ^{b,A *}	0.74 _{0.05} ^{b,A *}	0.70 _{0.07} ^{b,A}
G5	0.68 _{0.07} ^{c,A}	0.67 _{0.08} ^{de,A}	0.69 _{0.04} ^{c,A}	0.68 _{0.05} ^{bc,A}	0.69 _{0.05} ^{cd,A}	0.69 _{0.03} ^{b,A}
G2	0.67 _{0.05} ^{c,A}	0.67 _{0.05} ^{de,A}	0.67 _{0.04} ^{c,A}	0.65 _{0.06} ^{c,A}	0.64 _{0.07} ^{e,A}	0.69 _{0.05} ^{b,A}
G1	0.66 _{0.06} ^{c,A}	0.63 _{0.05} ^{e,A}	0.67 _{0.04} ^{c,A}	0.67 _{0.04} ^{bc,A}	0.67 _{0.03} ^{de,A}	0.69 _{0.05} ^{b,A}
Female candidates						
C11	0.45 _{0.02} ^{a,A}	0.45 _{0.02} ^{a,A}	0.45 _{0.02} ^{a,A}	0.45 _{0.02} ^{a,A}	0.45 _{0.02} ^{a,A}	0.45 _{0.02} ^{a,A}
G10	0.48 _{0.01} ^{ab,A}	0.48 _{0.01} ^{ab,A}	0.51 _{0.01} ^{b,B}	0.46 _{0.02} ^{ab,A *}	0.47 _{0.02} ^{ab,AB}	0.49 _{0.01} ^{b,B *}
G9	0.49 _{0.02} ^{b,A}	0.50 _{0.01} ^{b,B}	0.52 _{0.01} ^{b,C}	0.47 _{0.02} ^{ab,A *}	0.49 _{0.02} ^{bc,B}	0.52 _{0.01} ^{bc,C}
G8	0.51 _{0.01} ^{b,A}	0.51 _{0.01} ^{b,A}	0.54 _{0.01} ^{bc,B}	0.49 _{0.02} ^{bc,A *}	0.52 _{0.01} ^{cd,B}	0.53 _{0.01} ^{cd,C}
G5	0.51 _{0.01} ^{bc,A}	0.55 _{0.01} ^{c,B}	0.57 _{0.01} ^{c,C}	0.52 _{0.01} ^{cd,A}	0.55 _{0.01} ^{de,B}	0.57 _{0.01} ^{d,C}
G2	0.55 _{0.01} ^{cd,A}	0.57 _{0.01} ^{c,B}	0.57 _{0.01} ^{c,B}	0.55 _{0.01} ^{d,A}	0.56 _{0.02} ^{e,AB}	0.57 _{0.01} ^{d,B}
G1	0.56 _{0.01} ^{d,A}	0.56 _{0.01} ^{c,A}	0.56 _{0.01} ^{c,A}	0.55 _{0.01} ^{d,A}	0.56 _{0.01} ^{e,A}	0.56 _{0.01} ^{d,A}
Cows						
C11	0.48 _{0.03} ^{a,A}	0.48 _{0.03} ^{a,A}	0.48 _{0.03} ^{a,A}	0.48 _{0.03} ^{a,A}	0.48 _{0.03} ^{a,A}	0.48 _{0.03} ^{a,A}
G10	0.56 _{0.02} ^{b,A}	0.59 _{0.02} ^{b,B}	0.63 _{0.01} ^{b,C}	0.53 _{0.01} ^{b,A *}	0.56 _{0.01} ^{b,B *}	0.61 _{0.01} ^{b,C *}
G9	0.59 _{0.03} ^{bc,A}	0.63 _{0.02} ^{c,B}	0.70 _{0.01} ^{c,C}	0.57 _{0.02} ^{bc,A *}	0.62 _{0.02} ^{c,B}	0.68 _{0.02} ^{c,C *}
G8	0.62 _{0.02} ^{c,A}	0.67 _{0.02} ^{c,B}	0.74 _{0.02} ^{d,C}	0.60 _{0.02} ^{c,A *}	0.66 _{0.01} ^{d,B}	0.73 _{0.02} ^{d,C}
G5	0.70 _{0.02} ^{d,A}	0.77 _{0.01} ^{d,B}	0.79 _{0.02} ^{e,C}	0.69 _{0.02} ^{d,A}	0.76 _{0.01} ^{e,B}	0.78 _{0.02} ^{e,B}
G2	0.76 _{0.02} ^{e,A}	0.79 _{0.02} ^{d,B}	0.78 _{0.01} ^{e,AB}	0.76 _{0.01} ^{e,A}	0.77 _{0.02} ^{e,A *}	0.77 _{0.01} ^{de,A}

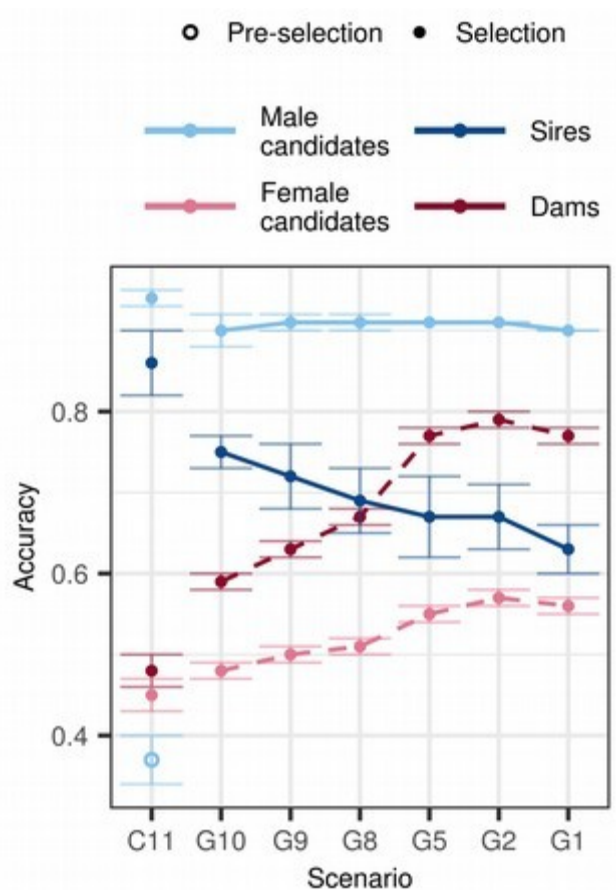
G1	0.77 _{0.02} ^{e,A}	0.77 _{0.02} ^{d,A}	0.77 _{0.01} ^{de,A}	0.76 _{0.01} ^{e,A}	0.76 _{0.02} ^{e,A}	0.76 _{0.02} ^{de,A}
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*The table presents the means and standard deviations (subscript) across 10 replicates for the conventional (C) and genomic (G) scenarios, with numbers indicating the number of phenotype records per lactation. The tables presents the results within three relative costs of phenotyping to genotyping (\$P:\$G). Conventional selection implemented two-stage selection for males, hence we present the accuracy of pre-selection of male candidates for progeny testing (S1) and the accuracy of selection of proven sires (S2). In genomic scenarios the male candidates were genotyped and non-phenotyped males. We also present the accuracy for sires currently used in artificial insemination (sires), for non-genotyped non-phenotyped females (female candidates), and for all active phenotyped cows and bull dams (cows). Lower-case letters denote statistically significant differences between scenarios within the same \$P:\$G and upper-case letters between different \$P:\$G within the same scenario. Stars denote statistically significant difference between corresponding scenarios with and without an initial training population.

Compared to the conventional scenario, genomic scenarios increased accuracy for young non-phenotyped male and female candidates, and cows, but decreased accuracy for sires. We show this in Figure 2 with the accuracy for male candidates, female candidates, sires, and cows with an initial training population and equal cost of phenotyping and genotyping. In Table S3 we compare accuracies at all three relative costs of phenotyping to genotyping. When the cost of phenotyping was equal to the cost of genotyping, the accuracy for young genomically tested male candidates ranged between 0.90 and 0.91 and did not depend on the amount of phenotyping and genotyping. This was 0.53-0.54 higher compared to the first stage of male selection in the conventional scenario (young un-phenotyped male candidates for progeny testing - same age point). However, this was 0.03 - 0.04 lower compared to the second stage of male selection in the conventional scenario (proven sires - same selection point). In contrast, the accuracy for sires decreased with reallocating phenotyping resources into genotyping. We observed the lowest accuracy for sires, 0.63, when we invested the most into genotyping (G1), and the highest, 0.75, when we invested the most into

337 phenotyping (G10). Compared to the conventional scenario, the accuracy for proven sires in the
338 genomic scenarios was between 0.11 and 0.23 lower. The accuracy for female candidates increased
339 with increasing genotyping, despite reduced phenotyping. We observed the highest accuracy for
340 female candidates, between 0.55 and 0.57, when we recorded five, two, or one phenotype record per
341 lactation and invested the rest into genotyping. Compared to the conventional scenario, the genomic
342 scenarios increased the accuracy for female candidates between 0.03 and 0.11. The accuracy for
343 cows followed the same trends, but with higher values. We observed the highest accuracy for cows,
344 between 0.77 and 0.79, by collecting five, two, or one phenotype record per lactation and investing
345 the rest in genotyping. Compared to the conventional scenario, genomic scenarios increased the
346 accuracy for cows between 0.11 and 0.29.

347 Changing the relative cost of phenotyping to genotyping affected primarily the accuracy for female
348 candidates and cows. We observed that in the majority of scenarios the accuracy increased with
349 decreasing the relative cost of genotyping, which enabled genotyping more animals. We observed
350 the largest difference of 0.06 for female candidates and 0.12 for cows when we changed the relative
351 cost of phenotyping from half to twice the cost of genotyping. Changing the relative costs, however,
352 did not change the trends.



353

354 **Figure 2 Accuracy by scenario with initial training population and equal cost of phenotyping**
 355 **and genotyping.** The figure presents the means (lines) and 95% confidence intervals (error bars)
 356 across 10 replicates for the conventional (C) and genomic (G) scenarios with numbers indicating the
 357 number of phenotype records per lactation. Conventional selection implemented two-stage selection
 358 for males, hence we present the accuracy of pre-selection of males for progeny testing (empty point)
 359 and the accuracy of selection of proven sires (solid point).

360 **Genetic gain and accuracy without an initial training population**

361 ***Genetic gain***

362 When an initial training population was not available, we increased the genetic gain of the
 363 conventional scenario between 31% and 134% by optimizing investment in phenotyping and
 364 genotyping. We show this in Figure 3 with the genetic gain, training population size, and accuracy
 365 by scenario without an initial training population and equal cost of phenotyping and genotyping.

366 The observed trends were in line with what we observed with an initial training population, that is,
367 increasing genotyping increased genetic gain despite reduced phenotyping. However, all
368 corresponding scenarios achieved between 2% and 28% smaller genetic gain than when an initial
369 training population was available. We show this in Tables S1 that compare the genetic gain of all
370 scenarios.

371 When the cost of phenotyping was equal to the cost of genotyping, genomic scenarios increased the
372 genetic gain of the conventional scenario between 51% and 131%. Compared to when we had an
373 initial training population, the corresponding scenarios achieved between 2% and 16% lower
374 genetic gain. We observed the largest difference in the scenario that invested the least into
375 genotyping (G10). In this scenario we needed six years to build an adequate training population and
376 implement genomic selection, since we only genotyped 355 cows per year. Increasing the
377 investment into genotyping decreased this difference. We observed the smallest difference in the
378 scenario that collected two phenotype records per lactations (G2) and implemented genomic
379 selection in the first evaluation year.

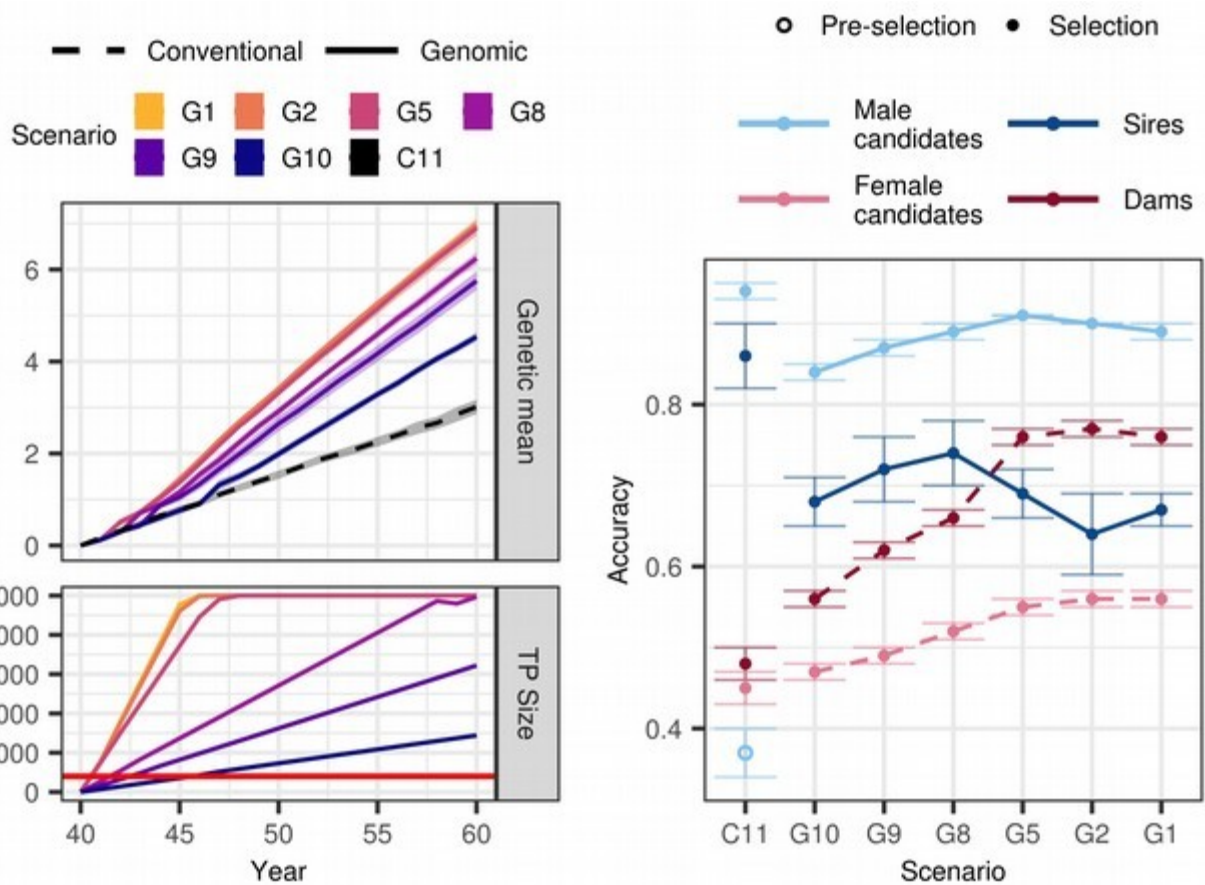
380 Changing the relative cost of phenotyping to genotyping did not change the overall trend, only the
381 level of genetic gain in the low-genotyping scenarios. When the cost of phenotyping was half the
382 cost of genotyping, the genomic scenarios increased genetic gain of the conventional scenario
383 between 31% and 126%. The corresponding scenarios achieved between 4% and 28% lower genetic
384 gain than when we had an initial training population. When the cost of phenotyping was twice the
385 cost of genotyping, the genomic scenarios increased the genetic gain of the conventional scenario
386 between 86% and 133%. The corresponding scenarios achieved between 3% and 14% lower genetic
387 gain than when we had an initial training population.

388 *Accuracy*

389 As when we had an initial training population, genomic scenarios without an initial training
390 population increased the accuracy for non-phenotyped male and female candidates, and cows. We

391 show this in Figure 3 with the accuracy without an initial training population and equal cost of
392 phenotyping and genotyping. In Table S3 we compare the accuracies of all scenarios. When the cost
393 of phenotyping was the same as the cost of genotyping, the accuracy for male candidates ranged
394 between 0.84 and 0.91. In contrast to scenarios with initial training population, the accuracy
395 increased with increasing the investment into genotyping, hence was significantly lower in the
396 scenario that invested the least into genotyping. The accuracy for sires ranged between 0.64 and
397 0.74. Contrary to when we had an initial training population, we observed no clear trend of either
398 increasing or decreasing accuracy. For female candidates the accuracy ranged between 0.47 and
399 0.56, and for cows between 0.56 and 0.76. For female candidates and cows the accuracies followed
400 the trends of when we had an initial training population, where increasing genotyping increased the
401 accuracy.

402 As in the scenarios with an initial training population, changing the relative cost of phenotyping to
403 genotyping affected the accuracy for female candidates and cows, but also male candidates. Here,
404 decreasing the relative cost of genotyping, and genotyping more animals, increased the accuracy in
405 the majority of the scenarios, particularly the low-genotyping ones.



406

407 **Figure 3 Genetic gain, training population size, and accuracy by scenario without initial**
 408 **training population (TP) and equal cost of phenotyping and genotyping.** The figure presents the
 409 means (lines or points) and 95% confidence intervals (polygons or errorbars) across 10 replicates
 410 for the conventional (C) and genomic (G) scenarios with numbers indicating the number of
 411 phenotype records per lactation. The red line marks the condition of 2,000 animal in the training
 412 population to implement genomic selection. Conventional selection implemented two-stage
 413 selection for males, hence we present the accuracy of the pre-selection stage for progeny testing
 414 (empty point) and the accuracy of selection for proven sires (solid point).

416 **Conclusions**

417 **Declarations**

418

419 **Ethics approval and consent to participate**

420 Not applicable

421 **Consent for publication**

422 Not applicable

423 **Availability of data and materials**

424 **Competing interests**

425 Not applicable

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429 **Authors' contributions**

430 JO designed the testing scenarios, ran the simulation, analyzed the data, wrote the papers and
431 interpreted the results. JJ participated in designing the scenarios, troubleshooting the simulation
432 problems, interpreting the results, and has substantially revised the manuscript. JMH participated in
433 the design of the work, interpretation of the results, and has substantially revised the manuscript.
434 GG has participated in designing the work, troubleshooting the problems, analysis of the data,
435 interpretations of the results, and has substantially revised the manuscript.

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439 **Author's information** (optional)

440 Not applicable.

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479 Additional file 1 Table S1

480 Format:

481 Title:

482 Description:

483 Additional file 2 Figure S1

484 Format:

485 Title:

486 Description:

Conventional selection, BLUP simulation, 100 sires

Number of records	Number of daughters / sire	Accuracy for sires	Accuracy for cows	Accuracy for non-phenotyped animals	Total number of phenotyped cows	Total number of phenotypes
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Variable resources for phenotyping

1	100	0.93	0.62	0.56	10,000	10,000
2	100	0.96	0.70	0.59	10,000	20,000
5	100	0.97	0.81	0.64	10,000	50,000
10	100	0.98	0.89	0.66	10,000	100,000

Fixed resources for phenotyping

1	1000	0.99	0.63	0.59	100,000	100,000
2	500	0.99	0.71	0.61	50,000	100,000
5	200	0.99	0.82	0.64	20,000	100,000
10	100	0.98	0.89	0.66	10,000	100,000

Genomic selection

Variable resources for phenotyping

1	-	-	0.62	0.53	10,000	10,000
2	-	-	0.70	0.58	10,000	20,000
5	-	-	0.81	0.64	10,000	50,000
10	-	-	0.89	0.68	10,000	100,000

Fixed resources for phenotyping

1	-	-	0.63	0.91	100,000	100,000
2	-	-	0.71	0.86	50,000	100,000
5	-	-	0.82	0.77	20,000	100,000
10	-	-	0.89	0.68	10,000	100,000