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1 **Genomic selection strategies for breeding adaptation and**  
2 **production in dairy cattle under climate change**

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16 RUNNING TITLE: Genomic selection for adaptation in dairy cattle

17

## **Abstract**

18 Livestock production both contributes to, and is affected, by global climate  
19 change, and substantial modifications will be required to increase its climate  
20 resilience. In this context, reliance on dominant commercial livestock  
21 breeds, featuring small effective population sizes, makes current production  
22 strategies vulnerable if their production is restricted to environments which  
23 may be too costly to support under future climate scenarios. The  
24 adaptability of animal populations to future environments will therefore  
25 become important. To help evaluate the role of genetics in climate  
26 adaptation, we compared selection strategies in dairy cattle using breeding  
27 simulations, where genomic selection was used on two negatively correlated  
28 traits for production (assumed to be moderately heritable) and adaptation  
29 (assumed to have low heritability). Compared to within population breeding,  
30 genomic introgression produced a more positive genetic change for both  
31 production and adaptation traits. Genomic introgression from highly adapted  
32 but low production value populations into highly productive but low  
33 adaptation populations was most successful when the adaptation trait was  
34 given a lower selection weight than the production trait. Genomic  
35 introgression from highly productive population to highly adapted  
36 population was most successful when the adaptation trait was given a higher  
37 selection weight than the production trait. Both these genomic introgression  
38 schemes had the lowest risk of inbreeding. Our results suggest that both

39 adaptation and production can potentially be improved simultaneously by

40 genomic introgression.

41 **Keywords:** adaptation, dairy cattle, introgression, simulation

## 42 **Introduction**

43 Adaptation of livestock to environmental challenges is becoming  
44 increasingly important in cost-effective animal production, especially as the  
45 climate becomes warmer, conditions for diseases are more favourable and  
46 production costs are set to rise (FAO, 2015; Phocas et al., 2016). Heat stress  
47 is one of the most pressing factors affecting livestock production (Niyas et  
48 al., 2015) and has been shown to cause a decrease in milk production (5-  
49 15%) and lower conception rates (Berman, 2011) in cattle. In addition,  
50 chronic stress triggers metabolic changes that result in stress-related disease  
51 and suppression of innate immunity (Das, 2016). However, selection can  
52 compensate for thermal stress with, for example, the slick hair coat  
53 phenotype being implicated in the thermoregulation of tropically adapted  
54 cattle breeds (Pitt et al., 2018).

55 In practice, adaptation comprises many traits including those influencing  
56 fitness, such as longevity and disease resistance. These traits typically have  
57 low heritability and have declined when milk production has increased (e.g.  
58 Mirkena et al., 2010). Genetic correlations have been estimated to range  
59 from -0.11 to -0.84 between milk yield and functional longevity (e.g.  
60 Sasaki, 2013; Pritchard et al., 2013a,b). Because adaptation to the local  
61 environment generally has a low heritability and possibly has antagonistic  
62 genetic correlations with milk production, long-term and efficient breeding  
63 strategies are required. In a rapidly changing environment, one approach is

64 to introgress locally adaptive genes found in autochthonous breeds into  
65 major production breeds or *vice versa* (Nardone et al., 2006; Hoffman,  
66 2010; Berman, 2011; Hoffman, 2013). Thus, an efficient strategy may be  
67 needed to introduce adaptive traits quickly into commercial breeds or these  
68 breeds may need to be replaced with better adapted populations (Åby and  
69 Meuwissen, 2014).

70 Introgression strategies commonly assume that one or more alleles in  
71 genes of interest or associated markers have been located in a donor  
72 population but are missing in the recipient population (e.g., Visscher et al.,  
73 1996). The aim is to select these favourable alleles from individuals within  
74 the donor population and use backcrossing and selection to introduce them  
75 into the recipient population, such that the favourable allele becomes fixed  
76 in the recipient population with as small as possible proportion of the rest of  
77 the donor's genome included. However, the allele(s) of interest need to be  
78 known and to be of large effect, which is unfortunately seldom the case.

79 Knowing the location of important genes affecting traits of interest may  
80 be unnecessary for introgression to succeed. Ødegård et al. (2009a)  
81 simulated a fish breeding population where introgression was applied for a  
82 major quantitative trait locus (QTL) affecting disease resistance by  
83 backcrossing a production line with a resistant donor line. In their study,  
84 classical selection, i.e., without genomic information, was inefficient but  
85 genomic selection without specific knowledge of the target QTL was

86 usually effective in preserving favourable alleles. Gaspa et al. (2015)  
87 investigated introgression of polledness in Holstein Friesian cattle by using  
88 simulations and concluded that a single gene strategy, applying genomic  
89 selection helped to speed up the process of introgression while  
90 simultaneously increasing the genetic gain of other important traits and  
91 reducing inbreeding.

92       Adaptation and production can be both assumed to be polygenic traits.  
93 Ødegård et al. (2009b) simulated a fish breeding scheme where both  
94 production and disease resistance were polygenic with either low or high  
95 heritability. The authors concluded that in contrast to classical selection,  
96 genomic selection increased genetic gain in introgression backcrossing  
97 schemes, with the largest gain being for low heritability traits and on traits  
98 not recorded in selection candidates.

99       Åby and Meuwissen (2014) simulated two divergent populations  
100 according to production and fitness profiles of livestock with pure and  
101 crossbreeding in discrete generations. Both production and fitness were  
102 polygenic traits having moderate heritability but no genetic correlation.  
103 According to their results, selection using breeding values estimated by  
104 genomic best linear unbiased prediction (GBLUP) outperformed  
105 conventional BLUP in terms of genetic increase in production and fitness.  
106 In general, results from the simulation studies suggest that genomic  
107 selection can be effective in introgression of a lowly heritable trait to a

108 target population with high production when traits (i.e. the introgressed trait  
109 and production) are polygenic and uncorrelated.

110 The aim of this study was to evaluate breeding strategies for the selection  
111 of rapid environmental (e.g. temperature) adaptation and production using  
112 dairy cattle as a model, by stochastic simulation. Breeding strategies include  
113 pure breeding and crossbreeding schemes involving a poorly adapted but  
114 high production population and a well-adapted population but of low milk  
115 yield. Adaptation and production traits were assumed to be negatively  
116 correlated and governed by many loci. We assumed production to have a  
117 higher heritability than adaptation and use bivariate genomic BLUP to  
118 estimate breeding values to improve both adaptation and production. A  
119 variety of breeding strategies using selection and introgression were  
120 considered. Introgression schemes included selection from well-adapted to  
121 poorly adapted population and *vice versa* when selection strategies applied  
122 different selection weights to the traits.

## 123 **Material and Methods**

124 Simulation of breeding programs followed two phases. First, QMSim  
125 (Sargolzaei and Schenkel, 2009) was used to simulate an initial historic  
126 population (HP) and the subsequent selection of two divergent lines, a  
127 production line (PL) and an adaptation line (AL). Second, the final breeding  
128 animals from these populations were available as breeding animals for  
129 alternative selection schemes. Five replicates were simulated using QMSim,



130 i.e. five sets of final breeding animals. Within a replicate, the studied  
131 breeding schemes selected the first breeding animals from the same  
132 population although different schemes could use different sets of animals.  
133 Table 1 shows the simulation parameters used.

#### 134 **Simulation of two populations using QMSim**

135 The HP in QMSim generates initial values of linkage disequilibrium (LD),  
136 mutation and drift. The simulated genome was assumed to have 30  
137 chromosomes of 100 cM each. To mimic a commercial Bovine 54K SNP  
138 chip, the genome had 54,000 evenly distributed bi-allelic SNP markers with  
139 equal frequencies (0.5) for the two alleles in the base population (1,800 bi-  
140 allelic SNP markers per chromosome). The HP consisted of 1,000  
141 individuals that were randomly mated for 95 generations (Figure 1). During  
142 the following five generations, the population was expanded to 12,000  
143 individuals to allow selection of two populations.

144 QMSim allows selection of one trait in the populations descending from  
145 the HP, and here this trait was chosen to represent milk production in dairy  
146 cattle. The production trait was assumed to have 30 randomly positioned  
147 QTLs within each chromosome, i.e., in total 900 QTLs. The mutation rate  
148 used was  $2.5 \times 10^{-5}$  per generation (e.g. Solberg et al. 2008). The number of  
149 recombinations per Morgan was sampled from a Poisson distribution with a  
150 mean of one and the cross-overs were randomly placed on the  
151 chromosomes. QTL effects of the production trait were introduced in the

152 last generation of the HP for a trait with a heritability of 0.30 which is close  
153 to heritability of 305-day milk yield in dairy cattle. The allelic effects were  
154 sampled from a gamma distribution with a shape parameter of 0.4 as  
155 implemented in QMSim, so that the QTLs explained all genetic variation.  
156 QTL allelic effects were scaled in QMSim such that the phenotypic variance  
157 in the last HP generation was one.

158 Animals for two populations or breeds (AL and PL) were selected from  
159 the HP, and subsequent breeding in QMSim was carried out separately  
160 within these breeds (Figure 1). For both populations, 2,800 females and 200  
161 males were selected from the last generation of the HP to be as breeding  
162 animals. The AL population animals were randomly selected but the PL  
163 population animals had the highest true breeding value for production. No  
164 animal was used in both populations. Within both populations each sire was  
165 mated to 14 dams, with each mating producing one offspring (50:50 birth  
166 sex ratio). This procedure yielded a total of 2,800 offspring (1,400 males  
167 and 1,400 females). In the following 10 generations in QMSim, selection of  
168 breeding animals in the AL population was random but in the PL population  
169 animals with highest pseudo EBVs (estimated breeding values) were  
170 selected for breeding.

171 Selection within the AL and PL populations allowed for overlapping  
172 generations. The breeding animals in each generation were selected from the  
173 current breeding animals and from the youngest mature generation. From

174 the 200 current breeding males, 60% (120 sires) were kept and 40% (80  
175 sires) were replaced. In the AL population, the 80 new sires were randomly  
176 selected from the youngest mature generation, and they replaced a randomly  
177 selected 80 older breeding males. In the PL population, the selection used  
178 the pseudo EBVs calculated by QMSim based on 20 daughter records. The  
179 breeding animals replaced had the lowest pseudo EBV among the current  
180 breeding males, and the selected new males had the highest pseudo EBV in  
181 the youngest mature generation. Correspondingly, 20% (560 females) were  
182 replaced among the 2,800 breeding females. In the AL population, the  
183 selection of replacements and replaced females were random. In the PL  
184 population, the selection used the pseudo EBVs based on the cow's own  
185 information. Thus, the two populations had the same random drift base  
186 population from which the PL population was selected for higher  
187 production, but the AL population continued with random selection. The AL  
188 population depicts a random drift population where there has been no  
189 efficient selection for production or adaptation which reflects the prevailing  
190 situation for many small local breeds. The breeding scheme was continued  
191 for 10 generations separately within AL and PL to produce two genetically  
192 different populations.

193 After this set of simulations, QTL effects for the adaptation trait were  
194 further simulated as a correlated trait to production. In the simulations, all  
195 the production QTL positions and effects were used to generate a correlated

196 trait which had a genetic correlation of -0.30 and heritability of 0.10 for all  
197 animals after the HP. Heritability of 0.10 is close to lowly heritable  
198 adaptation traits such as functional longevity that have moderately negative  
199 genetic correlation with milk production (Sasaki et al. 2013). In practice,  
200 there can be adaptation traits having lower heritability and possibly weaker  
201 or stronger genetic correlation with production, but use of different values  
202 would affect only absolute values, not the observed trends. The adaptation  
203 trait's QTL effects were scaled the same way as in QMSim for production in  
204 order to get the wanted genetic correlation of -0.3 between production and  
205 adaptation. However, the scaling of adaptation QTLs used information from  
206 one generation later than for the production QTLs because that was the first  
207 available generation with data from QMSim. Correlations of true breeding  
208 values (TBV) between the traits indicated that the wanted correlation of -0.3  
209 was realized. TBV of an animal was calculated using the true QTL values  
210 and the QTL genotypes of animal.

### 211 **Breeding program simulations**

212 Different breeding schemes were simulated for an additional ten simulation  
213 years after the QMSim simulation. These schemes used the final breeding  
214 animals from the QMSim simulation (Figure 1) but due to restrictions in the  
215 QMSim program, subsequent breeding program simulations were performed  
216 using a different set of computer programs. In every simulation scheme, a  
217 simulation year used current breeding animals to produce calves. A new set

218 of breeding animals were selected from the current breeding animals and  
219 calves maturing from previous year according to their EBVs (Table 2), i.e.  
220 breeding animals could be from a number of birth years. The basic  
221 principles in the simulation followed those described for QMSim. However,  
222 animals were simulated to mature after one year instead of immediately  
223 being available as in QMSim.

224 Selection was based on EBVs that used genomic information and  
225 observations from the final breeding animals in QMSim and subsequent  
226 years. EBVs were calculated using a two trait SNP-BLUP where the  
227 variance components were equal to the simulation parameters. This is  
228 equivalent to using GBLUP (Strandén and Garrick, 2009). A variety of  
229 breeding strategies were considered: (1) selection within a population; (2)  
230 selection within a new synthetic breed made from the AL and PL  
231 populations; (3) selection of females within a population but allowing  
232 selection of males from another population, i.e., genomic introgression by  
233 crossbreeding.

234 For the within population selection (strategies 1 and 2), selection of  
235 breeding animals was from the current breeding animals and mature calves.  
236 There were three types of breeding schemes denoted A, P and AP. Scheme  
237 A used the current AL breeding animals, scheme P used the PL individuals,  
238 and scheme AP used the combined AL and PL individuals. In AP, the first  
239 generation males were selected according to the selection index from the  $F_1$

240 individuals which were the offspring of male AL to female PL or male PL  
241 to female AL matings. Because the number of female  $F_1$  individuals was  
242 only 2,800, another 2,800 cows were selected from the current AL and PL  
243 population cows. Thus, the A and P schemes continued to use 200 males  
244 and 2,800 females but the AP scheme doubled the breeding population to  
245 400 males and 5,600 females keeping the same selection intensity.

246 Genomic introgression (strategy 3) was used to introduce favourable  
247 alleles of a trait from a donor population to a target population (Figure 2). A  
248 pure breed donor population was maintained along with the target  
249 population. In introgression from the AL to PL population (AiP), a pure AL  
250 population was maintained to allow selection of AL sires. Half of the  
251 selected breeding sires used in the target population were from the AL  
252 population, and the other half were from the current PL population. Thus,  
253 after four years, some of the PL population individuals were backcrosses.  
254 Note that the candidates for the next generation PL sires were the current PL  
255 sires and the mature PL male calves which (in both cases) were not  
256 necessarily pure PL breed animals either. The same logic was followed in  
257 the introgression breeding scheme from the PL to AL population (PiA).  
258 Note that in both introgression schemes selection in the pure line used the  
259 same selection index weights as in the target population. However, in  
260 practice the AL population is expected to continue its own selection scheme

261 in AiP. Thus, a genomic introgression scheme named rAiP was simulated  
262 where random selection was continued in the AL population.

### 263 **Simulation and the statistics calculated**

264 Each of the five QMSim simulations gave a set of final AL and PL breeding  
265 animals (Figure 1). The final breeding animals were available for the  
266 breeding schemes described. Unlike in the QMSim simulation schemes, the  
267 subsequent selection of animals in these breeding schemes was based on an  
268 index of EBVs by SNP-BLUP. Three alternative indices were used where  
269 the standardised EBVs of the adaptation and production traits were  
270 weighted differently. The EBVs were standardised trait wise by dividing by  
271 trait genetic standard deviations. The adaptation (A2P1) selection index had  
272 a weight 2 for adaptation and 1 for production EBVs. The equal weight  
273 (A1P1) selection index had equal weights for both of the EBVs. The  
274 production (A1P2) selection index weighted 1 for adaptation and 2 for  
275 production EBVs.

276 Two statistics were computed for both traits using the true breeding  
277 values of the progeny to breeding animals after the QMSim simulation:  
278 adjusted genetic level (G) and genetic change during the last nine simulation  
279 years ( $\Delta G$ ). Both statistics are reported in genetic standard deviation of trait.  
280 If selection is random or very mild, genetic change  $\Delta G$  stays at zero. When  
281 two traits are studied, selection of one of the traits will change the other as  
282 well due to correlated response. Genetic change ( $\Delta G$ ) in the target

283 population was computed as the difference in the mean genetic level over  
284 replicates between the final and the first year of the breeding scheme  
285 simulation, i.e., genetic change during the last 9 years. Adjusted genetic  
286 level (G) was computed as the average difference over replicates in genetic  
287 level between the last simulation year in the target population and the  
288 control level which was the last generation AL individuals of the QMSim  
289 simulation. Genetic level in a simulation year was mean of TBVs of animals  
290 born that year in the target population.

291 The adjusted genetic level (G) allowed comparison of the absolute  
292 genetic level, which illustrates changes in production and adaptation levels  
293 compared to the control level. After the QMSim simulation, the AL and PL  
294 lines were on different genetic levels. Consequently, comparisons according  
295 to the genetic change would provide a false impression on the short term  
296 genetic consequences of selection. Because the control level is the same for  
297 all schemes within a replicate, differences in absolute genetic level between  
298 the replicates could be corrected. The control level calculated from the last  
299 generation AL individuals of QMSim is from the random selection scheme,  
300 and is close to the genetic level after HP. Thus, for example, in AiP, the  
301 genetic change  $\Delta G$  has been calculated using the target PL population  
302 individuals only, but calculating the adjusted genetic level G we used the  
303 genetic level values of the last generation PL population and the last  
304 QMSim generation AL population. Note that the difference in G and  $\Delta G$



305 will not be the same in a single population (e.g. P) and introgression  
306 schemes (e.g., AiP) because the starting level in  $\Delta G$  is based on the genetic  
307 level of the progeny compared to the selected individuals. In a single  
308 population, the parents of progeny come from one of the pure lines but in  
309 the introgression schemes the parents come from both of the lines.

310 The rate of inbreeding per generation ( $\Delta F$ ) describes the risk of a  
311 breeding scheme. Inbreeding rate was estimated using pedigree information  
312 following the method of Gutierrez et al. (2009). The method used pedigree  
313 inbreeding coefficients to calculate individual rates of inbreeding which are  
314 averaged to estimate the population inbreeding rate.

315 Existing and new programs were combined in several Linux shell scripts.  
316 The first phase of the script was based on the QMSim software which  
317 generated the two breeding lines to be used in the subsequent breeding  
318 scheme simulation. Then, each breeding scheme used a script that was a set  
319 of programs written in Perl, R (all steps needing random numbers) or  
320 Fortran. Existing programs included RelaX2 (Strandén and Vuori, 2006) for  
321 effective population size calculation and MiX99 (Strandén and Lidauer,  
322 1999) for breeding value estimation by two trait SNP-BLUP.

## 323 **Results**

324 Genetic level in the final year of QMSim quantifies initial genetic level in  
325 the AL and PL populations before selection using the studied selection  
326 indices in the contrasted breeding schemes. In the final year of QMSim, the

327 average differences across replicates in adjusted genetic levels of adaptation  
328 and production between the AL and PL populations were 1.10 and -2.99  
329 genetic standard deviations of the traits, respectively. Because the difference  
330 was positive for adaptation but negative for production, genetically the AL  
331 population had higher adaptation but poorer production than in the PL  
332 population. The genetic level of the AL population can be considered a  
333 control level. Thus, adjusted genetic level values below 0 means that the  
334 trait has not reached the same level as in the AL population at the time the  
335 breeding scheme was started.

336 Genetic change and level were positive and high for adaptation in all  
337 schemes when the selection index A2P1 was used (Table 3). The genomic  
338 introgression and synthetic breeding schemes were able to achieve a higher  
339 genetic level for adaptation than the within line selection schemes. Genetic  
340 progress for adaptation was highest in the introgression scheme from AL to  
341 PL (AiP). However, because genetic change for production trait was  
342 negative in AiP, this scheme may be unrealistic in practice. In contrast,  
343 introgression from PL to AL (PiA) gave high genetic progress for both  
344 production and adaptation. Furthermore, the adjusted genetic level achieved  
345 for production was high and was moderately high for adaptation. The  
346 highest genetic increase in adaptation in the non-introgression schemes was  
347 achieved by the combined AP scheme, with genetic progress being higher  
348 than in the rAiP and PiA schemes. Similarly, genetic change and adjusted

349 genetic level were good in production in the AP scheme. The other non-  
350 introgression schemes showed low genetic increases in production.  
351 However, the P scheme, while giving the highest adjusted genetic level for  
352 production gave the lowest for adaptation.

353 When production and adaptation were weighted equally in the selection  
354 index, all schemes were able to make positive genetic change for both  
355 production and adaptation (Table 3) except rAiP, which showed a -0.20  
356 change in production. So, in contrast to the A2P1 index selection,  
357 introgression from AL to PL (AiP) gave positive genetic change in both of  
358 the studied traits. The final genetic level of adaptation was not as high as  
359 with A2P1 but the genetic level for production was quite high. The positive  
360 genetic progress of adaptation in the AiP scheme was due to applying the  
361 same selection index in the donor AL population scheme. When the  
362 selection was random in the donor population (rAiP), genetic progress in  
363 production was negative. Introgression from PL to AL (PiA) gave lower  
364 genetic progress in adaptation than in AiP, but the genetic level reached was  
365 still positive. However, both the genetic progress and level for production  
366 were very high. Thus, as the relative weight of adaptation decreased in the  
367 selection index (from A2P1 to A1P1), genetic change and the level of  
368 adaptation decreased. In this context, genomic introgression did not prove to  
369 be the best strategy. Instead, continuing selection within the PL population

370 (P) gave a high genetic increase in adaptation and a high genetic level in  
371 production. Likewise, the joint population AP scheme was competitive.

372 When the selection index A1P2 was used, genetic change and level in  
373 adaptation tended to be very low or even negative. Scheme P achieved  
374 minor improvement in adaptation, but the final level of adaptation was very  
375 low. Scheme A was able to maintain reasonable increases in adaptation  
376 although at a low level. The introgression scheme from AL to PL (AiP)  
377 gave the highest genetic increase in adaptation with the final genetic level  
378 value of adaptation being almost 0. In AiP, the genetic progress in  
379 production was lower than in the non-introgression schemes. However, the  
380 final genetic level of production was still high due to the high genetic level  
381 of production at the beginning of the breeding scheme. Thus, when the  
382 index weight for production increased, scheme AiP became more favourable  
383 than PiA because genetic change in both production and adaptation was  
384 positive.

385 Performance of the breeding schemes under different selection indices is  
386 illustrated in Figures 4 to 7. The P and PiA introgression schemes had the  
387 highest genetic change in production (Figure 4). The PiA scheme seemed  
388 superior when adaptation was given high weight. The AiP introgression  
389 scheme had the highest genetic change in adaptation although different non-  
390 introgression schemes were often close (Figure 5). The synthetic AP scheme  
391 reached highest genetic level in production but the single population P and

392 the introgression PiA schemes were competitive when production was given  
393 higher weight than adaptation (Figure 6). The A and AiP schemes achieved  
394 the highest genetic level in adaptation (Figure 7).

395 The introgression schemes from the AL donor population (AiP) used AL  
396 sires. The proportion of genes originating from the AL population depended  
397 on the selection index (Figure 3). The more adaptation was weighted in the  
398 selection index, the higher the influence of the AL population proved to be.  
399 The continued use of random selection in the AL population decreased the  
400 gene proportion of the original AL population considerably. In the last  
401 simulation year, the proportion of the AL population genes in AiP (rAiP)  
402 was 58% (39%) using A2P1, 44% (24%) using A1P1 and 34% (19%) using  
403 A1P2. These numbers were similarly ranked in AiP and rAiP as the genetic  
404 level G for adaptation in Table 3. When introgression was from the PL  
405 donor population (PiA), the proportion of AL genes decreased from the  
406 original 100% rapidly. In the final simulation year, the proportion of AL  
407 genes in PiA was 36% using A2P1, 29% using A1P1 and 27% using A1P2.  
408 For A2P1 and A1P1 these numbers were lower than those in AiP. The rate  
409 of inbreeding per generation  $\Delta F$  was highest in the within population  
410 schemes A and P (Table 3). The AP scheme showed a lower  $\Delta F$  and the  
411 genomic introgression schemes had an even lower  $\Delta F$ . These results can be  
412 expected because the genomic introgression schemes introduced animals  
413 with a lower than average relatedness to the target population, and the

414 combined breeding population AP had double the population size in  
415 comparison to the within line selection schemes A and P. Differences in  $\Delta F$   
416 within schemes using different selection indices were small.

## 417 **Discussion**

418 It should be anticipated that selection for a trait with high heritability will  
419 produce a higher genetic change than selection for a trait with low  
420 heritability when all the other conditions are the same. Thus, it should be  
421 easier to change a highly heritable trait such as production in this study than  
422 a less heritable trait such as adaptation. Consequently, PiA introgression  
423 should be preferred over AiP because it should be easier to breed high  
424 production into locally adapted animals than the other way around. Indeed,  
425 we found that PiA crossbreeding was more successful than AiP, but only  
426 when adaptation had a high weight in the selection index. In contrast, when  
427 production had a high weight, AiP exceeded PiA because adaptation  
428 increased in the former but decreased in the latter. This result is logical  
429 because when production is given a high weight in the selection index, PiA  
430 is efficient because adaptation is of less importance. However, when  
431 production has a high weight, AiP will lead to selection of favourable  
432 adaptive genes from the AL line, while maintaining a high genetic level of  
433 production.

434 In our study, the synthetic breed scheme AP combined the two divergent  
435 lines into one common population. This was the most successful non-

436 introgression strategy in terms of inbreeding rate and genetic change in  
437 production. Overall genetic diversity decreased if only one of the original  
438 populations was maintained. When the selection index weighted the traits  
439 equally, the AP scheme reached similar genetic change in production and  
440 higher genetic change in adaptation than the best introgression strategy  
441 (PiA). In some cases, the AP scheme may be the only way to conserve  
442 genes from both of the populations when either or both of the populations  
443 have too low number of animals to make a viable population. Because the  
444 potentially positive effects of heterosis were not considered in our study, the  
445 AP scheme may show even more positive results. However, heterosis  
446 effects would be expected to be lost rapidly in the AP scheme. In contrast,  
447 heterosis would contribute for a longer duration in the crossbreeding  
448 scheme, where each new generation would result in some heterosis because  
449 a separate donor line is maintained.

450 The rate of inbreeding  $\Delta F$  depends on the effective population size. The  
451 synthetic breed scheme AP increased population size by combining two  
452 breeds, leading to a lower rate of inbreeding than in the within breed  
453 schemes, which is expected. Similarly, genomic introgression schemes  
454 increase effective population size by incorporating genetic diversity from  
455 another population. However, in the simulated introgression schemes, the  
456 donor population remained separate during the simulation and allowed

457 continuous crossbreeding and thus featured a much lower rate of inbreeding  
458 than in the AP scheme.

459 Repeated crossbreeding or backcrossing between a locally adapted breed  
460 and a more productive breed has been used to breed locally adapted high  
461 milk yield cows. For example, in Yakutia, north-eastern Siberia, the locally  
462 adapted Yakutian cattle, which tolerate Siberian harsh cold environment,  
463 has been crossed with Simmental and Russian Kholmgor breeds to establish  
464 the Siberian Simmental and Siberian Kholmogor cattle populations,  
465 respectively (Li et al., 2005). These crossbreds have been backcrossed with  
466 the native Yakutian cattle to further develop two hybrid cattle populations.  
467 Breeding selection can be used for adaptation to local warm climate (e.g.  
468 Berman, 2011). In Ethiopia, the aim of crossbreeding native breeds to  
469 Holstein is to produce cows with at least 25% native and at most 75%  
470 Holstein breed proportions such that production is increased and adaptation  
471 is maintained (Negussie et al., 1999). Simulation results in our study support  
472 genomic introgression schemes from high production to adaptation (PiA)  
473 breeds to be reasonable when local adaptation is of high importance.  
474 However, the extent of crossbreeding varies in Africa even to such an extent  
475 that there is a risk of introgression into indigenous populations, and  
476 subsequent erosion of local genetic resources (Leroy et al., 2016). These  
477 risks are supported by our simulation results, where proportion of the AL



478 population genes decreased more rapidly in PiA than they increased in AiP,  
479 particularly when production was given a high weight.

480 In practice, any given farm is likely to have either high production or  
481 high adaptation animals. This influences the type of introgression preferred  
482 and possible. When a farm has high adaptation level animals and increasing  
483 production is desired, then the PiA scheme could be used. However, while  
484 increasing production and lowering adaptation may provide short term gains  
485 it incurs risks that will present themselves later. This is another reason to  
486 proceed cautiously using the PiA scheme. The use of AiP introgression is  
487 likely to show lower production but has the long-term benefit of adaptation.  
488 Climate change has direct and indirect effects on dairy cattle (Nardone et al.,  
489 2010; Kantanen et al., 2015). Indirect effects may be apparent earlier via  
490 extreme temperature or rainfall affecting feed production, which may  
491 require population replacement. The choice may then favour robust cattle  
492 that do not require high cost maintenance. The AL population had an  
493 adaptation level of zero at the beginning of the breeding scheme  
494 simulations. All schemes that showed a positive genetic level in adaptation  
495 in the last simulation year achieved the same level as the AL population at  
496 the beginning of the simulation. When adaptation was given a high weight,  
497 the genetic levels in adaptation were always positive. Even the PL  
498 population achieved high adaptation and was able to maintain high  
499 production during the simulation time of ten years.

500 Our simulation assumed a two-year generation interval, and ten years of  
501 selection. In practice, the absolute genetic levels and genetic change are  
502 unlikely to be this favourable over such a short period. First, we assumed  
503 that all animals were genotyped and genomic evaluation is in use. High but  
504 less efficient genetic change is likely to be achieved using single-step  
505 genomic evaluation (Aguilar et al., 2010; Christensen and Lund, 2010)  
506 when only some of the animals, e.g. all bulls, are genotyped. However, a  
507 basic assumption for the results to be applicable in practice is that an  
508 efficient breeding scheme is in place. Second, both traits in the simulation  
509 were assumed to be observed after the animal become mature, i.e. at the age  
510 of two years. In practice, first lactation milk yield is at the earliest available  
511 at the age of three, while adaptation data are available much later, depending  
512 on the defined trait (e.g., longevity). When genomic evaluation is used, it is  
513 important that the genotyped reference animals and their progeny have a  
514 sufficient number of observations. Thus, the more animals that have been  
515 genotyped, the higher the accuracy of genetic evaluation will be, and  
516 individual record information is less important. Third, the importance of  
517 genomic evaluation extends to the rate of inbreeding as well. When breeding  
518 value estimation is based on genomic information instead of pedigree  
519 information, using an animal model, selecting animals from different  
520 families becomes more likely, which translates to a lower rate of inbreeding.  
521 Fourth, the use of young two year old animals to selection allows short

522 generation interval and is feasible due to the use of genomic evaluation.  
523 However, calving at the age of 24 months may be too early. If a year in the  
524 simulation was extended to be 15 months, then the first calving would be at  
525 30 months. This would extend the simulation by 25% from ten to about 13  
526 years. Finally, it was assumed that both of the populations had an equally  
527 good recording system and that there were always breeding animals  
528 available. In practice, conserved local breeds may have too low a number of  
529 bulls with breeding values as accurate as in the major breed for an  
530 introgression scheme to succeed as well as in the simulations.

531 Our study design is quite unique and genomic introgression simulations  
532 including two selected traits have not been presented for dairy cattle.  
533 However, our results are similar to those in Ødegård et al. (2009b) where  
534 pure breed, synthetic breed and genomic introgression were simulated for  
535 fish. In particular, genetic increase in the simulated 5 years in production  
536 was higher (6.81 vs. 4.02) in the backcrossed scheme they used, similar to  
537 our PiA scheme (3.50 vs. 1.63) than in the pure breed scheme, but the  
538 opposite was the case for adaptation. Because each mating in fish produced  
539 20 offspring, selection intensity was higher, and the absolute values for  
540 genetic change were higher than achieved in our dairy cattle simulation.

541 All schemes featured a fairly low rate of inbreeding (Table 3). The major  
542 reason for this result was that even for the within population schemes, the  
543 number of selected males was quite high, and selection of females had low

544 intensity. However, the low rate of inbreeding also indicates moderate  
545 accuracy of the estimated breeding values. Accuracy of genomic evaluation  
546 by SNP-BLUP depends on the number of genotyped reference animals with  
547 records. The simulated population had many reference animals but only  
548 breeding bulls had a reasonable amount of information (20 daughter  
549 records). In practice, the reference animals are likely to have more accurate  
550 genomic evaluation which may give larger genetic differences between the  
551 schemes and higher rates of inbreeding.

552 We assumed a genetic correlation of -0.3 between adaptation and  
553 production. In addition, all loci affecting these traits were assumed to be  
554 shared. In practice, this would not be the case. However, this allowed a  
555 more realistic simulation than, for example, in Ødegård et al. (2009b) where  
556 no pleiotropic effects for QTL were assumed. The use of non-zero genetic  
557 correlations made selection to increase both the traits simultaneously more  
558 challenging, which also contributed to the lower genetic responses we found  
559 than were detected in the previous study of Ødegård et al. (2009b).

560 Changing genetic correlations and heritabilities will affect the absolute  
561 values achieved in our study. In particular, if heritability for production  
562 traits is higher and for adaptation traits is lower, increasing the genetic level  
563 of adaptation becomes more difficult, especially if the genetic correlation is  
564 more negative. However, the observed trends between the schemes under  
565 different selection index weights and conclusions should remain. For

566 example, our results confirm the value of conserving genetic resources for  
567 the benefit of introgressing their favourable characteristics into commercial  
568 breeding programs when the production trait has a high value.

569 Our simulations show that accelerated progress was achieved most  
570 efficiently by genomic introgression from the locally adapted into the  
571 production populations when (as is likely to be the case) production had a  
572 high weight in the selection index. This approach led to the selection of  
573 favourable locally adapted genes, while still maintaining a high level of  
574 production. Practical application of this scheme, however, should proceed in  
575 caution, especially focusing on locally adapted genes, ensuring that they are  
576 preserved in a separate local population. Knowing some or all of the  
577 favourable alleles of genes affecting the selected traits and using this  
578 information in the genetic evaluation can increase selection accuracy but  
579 further research is needed to quantify the change in genetic level and the  
580 likely increase in rate of inbreeding.

## 581 **Acknowledgements**

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583 Adaptation”) project funded by ERA-NET Plus on Climate Smart  
584 Agriculture Initiative.

## 585 **Conflict of Interest**

586 The authors declare that they have no conflict of interest.

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674 Figure Legends:

675 Figure 1.

676 QMSim simulation scheme.

677

678 Figure 2.

679 Repeated introgression backcrossing scheme of the production line (PL)

680 with the adaptation line (AL) for the first three years. For simplicity of

681 presentation, calves mature here after birth but in simulation after one year.

682

683 Figure 3.

684 Average proportion of AL population genes in cows by simulation year in

685 different introgression schemes from AL to PL (AiP). In the target

686 population selection index, adaptation and production were weighted by

687 ratio 2:1 (black), 1:1 (blue), and 1:2 (red). Selection index in the donor

688 population (AL) was the same as in the target population (solid line) or

689 random (dashed line).

690

691 Figure 4. Genetic change of production in genetic standard deviation by

692 selection index. The selection index weighted adaptation and production

693 equally in A1P1, by 2:1 ratio in A2P1 respectively, and by 1:2 ratio in A1P2

694 respectively. The non-introgression schemes A (circle), AP (square) and P  
695 (triangle) have solid lines, and the introgression schemes rAiP (cross), AiP  
696 (circle), and PiA (triangle) have dashed lines.

697

698 Figure 5. Genetic change of adaptation in genetic standard deviation by  
699 selection index. The selection index weighted adaptation and production  
700 equally in A1P1, by 2:1 ratio in A2P1 respectively, and by 1:2 ratio in A1P2  
701 respectively. The non-introgression schemes A (circle), AP (square) and P  
702 (triangle) have solid lines, and the introgression schemes rAiP (cross), AiP  
703 (circle), and PiA (triangle) have dashed lines.

704

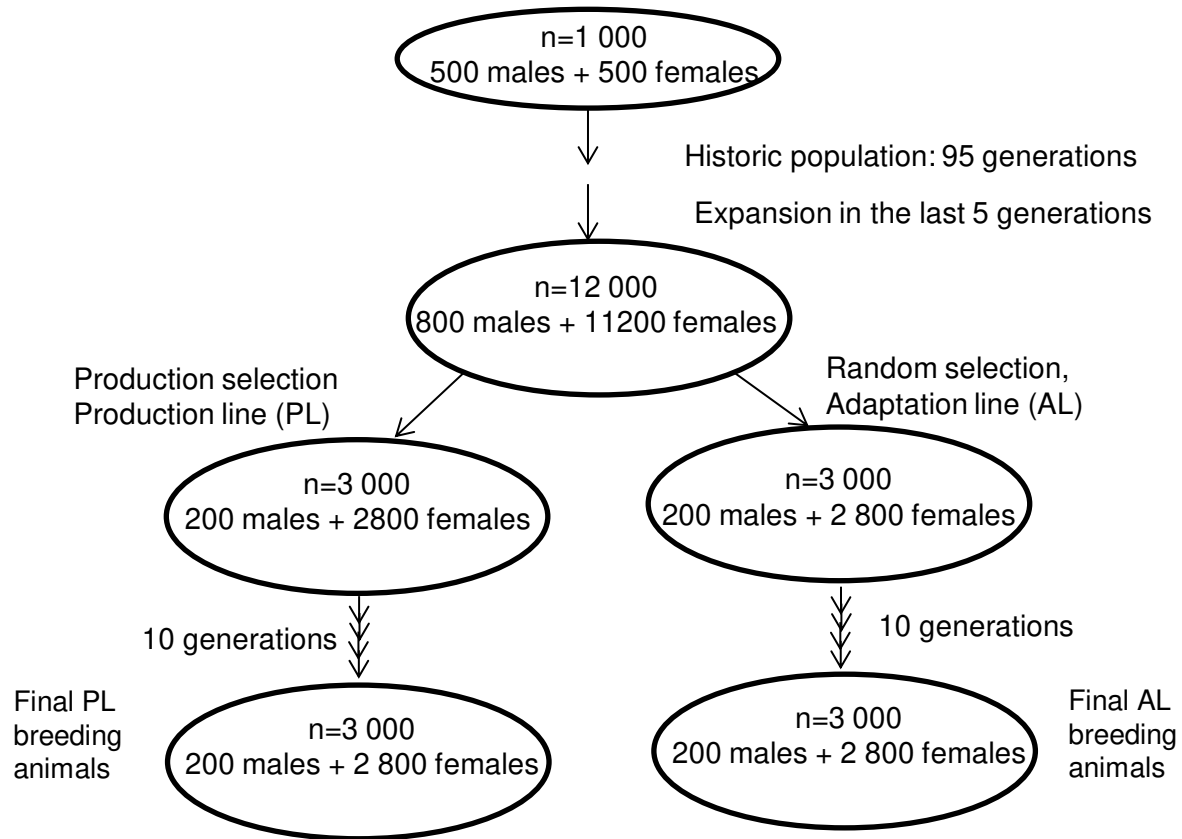
705 Figure 6. Genetic level of production in genetic standard deviation by  
706 selection index. The selection index weighted adaptation and production  
707 equally in A1P1, by 2:1 ratio in A2P1 respectively, and by 1:2 ratio in A1P2  
708 respectively. The non-introgression schemes A (circle), AP (square) and P  
709 (triangle) have solid lines, and the introgression schemes rAiP (cross), AiP  
710 (circle), and PiA (triangle) have dashed lines.

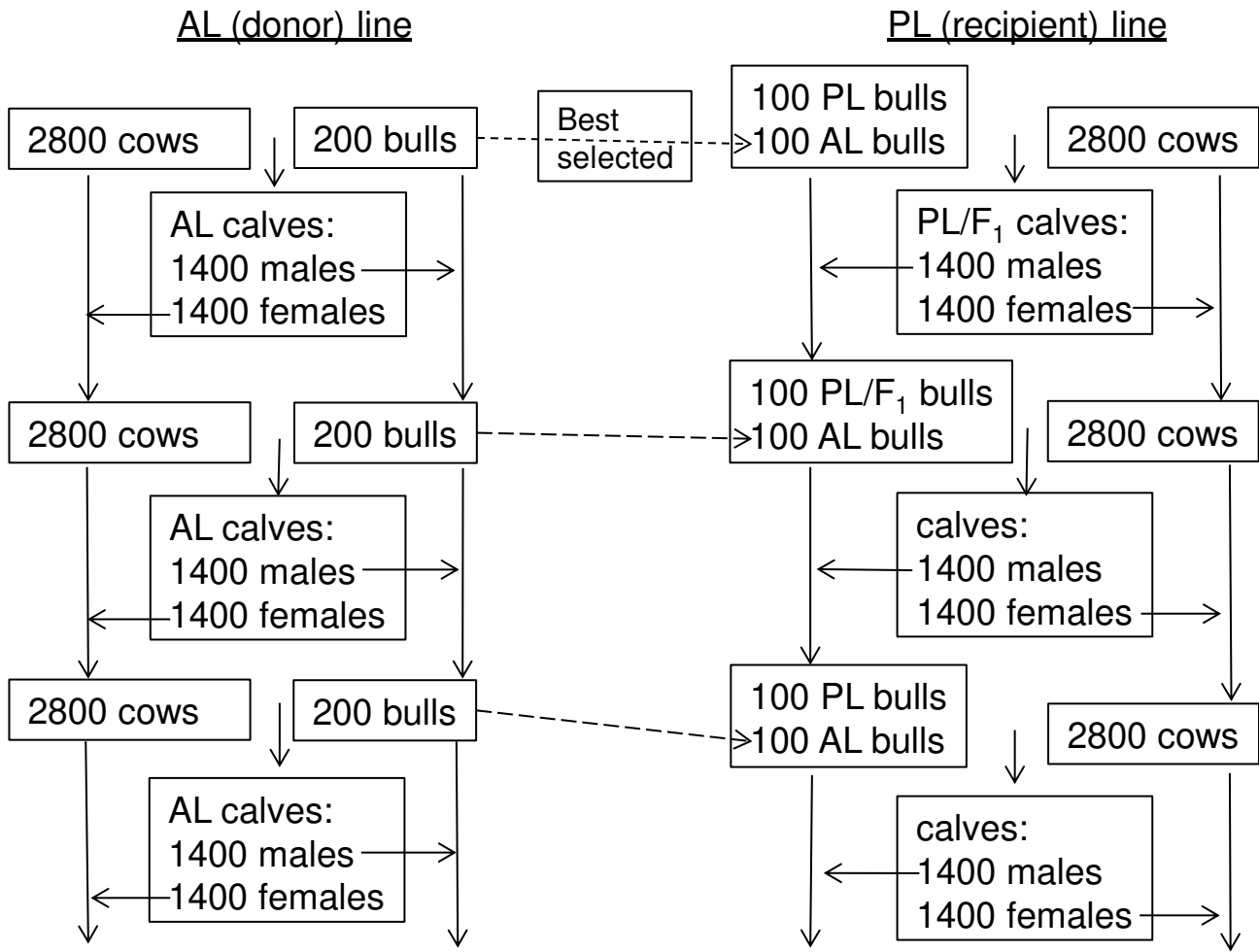
711

712 Figure 7. Genetic level of adaptation in genetic standard deviation by  
713 selection index. The selection index weighted adaptation and production

714 equally in A1P1, by 2:1 ratio in A2P1 respectively, and by 1:2 ratio in A1P2  
715 respectively. The non-introgression schemes A (circle), AP (square) and P  
716 (triangle) have solid lines, and the introgression schemes rAiP (cross), AiP  
717 (circle), and PiA (triangle) have dashed lines.

718



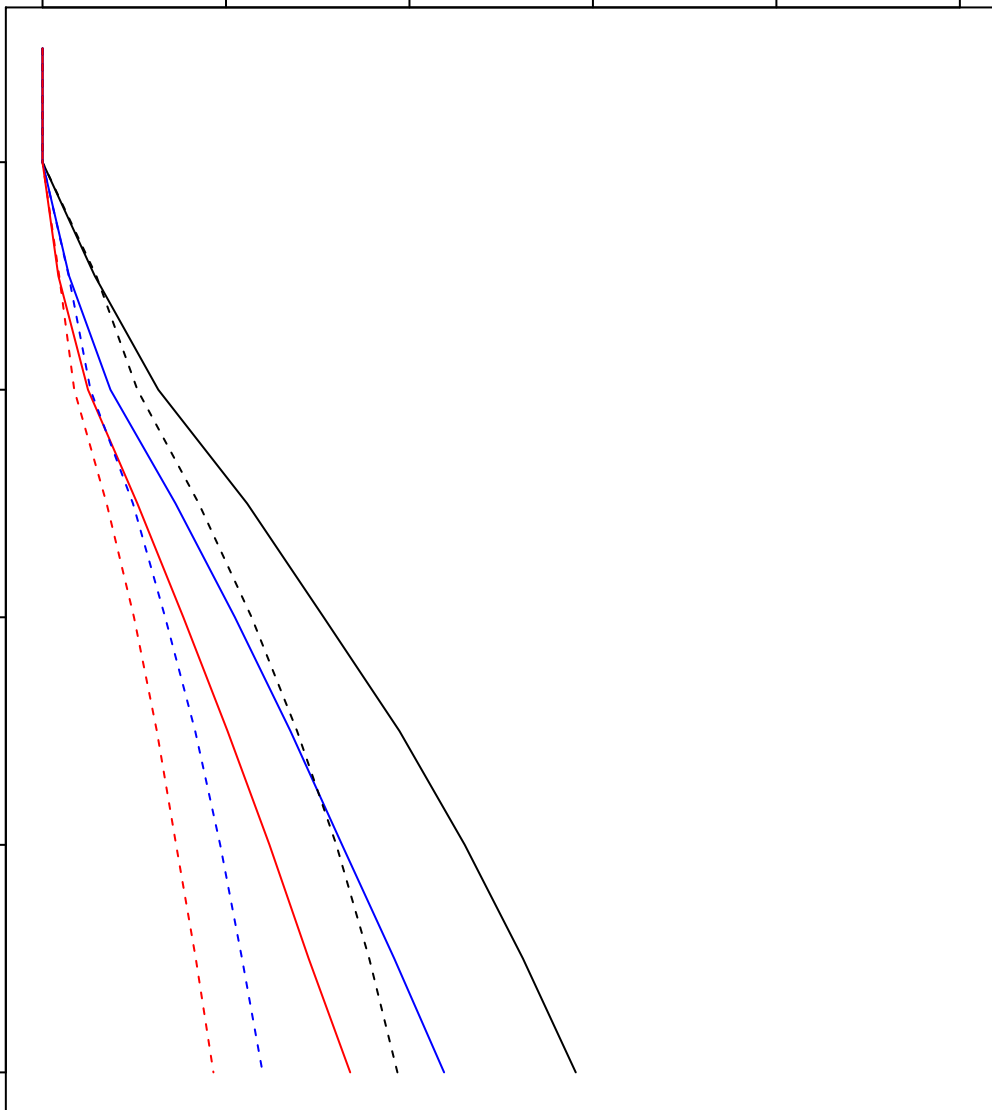


proportion AL genes

0.0 0.2 0.4 0.6 0.8 1.0

simulation year

2  
4  
6  
8  
10





Genetic change

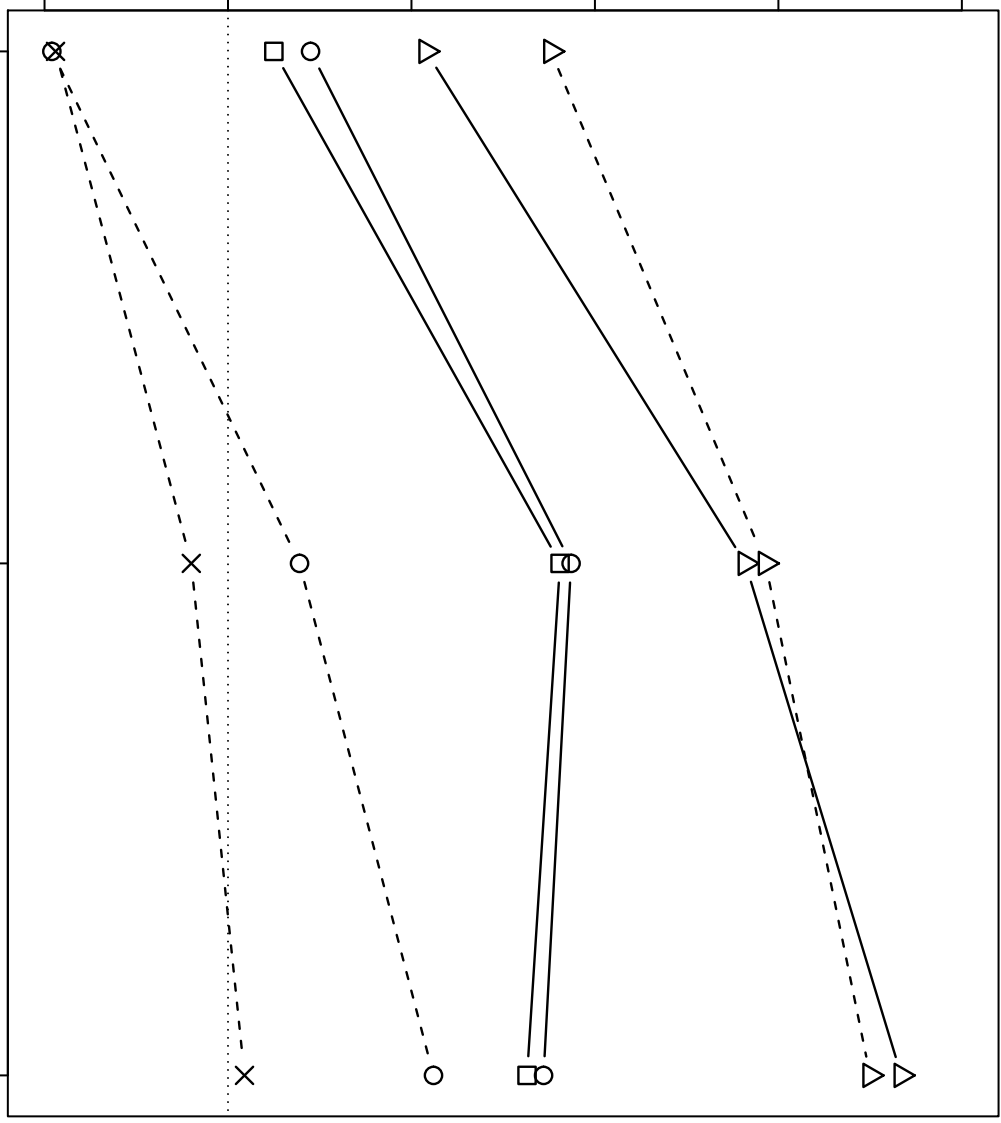
-1 0 1 2 3 4

A2P1

A1P1

A1P2

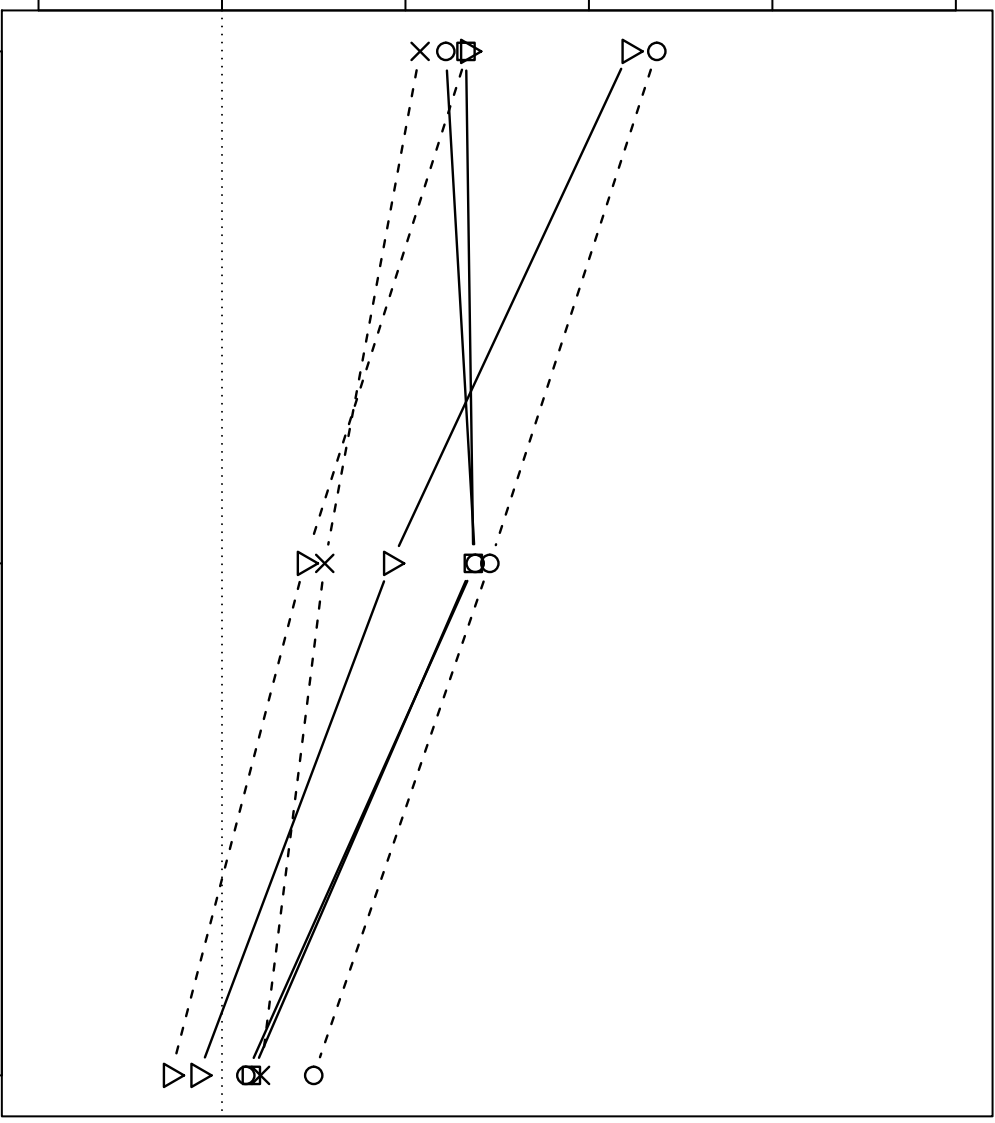
Index



# Genetic change

-1      0      1      2      3      4

A2P1  
A1P1  
A1P2  
Index



Genetic level

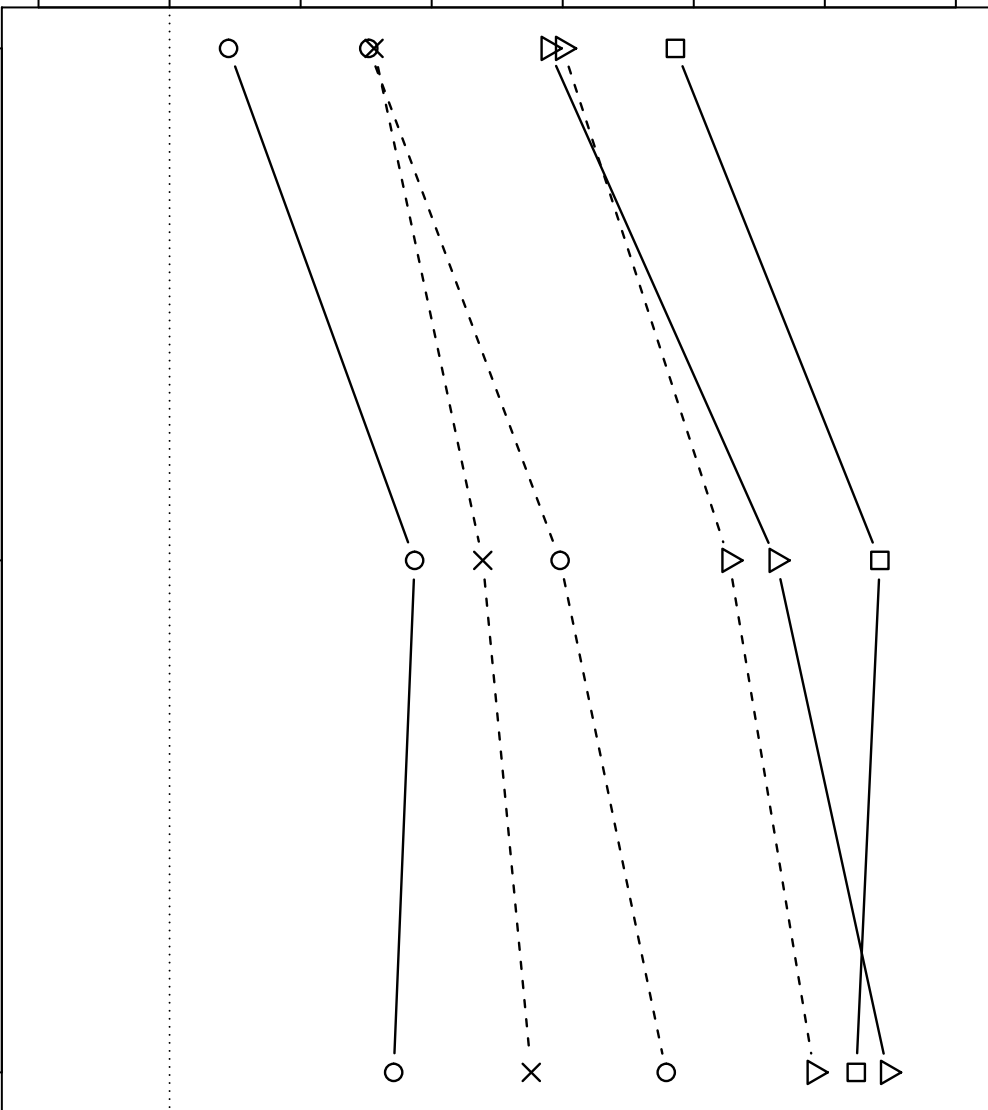
-1 0 1 2 3 4 5 6

A2P1

A1P1

A1P2

Index



Genetic level

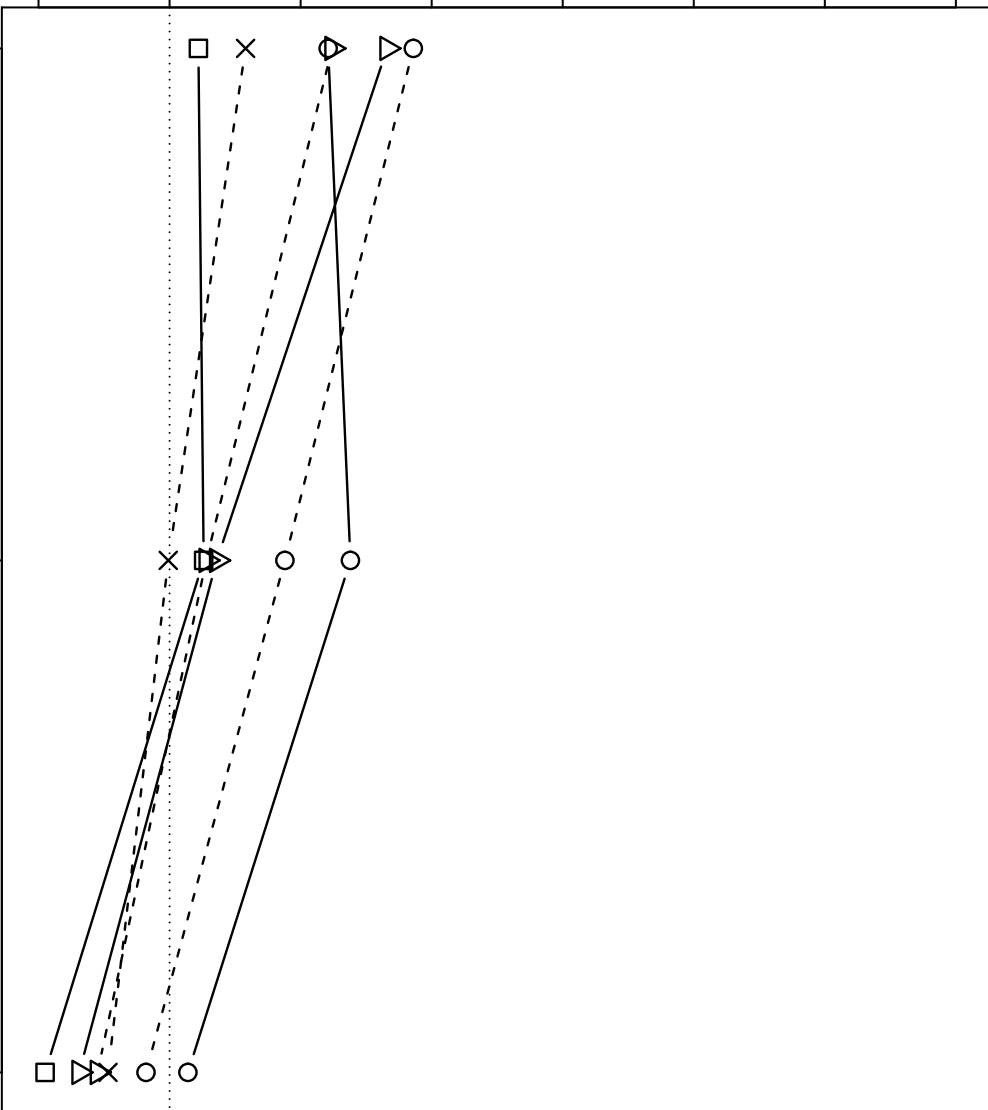
-1 0 1 2 3 4 5 6

A2P1

A1P1

A1P2

Index



1 Table 1. Parameters to simulation.

2

---

Parameter	Number
N breeding males	200
N breeding females	2,800
N progeny per mating	1
N females per male	14
$h^2$ , adaptation	0.1
$h^2$ , production	0.3
genetic correlation	-0.3
N chromosomes	30
Chromosome length	100 cM
N QTL simulated	900
N markers	54,000

---

3

1 Table 2. Steps in one simulation year after the QMSim simulation. Each  
2 step was a program in a script. In steps 1 to 5, current breeding animals are  
3 mated to produce calves. In steps 6 to 12, previous year calves mature and  
4 are included in genetic evaluation. These mature animals and current  
5 breeding animals are selection candidates for a new set of breeding animals.

---

Step Operation

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- 1) Search genotypes of breeding animals from all animals
  - 2) Make random mating pairs to the breeding animals in 1)
  - 3) Generate random recombination positions for the mating pairs in 2)
  - 4) Offspring genotypes by mating pairs in 2) using recombination positions in 3)
  - 5) Calculate true breeding values to the new genotypes in 4)
  - 6) Generate phenotypes to the maturing cows
  - 7) Generate pseudo phenotypes to the maturing bulls
  - 8) Extract all phenotype data for genetic evaluation by SNP-BLUP
  - 9) Extract genotypes for animals in 8)
  - 10) Calculate estimated breeding values by SNP-BLUP using data from 8) and 9)
  - 11) Calculate index (A1P1, A2P1 or A1P2) using estimated breeding values
  - 12) Select new breeding animals from the current breeding and the mature animals
- 

6



1 Table 3. Genetic change in last nine years ( $\Delta G$ ) and genetic level in the last year ( $G$ ) within scheme measured in genetic  
2 standard deviation units of the trait (production or adaptation), and rate of inbreeding per generation ( $\Delta F$ ) in percentages with  
3 standard error (SE) over five replicates. The selection index weighted adaptation and production equally in A1P1, by 2:1 ratio  
4 in A2P1 respectively, and by 1:2 ratio in A1P2 respectively.

5

Scheme*	Index	Production		Adaptation		$\Delta F$
		$\Delta G$ (SE)	G (SE)	$\Delta G$ (SE)	G (SE)	
A	A2P1	0.45 (0.05)	0.45 (0.05)	1.22 (0.04)	1.21 (0.03)	0.12 (0.004)
P	A2P1	0.25 (0.02)	3.86 (0.02)	1.33 (0.06)	0.22 (0.08)	0.17 (0.011)
AP	A2P1	1.08 (0.10)	2.89 (0.10)	2.22 (0.03)	1.66 (0.01)	0.07 (0.004)
rAiP	A2P1	-0.94 (0.06)	1.56 (0.05)	1.08 (0.05)	0.58 (0.03)	0.03 (0.002)
AiP	A2P1	-0.96 (0.09)	1.52 (0.07)	2.37 (0.04)	1.86 (0.03)	0.05 (0.004)
PiA	A2P1	1.76 (0.08)	3.00 (0.09)	1.34 (0.05)	1.24 (0.06)	0.04 (0.001)
A	A1P1	1.87 (0.06)	1.87 (0.06)	1.38 (0.05)	1.38 (0.05)	0.13 (0.006)
P	A1P1	1.81 (0.07)	5.42 (0.07)	1.37 (0.05)	0.26 (0.06)	0.20 (0.007)
AP	A1P1	2.82 (0.03)	4.63 (0.04)	0.92 (0.05)	0.36 (0.07)	0.09 (0.007)
rAiP	A1P1	-0.20 (0.04)	2.39 (0.01)	0.56 (0.03)	-0.01 (0.06)	0.04 (0.001)
AiP	A1P1	0.39 (0.06)	2.98 (0.07)	1.46 (0.06)	0.88 (0.07)	0.05 (0.003)
PiA	A1P1	2.93 (0.09)	4.27 (0.10)	0.45 (0.10)	0.28 (0.12)	0.04 (0.003)
A	A1P2	1.72 (0.08)	1.71 (0.07)	0.13 (0.04)	0.14 (0.04)	0.11 (0.009)
P	A1P2	1.63 (0.06)	5.24 (0.07)	0.16 (0.04)	-0.95 (0.10)	0.19 (0.007)
AP	A1P2	3.67 (0.04)	5.48 (0.05)	-0.13 (0.07)	-0.69 (0.10)	0.10 (0.005)
rAiP	A1P2	0.09 (0.05)	2.76 (0.03)	0.21 (0.03)	-0.47 (0.06)	0.04 (0.001)
AiP	A1P2	1.12 (0.04)	3.79 (0.04)	0.50 (0.03)	-0.18 (0.07)	0.05 (0.003)
PiA	A1P2	3.50 (0.05)	4.92 (0.07)	-0.28 (0.09)	-0.55 (0.12)	0.04 (0.003)

6

2

7 \*The A, P, and AP schemes used only adaptation line (AL), production line (PL), or combined AL and PL synthetic line  
8 individuals, respectively. The AiP scheme used introgression from AL to PL, and the PiA scheme used introgression from PL  
9 to AL. In the rAiP scheme, there was no selection in the AL donor line used in introgression.