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1 **IMPUTATION FOR GENOMIC EVALUATION IN LAYERS**

2 **Interest of using imputation for genomic evaluation in layer chicken**

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8 **GENETICS AND GENOMICS**

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26 **ABSTRACT**

27 With the availability of the 600K Affymetrix® Axiom® high-density (HD) single  
28 nucleotide polymorphism (SNP) chip, genomic selection has been implemented in broiler and  
29 layer chicken. However, the cost of this SNP chip is too high to genotype all selection  
30 candidates. A solution is to develop low density SNP chip, at a lower price, and to impute all  
31 missing markers. But to routinely implement this solution, the impact of imputation on  
32 genomic evaluation accuracy must be studied. It is also interesting to study the consequences  
33 of the use of low density SNP chips on genomic evaluation accuracy. In this perspective, the  
34 interest of using imputation in genomic selection was studied in a pure layer line.

35 Two low density SNP chip design were compared: an equidistant (EQ) methodology  
36 and a methodology based on linkage disequilibrium (LD). Egg weight, egg shell color, egg  
37 shell strength and albumen height were evaluated with single-step GBLUP methodology. The  
38 impact of imputation errors or the absence of imputation on the ranking of the male selection  
39 candidates was assessed with a genomic evaluation based on ancestry. Thus, genomic  
40 estimated breeding values (GEBV), with imputed HD genotypes or low density genotypes,  
41 were compared to GEBV obtained with the HD SNP chip. The relative accuracy of GEBV  
42 was also investigated by considering as reference GEBV estimated on offspring.

43 A limited reordering of the breeders, selected on a multi-trait index, was observed.  
44 Spearman correlations between GEBV on HD genotypes and GEBV on low density  
45 genotypes (with or without imputation) were always higher than 0.94 with more than 3K  
46 SNPs. For the genetically closer top 150 individuals for a specific trait, with imputation, the  
47 reordering was reduced with correlation higher than 0.94 with more than 3K SNPs. Without  
48 imputation the correlations remained below 0.85 with less than 3K and 16K SNPs for EQ and  
49 LD methodology, respectively. The differences in GEBV correlations between both  
50 methodologies never were significant. The conclusions were the same for all studied traits.

51 Key words: Genomic selection, layer chicken, low density panel, imputation accuracy,  
52 genomic evaluation accuracy

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## INTRODUCTION

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77       The availability of single nucleotide polymorphisms (SNP) enabled the development  
78 of high-throughput genotyping technologies leading to the use of the 600K Affymetrix®  
79 Axiom® high density (HD) genotyping array, a high-density genotyping chip developed by  
80 Kranis et al. in 2013, in layer and broiler breeding. Genomic selection as described by  
81 Meuwissen et al. (2001) has then been implemented in many livestock species with different  
82 statistical methods like genomic best linear unbiased prediction methods (GBLUP) (Legarra  
83 et al., 2009; Goddard et al., 2011) or Bayesian methods (Meuwissen et al., 2001; Xu, 2003;  
84 Habier et al., 2009). From a reference population with genotypes and phenotypes, it is  
85 possible to estimate the genomic value of the genotyped selection candidates with or without  
86 phenotype. The main objective is to choose among the selection candidates of generation  $N$ ,  
87 the best breeders for one or more traits to produce the individuals of the generation  $N+1$ . In  
88 addition, compared to a genetic selection, genomic selection may increase the genetic gain  
89 through the decrease in generation interval, most particularly for species with high generation  
90 interval, through the increase in selection intensity by genotyping many selection candidates  
91 and through the increase in evaluation accuracy.

92       However, the high cost of such high density (HD) SNP chip is still a problem for all  
93 livestock species. To reduce the cost of genomic selection, low density SNP chips can be  
94 developed. The idea is to select a subset of markers from the HD SNP chip and to impute the  
95 genotypes at missing markers. Three main methods to select the marker panel have been  
96 developed: (1) selection of a subset of SNPs chosen at regular intervals along each  
97 chromosome taking into account or not the MAF of the selected SNPs (Habier et al., 2009;  
98 Weigel et al., 2009; Zhang et al., 2011; Cleveland & Hickey, 2013; Wang et al., 2013; Herry  
99 et al., 2018), (2) selection of a subset of SNPs having high effects on different traits of interest  
100 (Weigel et al., 2009, Zhang et al., 2011), or (3) selection of a subset of SNPs based on linkage

101 disequilibrium (LD) between markers (Herry et al., 2018). This latter method was studied  
102 because of the particularities of the Gallus gallus genome (International Chicken Genome  
103 Sequencing Consortium, 2004) and the particular structure of the avian linkage disequilibrium  
104 (Megens et al., 2009; Qanbari et al., 2010; Héroult et al., 2018).

105 Factors influencing imputation accuracy are well documented as well as the relation  
106 between imputation accuracy and genomic evaluation of the selection candidates.  
107 Theoretically, due to imputation errors, genomic evaluation accuracy with imputed genotypes  
108 is expected to be lower than a genomic evaluation done with HD genotypes. The literature  
109 confirms it for very low density SNP chip (from few SNPs to 3K SNPs) with a decrease in  
110 genomic evaluation accuracy with a decrease, sometimes limited, in imputation accuracy  
111 (Weigel et al., 2009; Weigel et al., 2010; Mulder et al., 2012; Cleveland & Hickey, 2013,  
112 Raoul et al., 2017). But concerning intermediate low density SNP chip (between 6K and 20K  
113 SNPs), other studies showed that the impact of imputation errors was very limited (Weigel et  
114 al., 2010; VanRaden et al., 2011; VanRaden et al., 2012; Moghaddar et al., 2015; Wang et al.,  
115 2016). However, few studies about the impact of imputation on genomic evaluation have been  
116 led on chickens (Wang et al., 2013).

117 In addition, several studies showed that for traits affected by few large QTL, genomic  
118 evaluations are more sensitive to imputation errors. This was shown by Habier et al. (2009)  
119 and Zhang et al. (2011) in simulation studies and confirmed by Chen et al. (2014) on real  
120 data. They showed, in Holstein bulls, that the accuracy of direct genomic value (DGV) for  
121 milk fat percentage, a trait affected by few large QTL, decreased by 34% via GBLUP using  
122 imputed genotypes. Conversely, they showed that the accuracy of DGV for the somatic cell  
123 score, a trait affected by many small QTL, decreased only by 15%. In layer chickens, most of  
124 studied traits are affected by many small QTL. This could indicate that genomic evaluation  
125 would not be severely impacted by imputation errors.

126 Finally, most studies investigated the impact of imputation on genomic evaluation  
127 accuracy, but only few studies focused on the impact of the use of medium density SNP chip  
128 (Su et al., 2012; Moghaddar et al., 2015) or low density SNP chip (Weigel et al., 2009; Harris  
129 & Johnson, 2010) without imputation on genomic evaluation.

130 The main objective of a company is to select their breeders and to describe the  
131 consequences on the loss of selection response and on genetic progress by investigating if the  
132 ranking of their best candidates would be modified with the use of low density SNP chip.  
133 Thus, focusing on four generations of a pure line of laying hens, the first objective of this  
134 study was to investigate the impact of imputation errors on genomic evaluation with an  
135 evaluation based on ancestry of the candidates of the second generation with true HD  
136 genotyping or imputed HD genotyping. The second objective was to study the impact of a  
137 direct use of low density SNP chips, without imputation, on genomic evaluation. To do so, a  
138 comparison was done between the same previous genomic evaluation of the candidates based  
139 on ancestry with true HD genotyping or with low density genotyping without imputation.  
140 Then, to get closer to the true breeding values of the candidates, their genomic estimated  
141 breeding values (GEBV) was estimated with a genomic evaluation with optimal information  
142 (phenotypes on descendants). Thus, the third objective was to assess the relative accuracy of  
143 genomic evaluation by comparing the GEBV of the candidates of the second generation with  
144 optimal information (phenotypes on their descendants of the third and fourth generations) and  
145 their GEBV based on ancestry with imputed HD genotyping. Finally, imputed HD genotyping  
146 of the candidates were replaced by their low density genotyping without imputation.  
147 Therefore, the fourth objective was to assess the relative accuracy of genomic evaluation of  
148 the candidates without imputation.

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## MATERIAL AND METHODS

### 153 ***Ethics Statement***

154 All blood samples were carried out as part of the commercial and selection activities  
155 of Novogen. These animals studied and the scientific investigations described herein are  
156 therefore not to be considered as experimental animals per se, as defined in EU directive  
157 2010/63 and subsequent national application texts. As a consequence, we did not seek ethical  
158 review and approval of this study as one including the use of experimental animals. All  
159 animals were reared in compliance with national regulations pertaining to livestock  
160 production and according to procedures approved by the French Veterinary Services.

161

### 162 ***Animals***

163 All animals studied were detailed in Herry et al. (2018). They consisted in a  
164 commercial pure line of Rhode Island (RI) laying hens. This line was created and selected by  
165 Novogen (Plédran, France). The population studied was comprised of 21,475 chickens split in  
166 four generations. Each generation was divided in three batches and a new batch was bred  
167 every six months from 2010 to 2015 (Figure 1).

168 Concerning the laying hens, phenotypic data were recorded from 60 to 90 weeks of age, when  
169 birds were bred in individual cages. Each data collected was associated with a laying hen.  
170 There were 75,121 measures recorded for 7983 birds. Finally, the sires were bred in  
171 individual cages.

172 Genomic selection was implemented in 2015 on males of this line. However, females were  
173 still selected based on pedigree and performances, and not with genomic selection. Thus, this  
174 study concerned male selection candidates. In addition, among the different parameters



175 studied and detailed in a next section, the relative accuracy of genomic selection was  
176 investigated. To calculate this relative accuracy, it is necessary to have a set of male selection  
177 candidates with information on their offspring. These male selection candidates were the 67  
178 male breeders of the generation G1.

179

## 180 ***Genotyping***

181 Genotyping are briefly described because detailed in Herry et al. (2018). 2370 animals  
182 were genotyped for 580,961 SNPs using the 600K Affymetrix<sup>®</sup> Axiom<sup>®</sup> HD genotyping array  
183 (Kranis et al., 2013).

184 Based on the fifth annotation release of *Gallus gallus* genome (Warren et al., 2017),  
185 these SNPs were distributed on macro-chromosomes (1 to 5), intermediate chromosomes (6 to  
186 10), micro-chromosomes (11 to 28 and 33), one linkage group (LGE64), two sexual  
187 chromosomes Z and W, as well as a group of 3,724 SNPs with unknown location.

188 Genotypes were filtered through six successive steps (Table 1) including individual  
189 call rate (<95%), MAF (<0.05), SNP call rate (<95%) and Hardy-Weinberg equilibrium ( $P <$   
190  $10^{-4}$ ). SNPs with unknown location or located on sexual chromosome W were removed, as  
191 well as the animals showing pedigree incompatibilities. Most of the SNPs had to be removed  
192 because they showed zero MAF. Finally, 300,351 SNPs and 2362 individuals remained  
193 available for the analyses.

194

## 195 ***Low Density SNP Chips Design***

196 Several low density SNP chips were previously designed in silico by selecting a subset  
197 of SNPs (Herry et al., 2018) from the HD SNP chip.

198 An equidistant (EQ) methodology was studied by selecting SNPs at regular physical  
199 intervals (in pb) along each chromosome. In addition, for each interval, the SNP with the

200 highest MAF, or the one located furthest on the left, in case of equivalent MAF, was selected.  
201 12 low density “equi” SNP chips were designed according to this method with different SNP  
202 densities: 1K, 2K, 3K, 4K, 5K, 7.5K, 10K, 15K, 20K, 30K, 40K and 50K SNPs.

203 A linkage disequilibrium (LD) methodology was studied considering the particular  
204 structure of the chicken linkage disequilibrium (Robert et al., 2015). Low density SNP chips  
205 were designed using the SS4I software (Hérault et al., 2016). This software enabled to obtain  
206 clusters of SNPs according to a chosen LD threshold. For each cluster, the SNP with the  
207 highest MAF was selected and used as representative of this cluster. 9 low density “LD” SNP  
208 chips were designed with different LD thresholds: 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7 and 0.8.

209

### 210 ***Imputation Accuracy***

211 In our study, the selection candidates were the 580 sires of the second generation (G1)  
212 with simulated low density genotyping. The selection candidates were imputed from the high  
213 density genotyping of the 447 sires of the first generation (G0). These 447 individuals were  
214 the fathers or the fathers’ half-brothers of the selection candidates. Thus, the selection  
215 candidates were directly related to them.

216 For each low density SNP chip designed, imputation accuracy of the selection  
217 candidates was previously assessed as the mean correlation between true and imputed  
218 genotypes (Herry et al., 2018). Correlations were calculated one SNP at a time for all the  
219 candidates, as suggested in Pearson’s method. The mean correlation was then estimated on  
220 300,351 correlations. The mean correlations obtained were subsequently compared for the  
221 different low density SNP chips and/or scenarios, using Student tests with type 1 error rate of  
222 0.1%.

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## 226 **Measurement of Traits**

227 Four distinct traits were studied in this paper. They are named according to Animal  
228 Trait Ontology for Livestock (Atol Ontology, 2012). From 60 to 75 weeks, egg production  
229 was recorded each day for all individuals. There were individual data. 75,121 eggs concerning  
230 7983 birds were measured from (G0) to (G3).

231 One egg was collected per layer and per week, between 60 and 75 weeks, for all  
232 layers. These eggs were then transferred at Zootests (Ploufragan, France) to study egg quality  
233 traits. The first step was to measure Egg Weight (EW, in g). Then, three traits concerning egg  
234 shell color were estimated with a Minolta Chroma Meter: redness ( $a^*$ ), yellowness ( $b^*$ ) and  
235 lightness ( $L^*$ ) of egg shell. Egg Shell Color (ESC) was then calculated as  $ESC =$   
236  $100 - (L^* - a^* - b^*)$ . The next step consisted in measuring Egg Shell Strength (ESS, in N)  
237 by using a compression machine to evaluate the shell static stiffness. ESS corresponded to the  
238 maximum force recorded before fracturing the shell. Finally, each egg was broken and  
239 Albumen Height (AH) was measured using a tripod.

240

## 241 **Genomic Evaluation Strategies**

242 EW, ESC, ESS and AH were evaluated with single-step GBLUP methodology  
243 (Legarra et al., 2009) using BLUPF90 programs (Misztal et al., 2002).

244 The first part aimed to investigate the impact of imputation errors on genomic  
245 evaluations (Figure 2a). To do so, a genomic evaluation based on ancestry “Anc\_HD” was  
246 done using true HD genotyping of the 447 G0 sires and selection candidates (G1), and  
247 phenotypes of the first generation (G0). A second genomic evaluation based on ancestry  
248 “Anc\_Imputed” was done using the same data for the 447 G0 sires and imputed HD  
249 genotyping of the selection candidates (G1) from simulated low density SNP chips previously

250 designed. For each low density SNP chip and for each trait, Spearman correlations, that  
251 enabled to estimate the reordering of the selection candidates, were calculated between true  
252 “Anc\_HD” Genomic Estimated Breeding Value (GEBV) and “Anc\_Imputed” GEBV.  
253 Spearman correlations were calculated for the top 150 individuals from G1 according to each  
254 trait. Spearman correlations were limited to the top 150 males to better describe the  
255 consequences of imputation errors on the reordering of these individuals, and thus to better  
256 describe the consequences on the loss of selection response and on genetic progress. The  
257 objective was to identify the good candidates and to successfully rank them among  
258 themselves. We did not focus on the ranking of the less good candidates. There were also  
259 calculated for the 67 breeders from G1 having at least 10 offspring in G2.

260 Then, concerning the second objective, imputed HD genotyping of the candidates were  
261 replaced by their low density genotyping without imputation, allowing to simulate the impact  
262 of the direct use of the different low density SNP chips without imputation (Figure 2b). This  
263 part also implied the use of low density genotyping without imputation for the reference  
264 population. For each low density SNP chip and for each trait, Spearman correlations were  
265 calculated between the same previous true “Anc\_HD” GEBV and “Anc\_Not\_Imputed”  
266 GEBV obtained with low density genotyping (without imputation). These correlations were  
267 calculated for the same 67 breeders of G1 and the top 150 individuals from G1 according to  
268 each trait.

269 The third objective was to study the attainable relative accuracy with imputation  
270 (Figure 2c). To calculate this relative accuracy, it is necessary to have a set of male selection  
271 candidates with information on their offspring. On one hand, males don't have own  
272 phenotypes and only a few of them have daughter records. Thus, information from them is  
273 limited. On the other hand, Generation 2 had 662 genotyped females with own performances  
274 and some of them with progeny records. They would provide a more reliable validation set

275 with GEBVs using all available information fairly close to the true breeding values. However,  
276 females were still selected based on pedigree and performances, and not with genomic  
277 selection. Thus, this study focused on male selection candidates. To get closer to the true  
278 breeding values for the males, a genomic evaluation “Full\_HD” of the G1 candidates was  
279 done with all available information (phenotypes and genotypes) from (G0) to (G3). These  
280 “Full\_HD” GEBV led to closer to the true breeding values of the G1 candidates which  
281 cannot be calculated. These “Full\_HD” GEBV represented the maximum of relative accuracy  
282 attainable regarding this genomic evaluation with all information and were calculated only for  
283 the 67 G1 breeders which had at least 10 offspring in G2. Then, these “Full\_HD” GEBV were  
284 compared by Pearson correlations with the previous GEBV based on ancestry “Anc\_Imputed”  
285 with imputed HD genotyping of the breeders, for each simulated low density SNP chip.

286 Finally, imputed HD genotyping of the candidates were replaced again by their low  
287 density genotyping without imputation. The “Full\_HD” GEBV of the 67 G1 breeders were  
288 compared by Pearson correlations with their GEBV obtained with low density genotyping  
289 without imputation (“Anc\_Not\_Imputed” GEBV). The fourth objective was thus to  
290 investigate the impact of a direct use of low density SNP chips without imputation on relative  
291 accuracy of genomic evaluation (Figure 2d).

292 The four traits were jointly estimated according to a classical multi-trait animal model:  
293  $Y = 1\mu + X\beta + Zu + \varepsilon$ .  $Y$  is a vector of the four traits of each individual,  $\mu$  is the vector of  
294 means of each trait,  $\beta$  is a vector of fixed effects including batches, battery and position in the  
295 battery,  $u$  is a vector of genomic breeding values and  $\varepsilon$  is a vector of random residual effects.  
296  $X$  and  $Z$  are design matrixes relating respectively phenotypes to fixed effects and phenotypes  
297 to genomic breeding values ( $u$ ). It is assumed that  $u \sim N(0, H \otimes W)$  where  $H$  is the genetic  
298 relationship matrix combining SNP information and pedigree data (Legarra et al., 2009) and  
299  $W$  is the matrix of variance and covariance of the genomic breeding values of the four traits.

300 Finally,  $\varepsilon \sim N(0, I \otimes R)$  where  $I$  is the identity matrix and  $R$  is the matrix of residual variance  
301 and covariance of the four traits.

## 302 ***Software***

303 FImpute V2.2 (Sargolzaei et al., 2014) was used to impute the selection candidates  
304 with low density genotyping to high density genotyping from the individuals of G0 with high  
305 density genotyping.

306 The scenario with all available information (Full\_HD) was used to estimate the genetic  
307 parameters of the model. Remlf90 (Misztal et al., 2002) was used to estimate the genetic and  
308 residual variance components. Once fixed, all different genomic evaluations based on  
309 ancestry were performed with Blupf90. The variance components were compared to  
310 components estimated with a pedigree based model using all phenotypes. They were highly  
311 correlated (Picard Druet et al., 2019).

312

## 313 **RESULTS AND DISCUSSION**

### 314 ***Imputation Accuracy***

315 All the results concerning imputation accuracy were presented in Herry et al. (2018)  
316 but the evolution of the mean correlations between true and imputed genotypes for the two  
317 different methodologies were recalled in Figure 3. For both methodologies, there was an  
318 increase in mean correlation with an increase in the number of SNPs on the different low  
319 density SNP chips. Better imputation accuracies were obtained with the LD methodology at  
320 an equivalent SNP density. The differences observed in mean correlation between the two  
321 methodologies were all significant. In addition, for the EQ methodology at a very low density  
322 of 1K SNPs, the mean correlation was 0.7098 indicating a quite deteriorated imputation  
323 accuracy. This corresponded to a genotyping imputation error rate of 18.5%.

324           These results were consistent with those found in the literature (Dassonneville et al.,  
325 2012; Carvalheiro et al., 2014) where an increase in the number of SNPs on low density SNP  
326 chip led to better imputations.

### 327 ***Impact of Imputation Errors***

328           The impact of imputation errors was investigated by comparing the results of a  
329 genomic evaluation based on ancestry, with true HD genotyping or with imputed HD  
330 genotyping. Only the results for Egg Weight (EW) were shown to simplify the reading and  
331 because of the similarity of the results for the other traits.

332

### 333 ***Results For The Top 150 Individuals.***

334           For both methodologies (Figure 4a), there was an increase in Spearman correlations  
335 between “Anc\_HD” GEBV and “Anc\_imputed” GEBV with an increase in SNP density.  
336 Indeed, for the LD0.05 and LD0.8 SNP chips, the mean correlations were respectively 0.8661  
337 and 0.9931. For the 3Kequi and 20Kequi SNP chips, there were respectively 0.9045 and  
338 0.9885. These results are in agreement with imputation accuracies obtained with the different  
339 low density SNP chips. There was an increase in mean correlation concerning the evaluations  
340 with an increase in imputation accuracy which is consistent with the literature. Moghaddar et  
341 al. (2015) showed, for Merino sheep, that the mean correlations between GEBV based on true  
342 genotypes (50K) and GEBV based on imputed genotypes (50K imputed from 12K) increased  
343 with imputation accuracies.

344           It was noticed that for both methodologies, with more than 5K SNPs, the mean  
345 correlations were above 0.90 indicating a re-ranking rather reduced of the best individuals for  
346 EW. However, for the 1Kequi SNP chip, the mean correlation was 0.7833 indicating a  
347 reordering quite important of the best individuals for egg weight.

348 Finally, at equivalent SNP density of 3K SNPs, the EQ methodology seemed to  
349 present higher results than the LD methodology with mean GEBV correlations of respectively  
350 0.9045 and 0.8661 for the 3K<sub>equi</sub> and LD0.05. But the differences were not significant since  
351 the standard errors were  $\pm 0.04$  for both SNP chips. At a density of 20K SNPs, both  
352 methodologies were equivalent with mean GEBV correlations of respectively 0.9885 and  
353 0.9931 for the 20K<sub>equi</sub> and LD0.8. However, as seen previously, the LD methodology  
354 appeared to be better to get good imputation accuracies. Thus, higher imputation accuracies  
355 with the LD methodology were not synonymous of better mean correlations between GEBV  
356 compared to the EQ methodology. This could be due to the methodology itself. Indeed, Harris  
357 and Johnson (2010) and Weigel et al. (2010) said that an equidistant methodology was better  
358 to get good genomic evaluation results for traits controlled by many small QTL, which is the  
359 case for the four traits studied. On the contrary, genomic evaluations concerning traits  
360 controlled by few large QTL were more sensitive to equidistant methodology which was  
361 consequently not the most appropriated methodology. Moreover, ssGBLUP methodology  
362 considers a same variance for each SNP (Legarra et al., 2009) and consequently would favor  
363 the EQ methodology. Finally, another reason could be due to the errors done with imputation.  
364 Some imputation errors from LD SNP chips could degrade more the GEBV estimation than  
365 imputation errors from equidistant SNP chips. The EQ methodology would be more robust  
366 than the LD methodology in case of imputation errors.

367

### 368 ***Results For The Breeders.***

369 Spearman correlations between “Anc<sub>HD</sub>” GEBV and “Anc<sub>Imputed</sub>” GEBV were  
370 also calculated for the 67 G1 breeders having at least 10 offspring in the next generation G2.  
371 For both methodologies (Figure 4b), there was an increase in Spearman correlations with an  
372 increase in SNP density. Indeed, for the LD0.05 and LD0.08 SNP chips, the mean GEBV



373 correlations were respectively 0.9777 and 0.9979. For the 3Kequi and the 20Kequi SNP chips,  
374 the results were respectively 0.9771 and 0.9972. Thus, the results were higher compared to  
375 the results for the top 150 individuals. This is due to the distribution of the 67 breeders which  
376 were not the best breeders of G1 for EW, but the best for a set of selection criteria. This was  
377 confirmed by plotting the normal distribution of HD GEBV estimated on ancestry with true  
378 HD genotyping for all G1 candidates (Figure 5). The 67 breeders (in red on the plot) were  
379 well distributed among the 580 individuals of G1 which reduced the reordering of the  
380 individuals.

381 The results also showed that even with a SNP density superior to 2K SNPs, good mean  
382 correlations (superior to 0.95) could be obtained indicating a very reduced re-ranking of the  
383 individuals. With only 5K SNPs imputed to the HD SNP chips, mean correlations above 0.98  
384 could be reached.

385         However, with the 1Kequi SNP chip, the mean GEBV correlation was under 0.95.  
386 This decrease in correlation was also illustrated by Cleveland and Hickey (2013) in pig. They  
387 used only 450 SNPs imputed to the Illumina PorcineSNP60 BeadChip which resulted in a  
388 decrease in correlation to 0.866 (for an imputation accuracy of 0.914). Thus, by decreasing to  
389 much the SNP density, the reduced imputation accuracies can have negative consequences on  
390 genomic evaluations.

391         Finally, our results did not show any difference between EQ and LD methodologies.

392

### 393 ***Impact of the Absence of Imputation***

394         Given the good results of genomic evaluations with imputed genotyping, the impact of  
395 the absence of imputation was studied. Only the results for Egg Weight (EW) were shown to  
396 simplify the reading and because of the similarity of the results for the other traits.

397

398 ***Results For The Top 150 Individuals.***

399 For the top 150 individuals for both methodologies (Figure 6a), there was an increase  
400 in Spearman correlation between “Anc\_HD” GEBV and “Anc\_Not\_Imputed” GEBV with an  
401 increase in SNP density. Indeed, the mean correlations for the 3Kequi and the 20Kequi SNP  
402 chips were respectively 0.8507 and 0.9379. For the LD0.05 and the LD0.8 SNP chips there  
403 were respectively 0.7816 and 0.8658. Zhang et al. (2011) showed in simulation studies that  
404 compared to the results of a genomic evaluation done with HD SNP chip, the results of  
405 genomic evaluations done with low density SNP chips without imputation also decreased.  
406 With an effective population size of 100, heritability of 0.5, 241 QTL, and a SNP chip of 10K  
407 markers, the relative accuracy of the GBLUP evaluation decreased from 0.88 with 5K  
408 markers to 0.69 with only 200 markers.

409 For both methodologies, there was a consequent decrease in mean correlations  
410 compared to the results of the genomic evaluations done with imputed HD genotyping. For  
411 the 1Kequi and the 50Kequi SNP chips, both imputed, the results were respectively 0.7833  
412 and 0.9964. Without imputation, the results were respectively 0.6261 and 0.9503. Likewise,  
413 for the LD0.05 and the LD0.8 SNP chips with imputation, the results were respectively  
414 0.8661 and 0.9931. Without imputation, the results decreased respectively to 0.7816 and  
415 0.8658. Furthermore, from 20K SNPs, the results for the EQ methodology seemed to reach a  
416 mean correlation threshold of 0.95 whereas with imputation the mean correlations were above  
417 0.99. Thus, imputations enabled to increase significantly the mean correlations, mainly for  
418 very low density SNP chips. In addition, these results indicate that the ranking of the best 150  
419 individuals of G1 for EW obtained without imputation was quite different from the ranking  
420 obtained with HD genotyping. The lower results obtained for very low SNP density indicated  
421 that using few SNPs could not be sufficient to accurately rank individuals having very close  
422 genomes.

423 Finally, at equivalent SNP density, a tendency to get higher results with the EQ  
424 methodology was observed. Indeed, at 3K SNPs, the difference in mean correlation between  
425 3Kequi and LD0.05 SNP chips was equal to 0.07. The same difference was obtained between  
426 20Kequi and LD0.8 SNP chips. Such differences were higher than with imputation but were  
427 not significant. However, we can note that the correlations remained always below 0.90 for  
428 the top 150 individuals whatever the SNP density with the LD methodology without  
429 imputation. The differences between methodologies are consistent with the genetic  
430 determinism of the four traits as explained in the previous part (Harris and Johnson, 2010;  
431 Weigel et al., 2010). In addition, the EQ methodology enabled a covering of all chromosomes  
432 more optimal than the LD methodology (Herry et al., 2018). With the LD methodology, there  
433 were some gaps on chromosomes without SNPs selected on low density SNP chips. With the  
434 EQ methodology, the number of gaps was decreased, or at least their size was lower.

435

#### 436 ***Results For The Breeders.***

437 Spearman correlations between “Anc\_HD” GEBV and “Anc\_Not\_Imputed” GEBV  
438 were also calculated for the 67 breeders (Figure 6b). For both methodologies, there was an  
439 increase in Spearman correlations with an increase in SNP density. At equivalent SNP  
440 density, the results for the 3Kequi and 20Kequi SNP chips were respectively 0.9484 and  
441 0.9802. For the LD0.05 and LD0.8 the results were respectively 0.9349 and 0.9665.  
442 Compared to the results for the top 150 individuals, the results were better for the 67 breeders  
443 as shown previously in the scenario with imputation. Finally, for a SNP density higher than  
444 3K, the mean correlations were above 0.94 for both methodologies, indicating a reordering  
445 rather reduced of the 67 breeders. In bovine, Weigel et al. (2009) showed that compared to the  
446 top 500 bulls selected from progeny testing, 306 were truly selected with 32K SNPs chosen  
447 from the Illumina BovineSNP50 Bead Chip. With 2K equally spaced SNPs, 292 bulls were

448 chosen. With only 500 equally spaced SNPs, 247 bulls were chosen. This illustrates that  
449 compared to the HD SNP chip, the re-ranking was limited and that even with few SNPs, the  
450 reordering of the individuals was limited.

451 Compared to the results obtained with imputation, there was a slight decrease in  
452 correlations with “Anc\_HD” GEBV. Indeed, for the 1Kequi and 50Kequi SNP chips, the  
453 results were respectively 0.9316 ( $\pm 0.0451$ ) and 0.9983 ( $\pm 0.0072$ ) with imputation, and 0.8718  
454 ( $\pm 0.0608$ ) and 0.9815 ( $\pm 0.0238$ ) without imputation. Likewise, for the LD0.05 and the LD0.8,  
455 the results were respectively 0.9777 ( $\pm 0.0261$ ) and 0.9979 ( $\pm 0.0080$ ) with imputation, and  
456 0.9349 ( $\pm 0.0440$ ) and 0.9665 ( $\pm 0.0318$ ) without imputation. Thus, the differences observed  
457 for both methodologies were not significant and the results were still high whatever the SNP  
458 chip used. These results were rather different from those obtained by Aliloo et al. (2018).  
459 They showed in bovine, for 1034 individuals, that correlations between HD GEBV (on 777K  
460 genotypes) and GEBV based on imputed HD genotyping were significantly higher than  
461 without imputation. Indeed, according to their MAFI (Minor Allele Frequency within  
462 Interval) method which was the closest to our EQ methodology, using 4013 and 25,410 SNPs  
463 imputed to 777K SNPs resulted respectively in correlations of 0.9398 and 0.9927. These  
464 results decreased dramatically without imputation with correlations of respectively 0.6485 and  
465 0.8598. Such a large decrease was not observed in our study.

466 Finally, the differences observed between the two methodologies were also not  
467 significant. Consequently, the simpler EQ methodology seems to be sufficient to get good  
468 genomic evaluation results for traits controlled by many small QTL, which is the case for the  
469 four traits studied.

470

471 ***Impact Of Imputation On Relative Accuracy Of Genomic Evaluation***

472 The impact of imputation on the attainable relative accuracy of genomic evaluations  
473 was studied by comparing a genomic evaluation “Full\_HD” of the 67 G1 breeders using all  
474 available information (phenotypes and genotypes) from generation (G0) to (G3) and GEBV of  
475 the G1 breeders based on ancestry with imputed HD genotyping (“Anc\_Imputed” GEBV), for  
476 each low density SNP chip. Only the results for Egg Weight (EW) were shown to simplify the  
477 reading and because of the similarity of the results for the other traits.

478 It was noticed (Figure 7) for the EQ methodology a slight increase in Pearson  
479 correlations from very low density SNP chips to 20K SNPs. Indeed, for the 1Kequi and the  
480 20Kequi SNP chips, the mean correlations were respectively 0.4472 and 0.4854. But for the  
481 LD methodology, the results were rather stable with mean correlations of respectively 0.4917  
482 and 0.4875 for the LD0.05 and LD0.8 SNP chips. For both methodologies, the results varied  
483 slightly up to 20K SNPs. They became steady for the EQ methodology from 20K to higher  
484 SNP densities. Finally, for both methodologies, the correlations of “Anc\_Imputed” GEBV  
485 with “Full\_HD” GEBV were not significantly different from those obtained by comparison  
486 between true HD GEBV on ancestry and “Full\_HD” GEBV. The mean correlation was  
487 0.4848 and corresponded to a theoretical maximum value attainable. The standard error for  
488 each low density SNP chip was  $\pm 0.11$  indicating that there was no difference with the  
489 theoretical maximum value. For information purposes, the mean correlations for ESC, ESS  
490 and AH were  $0.2618 \pm 0.12$ ,  $0.4027 \pm 0.11$  and  $0.4802 \pm 0.11$ . This is consistent with the  
491 previous results showing a very slight impact of imputations errors on GEBV estimations of  
492 the 67 breeders on ascendance. For both methodologies, from a density of 5K SNPs imputed  
493 to the HD SNP chip, the mean correlations were above 0.98 between “Anc\_HD” GEBV and  
494 “Anc\_Imputed” GEBV. These results are also in agreement with the literature. Indeed, Harris  
495 and Johnson (2010) showed that in bovine, from 5K to 1000K SNPs, the increase in  
496 correlations between true phenotypes and predicted phenotypes was very limited (0.62 to

497 0.65). VanRaden et al. (2012) showed that, for 28 traits tested in bovine, in average, the  
498 estimated genomic reliability was 61.1% with 300K SNPs and decreased to only 60.7% when  
499 they used 45K SNPs. In the study of Wellman et al. (2013), 768 SNPs imputed to the Illumina  
500 PorcineSNP60 BeadChip (60K SNPs) led to a negligible loss in genomic evaluation accuracy.  
501 Likewise, Chen et al. (2014) estimated in bovine that the accuracy of genomic prediction with  
502 observed 50K or imputed 50K (from 6K) genotypes was 0.61 for milk yield and 0.62 for  
503 somatic cell score (SCS).

504         However, a decrease in relative accuracy was observed with the 1Kequi SNP chip with  
505 a mean correlation of 0.4472. The highest decrease was observed for albumen height (AH)  
506 where the mean correlation for the 1Kequi SNP chip was 0.4045 ( $\pm 0.11$ ) and the theoretical  
507 maximum value was 0.4802. One cannot conclude about the significance of this difference  
508 but this decrease was also expected because the results regarding the impact of imputation  
509 accuracies showed a mean correlation of 0.9316 for the 1Kequi SNP chip. Other studies  
510 showed that decreasing too much the SNP density has consequences on genomic evaluation  
511 accuracies. Raoul et al. (2017) illustrated this point in Merino sheep where using only 500 or  
512 250 SNPs imputed to the Illumina OvineSNP50 BeadChip resulted respectively in a decrease  
513 in accuracies from 0.53 (with HD SNP chip) to 0.45 and 0.38. Wellman et al. (2013) showed  
514 that 384 SNPs imputed to the Illumina PorcineSNP60 BeadChip led to a loss of 3% in  
515 genomic evaluation accuracy. Likewise, Chen et al. (2014) showed that the accuracy of  
516 genomic prediction decreased from 0.61 to 0.49 for milk yield and from 0.62 to 0.53 for SCS  
517 with imputed 50K genotypes from 384 SNPs.

518         Consequently, we can conclude that the effects of imputation errors on GEBV relative  
519 accuracies were very limited even if slightly more important for very low densities.

520

521 ***Impact of the Direct Use of Low Density SNP Chips Without Imputation on***

522 ***Relative Accuracy of Genomic Evaluation***

523 The impact of the direct use of low density SNP chips on relative accuracy of genomic  
524 evaluation was studied by comparing the “Full\_HD” GEBV of the G1 and GEBV of the G1  
525 breeders on ancestry with low density genotyping without imputation (“Anc\_Not\_Imputed”  
526 GEBV), for each low density SNP chip. For both methodologies, only the results for Egg  
527 Weight (EW) were shown to simplify the reading and because of the similarity of the results  
528 for the other traits.

529 Both methodologies were rather stable with slight variations in Pearson correlations up  
530 to 20K SNPs (Figure 8). The results for the 3Kequi and 20Kequi SNP chips were respectively  
531 0.4471 and 0.4675. For the LD0.05 and LD0.8 the correlations were respectively 0.4583 and  
532 0.4888. However, the standard errors associated to these results were  $\pm 0.11$  and the  
533 correlation between the “Full HD” GEBV and the HD GEBV based on ancestry was 0.4848.  
534 This indicates that the differences observed between each low density SNP chip, and  
535 consequently between the two methodologies, were not significant. These results are in  
536 agreement with the previous results showing a very slight impact of the absence of imputation  
537 on GEBV estimation of the 67 breeders on ascendance. However, the results for the 1Kequi  
538 was 0.4018 ( $\pm 0.11$ ). This lower but non-significant result was also expected because the  
539 correlation between “Anc\_HD” GEBV and “Anc\_Not\_Imputed” GEBV was lower (0.8718  
540  $\pm 0.0608$ ) than those obtained with higher SNP densities. This was the case for all traits  
541 studied.

542 The results found in the literature are contrasted. Moghaddar et al. (2015) showed in  
543 Merino sheep, that the accuracy of genomic prediction based on observed 50K genotypes was  
544 0.446 for post-weaning weight (PWW) and 0.219 for post-weaning eye muscle depth  
545 (PW\_EMD). Based on genotypes imputed from 12K to 50K genotypes, with imputation

546 accuracy comprised between 0.88 and 0.99, the accuracy of genomic prediction was 0.443 for  
547 PWW and 0.219 for PW\_EMD. Based on observed 12K genotypes, the accuracy was 0.412  
548 for PWW and 0.205 for PW\_EMD. Thus, the results were slightly better with imputation  
549 compared to a direct use of the 12K without imputation, but in both cases, there was not a  
550 dramatic decrease in genomic prediction accuracy despite a significant gap of SNP density  
551 between HD and low density chips. Weigel et al. (2009) had a gap of SNP density closer to  
552 our but the results were rather different. The correlation between the results from progeny  
553 testing and the genomic result with a HD SNP chip of 32K was 0.612. With 300, 1K and 2K  
554 equally spaced SNPs, the results were respectively 0.253, 0.422 and 0.539. Contrary to the  
555 results of Moghaddar et al. (2015), there was a significant decrease in their results with the  
556 use of low density SNP chips without imputation. In 2010, they showed that their results were  
557 better with imputation.

558 Finally, for a SNP density higher than 3K, using low density SNP chips without  
559 imputation led to results as good as those obtained with the HD SNP chip itself.

560

561

## CONCLUSIONS

562 This study showed a very limited reordering of the breeders, selected on a multi-traits  
563 index, with low density genotyping (with or without imputation) instead of HD genotyping.  
564 Indeed, Spearman correlations between GEBV on HD genotyping and GEBV on low density  
565 genotyping were always higher than 0.94 with more than 3K SNP. For the top 150  
566 individuals, who are genetically closer than the breeders, the reordering was a bit more  
567 important. Thus, the correlations between GEBV with HD genotyping and GEBV with low  
568 density genotyping remained below 0.85 with less than 3K SNP with the EQ methodology  
569 and less than 16K SNP (LD0.6) with the LD methodology. The differences in GEBV



570 correlations between the two methodologies were never significant but seemed to indicate that  
571 the simpler EQ methodology was sufficient to obtain similar results.

572 Thus, using directly low density SNP chips designed with the EQ methodology with  
573 more than 5K SNPs could enable to get good results of genomic evaluation and could be a  
574 cost effective solution for genomic selection. However, only four traits were studied. These  
575 four traits were controlled by many small QTL, which explained why the equidistant  
576 methodology was more appropriated to realize genomic evaluation with ssGBLUP than the  
577 LD methodology, whereas the results on imputation accuracies were inverted. Further  
578 investigations on other traits with different genetic architectures should be conducted.

579 Finally, as shown by Habier et al. (2009), there could be a decrease in genomic  
580 evaluation accuracy over the generations with low density genotyping. This would require to  
581 genotype at higher density birds selected at each generation to avoid a decrease in genomic  
582 evaluation accuracy which could be prejudicial for genomic selection. In addition, in our  
583 study, only the males were genotyped but having both parents genotyped could lead to higher  
584 genomic evaluation accuracies.

585

586

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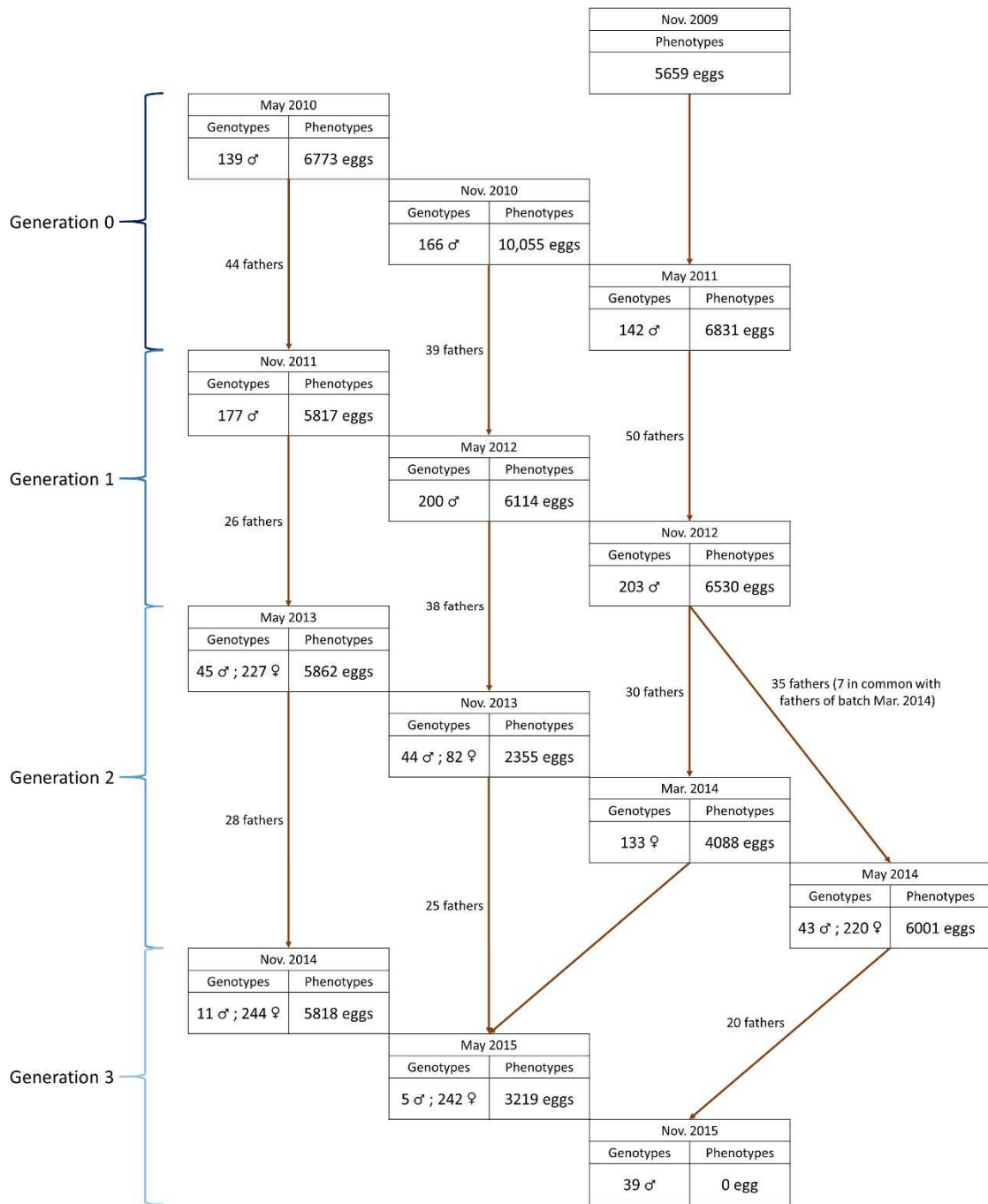
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Table 1. Summary of the different steps of quality control

<b>Genotypes filtration</b>	<b>RI Line</b>
Individual Call Rate (<95%)	8
MAF (=0)	204,122
MAF (<0.05)	54,650
SNP Call Rate (<95%)	7541
Hardy-Weinberg equilibrium ( $P < 10^{-4}$ )	12,538
SNP with unknown location or on chromosome W	1759
Pedigree Incompatibility	0
<b>SNP retained for analyses</b>	<b>300,351</b>
<b>Animals retained for analyses</b>	<b>2362</b>

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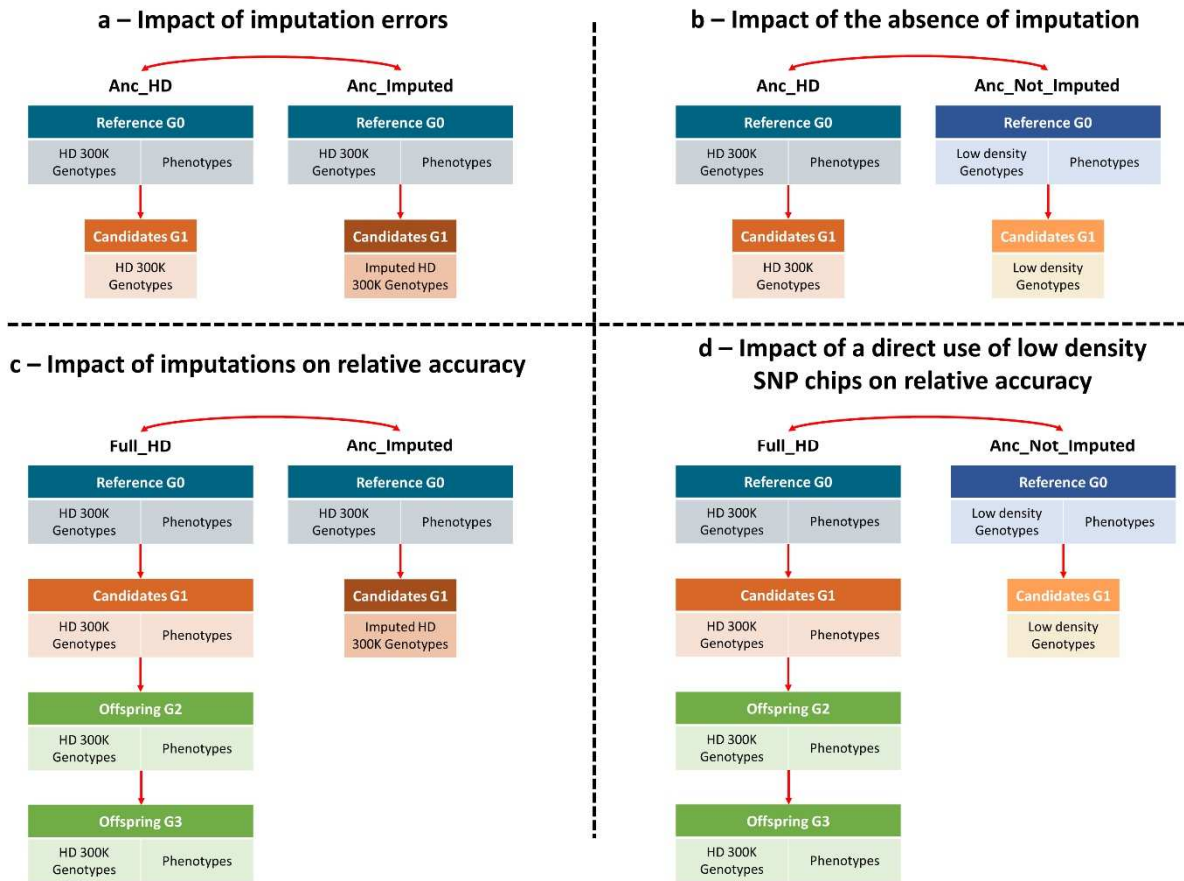
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733 **Figure 1.** Population structure of the RI line

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735

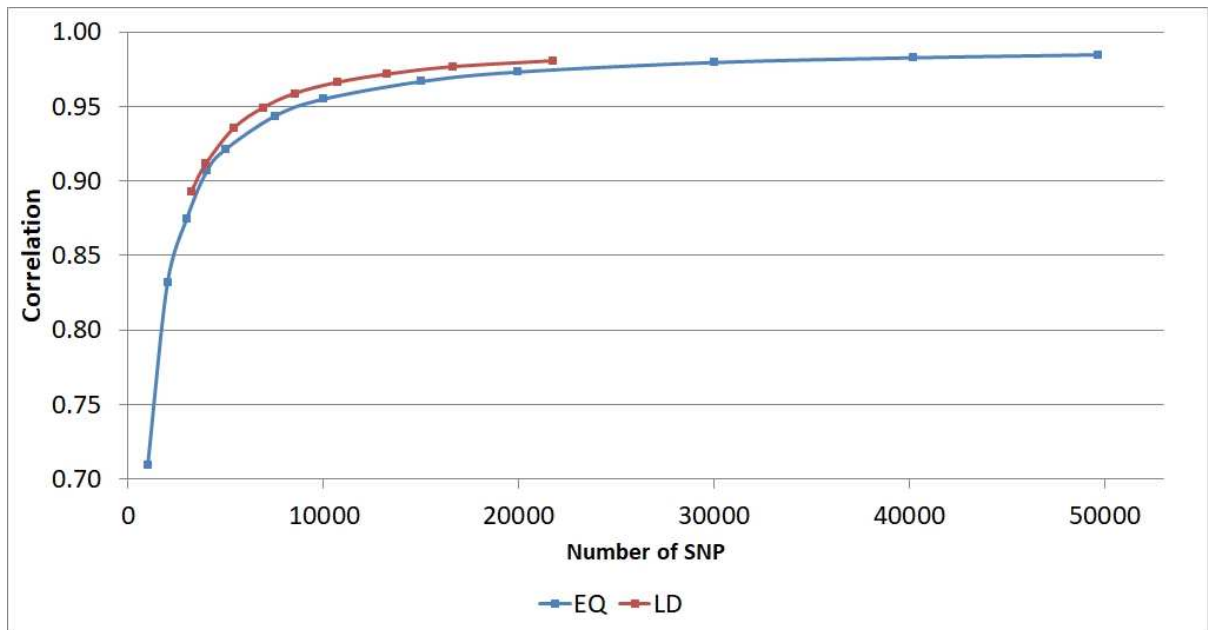




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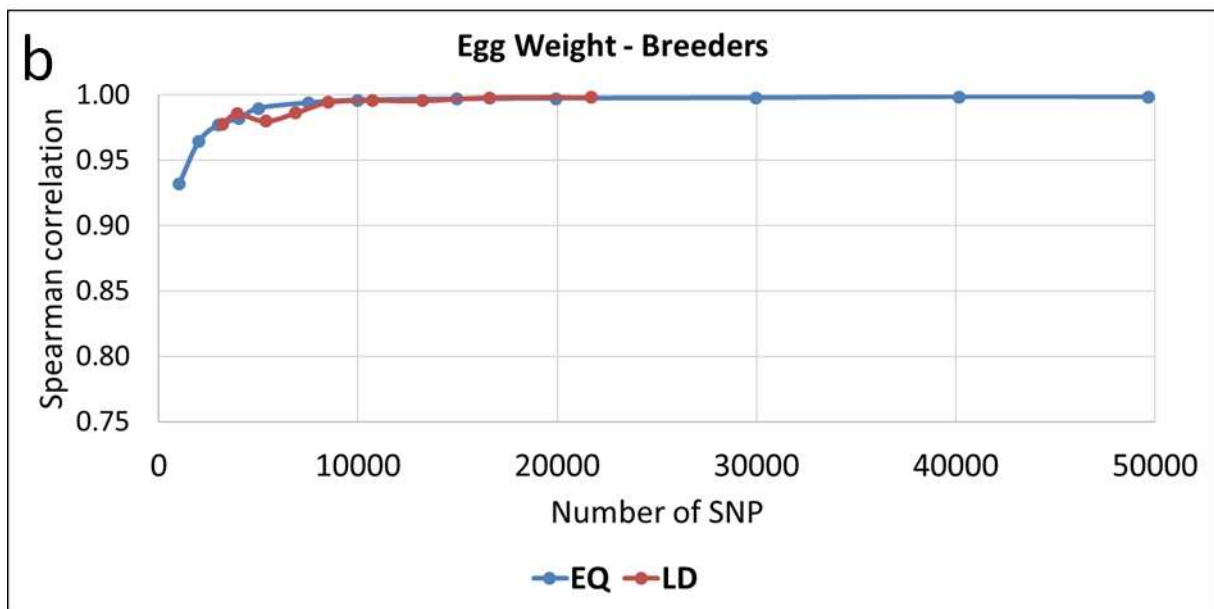
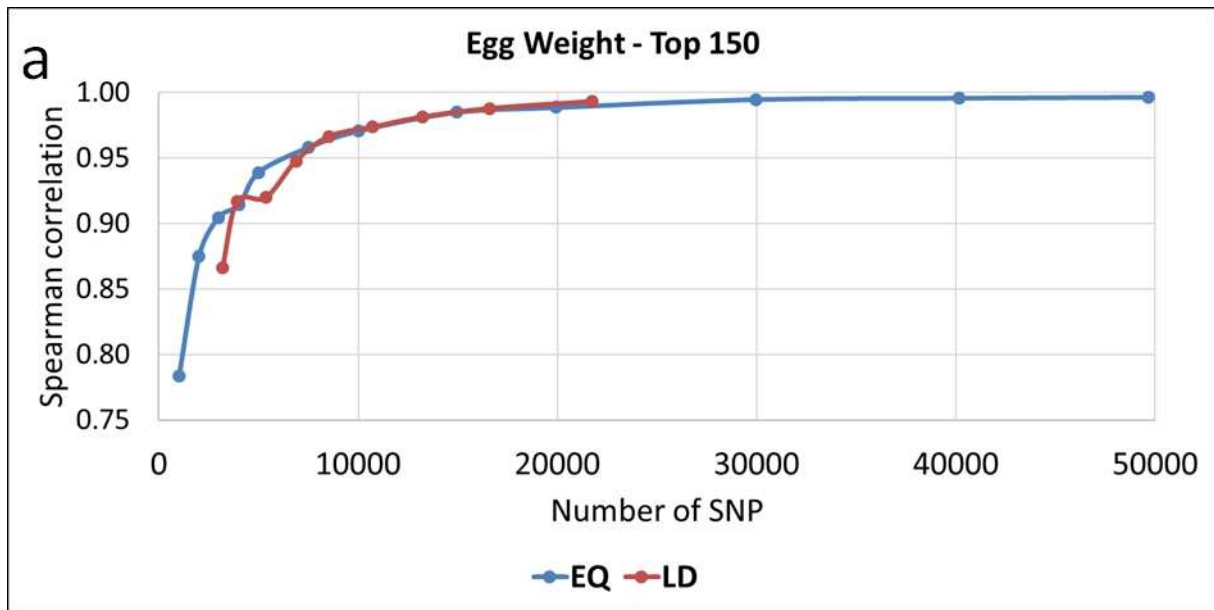
737 **Figure 2.** Summary of all different genomic evaluation strategies studied

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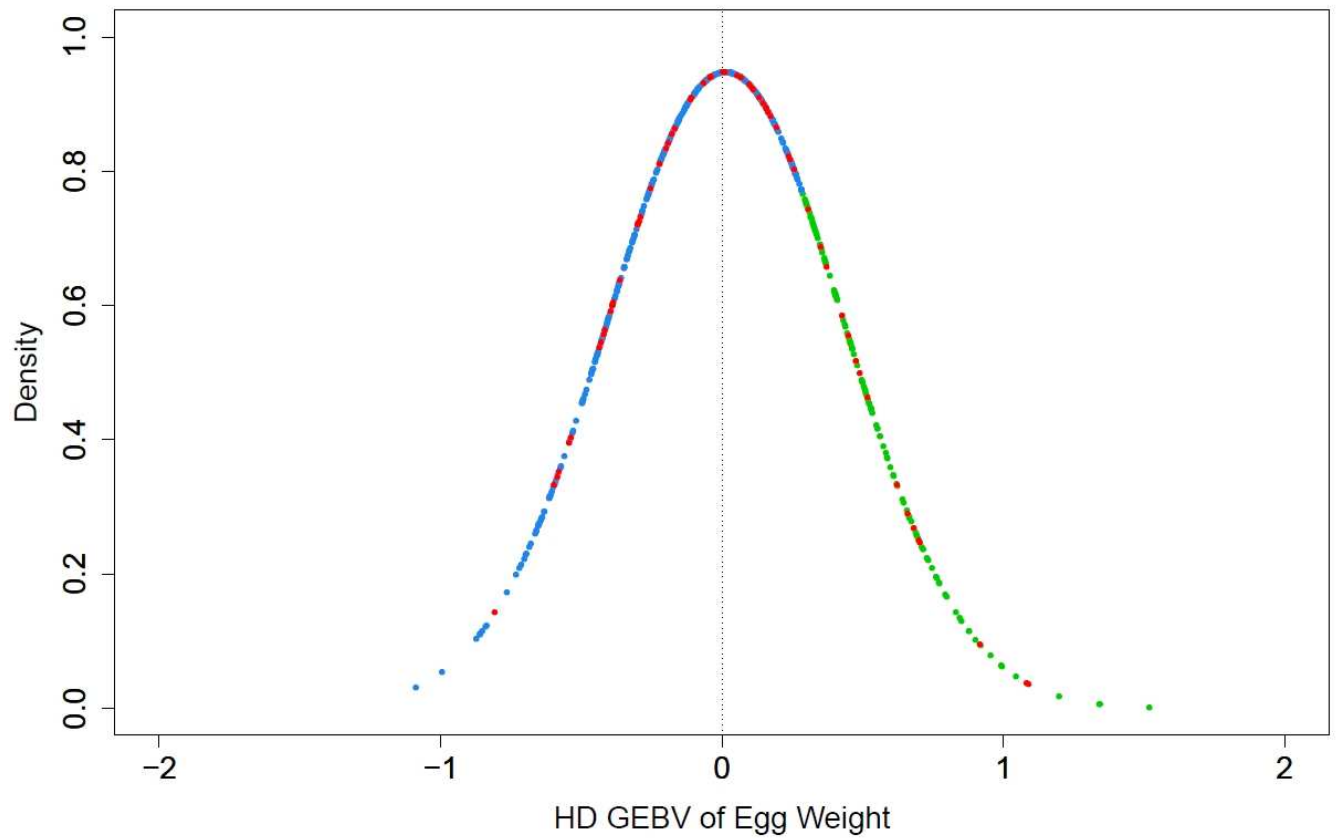
740 **Figure 3.** Mean correlations between true and imputed genotypes according to the number of  
 741 SNPs on low density SNP chips for EQ and LD methodologies.



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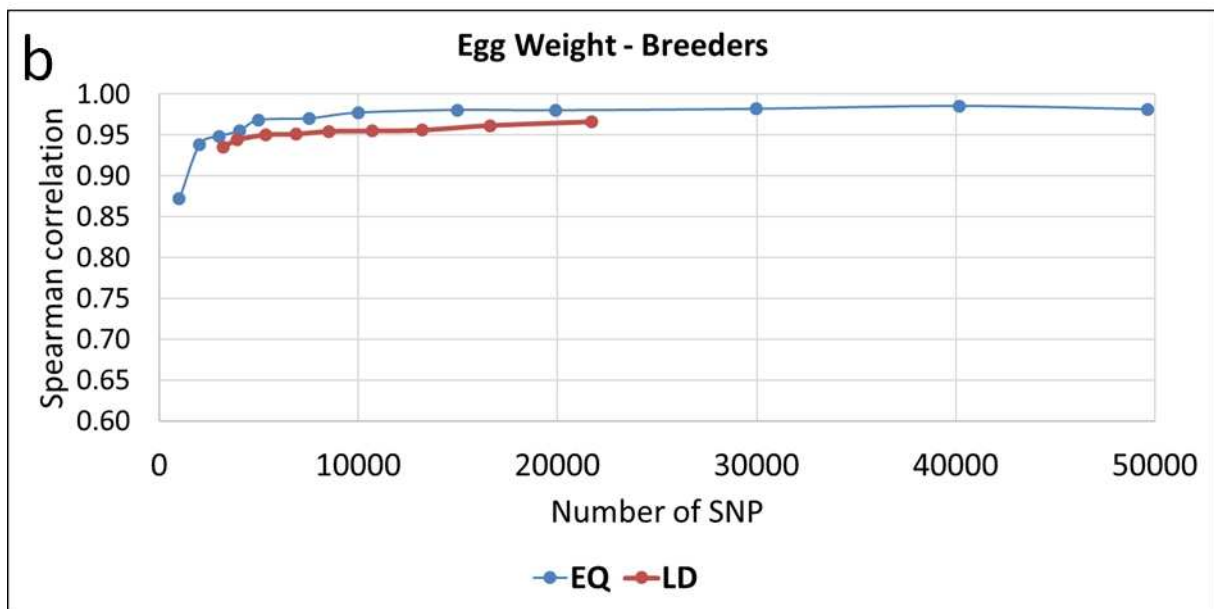
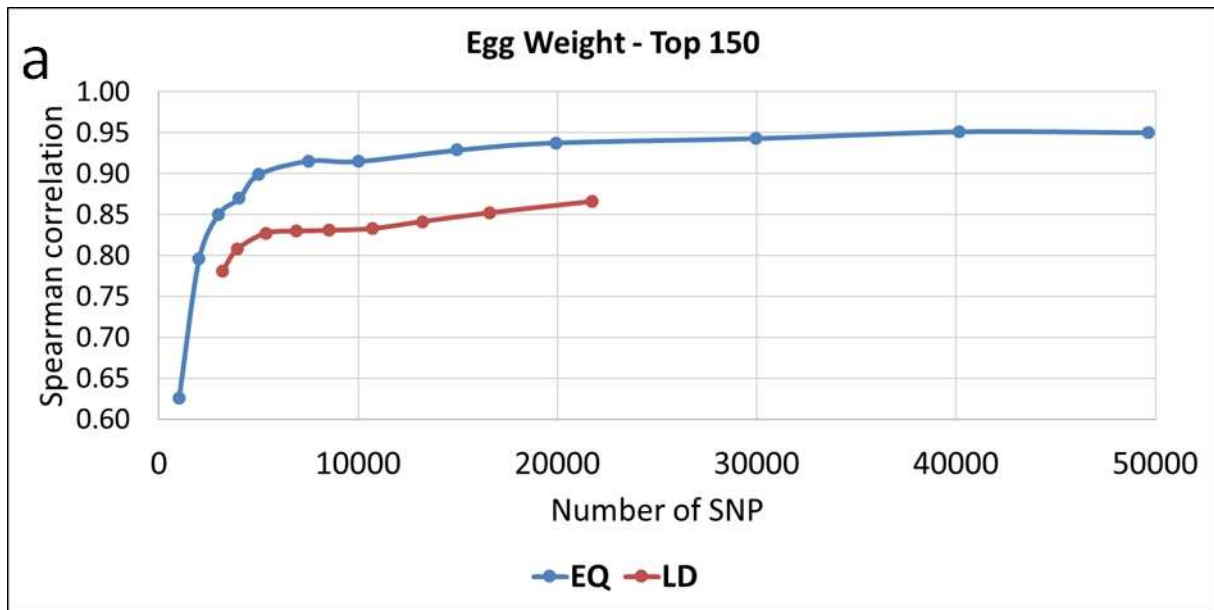
743 **Figure 4.** Spearman correlations between GEBV based on ancestry obtained with true HD  
 744 genotyping and GEBV based on ancestry obtained with imputed HD genotyping. Results are  
 745 shown for egg weight and for the top 150 individuals (a) or the 67 breeders (b) according to  
 746 the number of SNPs on low density SNP chip for both methodologies.

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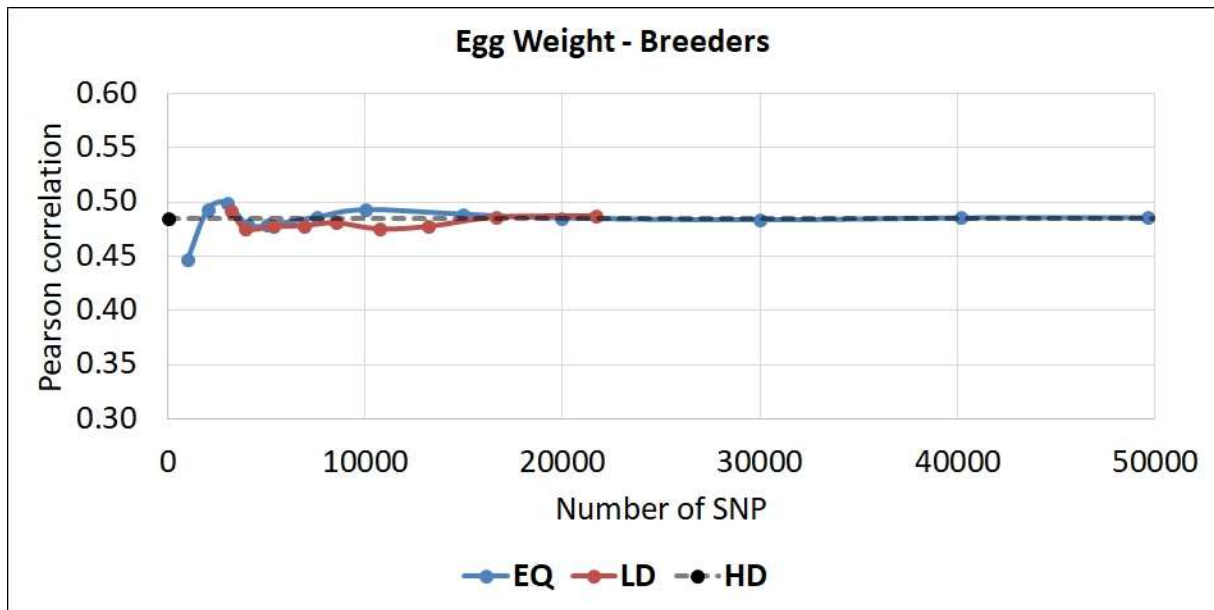
749 **Figure 5.** Normal distribution of all G1 selection candidates according to their HD GEBV of  
750 Egg Weight estimated on ancestry with true HD genotyping. Red dots represent the 67 G1  
751 breeders, green dots represent the top 150 individuals for EW, and blue dots represent the  
752 other selection candidates.



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754 **Figure 6.** Spearman correlations between GEBV based on ancestry obtained with true HD  
 755 genotyping and GEBV based on ancestry obtained with low density genotyping (without  
 756 imputation). Results are shown for egg weight and for the top 150 individuals (a) or the 67  
 757 breeders (b) according to the number of SNPs on low density SNP chip for both  
 758 methodologies.

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760

761 **Figure 7.** Pearson correlations between “Full\_HD” GEBV based on offspring with true HD  
 762 genotyping and GEBV based on ancestry with imputed HD genotyping. Results are shown for  
 763 egg weight and for the 67 G1 breeders according to the number of SNPs on low density SNP  
 764 chip for both methodologies.

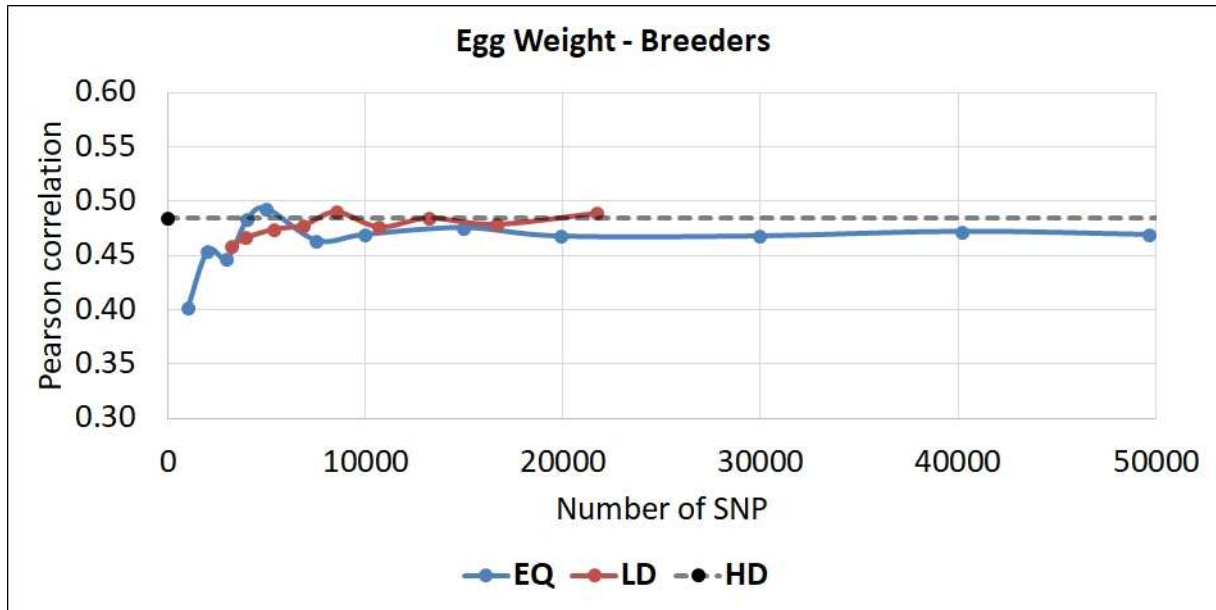
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771 **Figure 8.** Pearson correlations between “Full\_HD” GEBV based on offspring with true HD  
 772 genotyping and GEBV based on ancestry with low density genotyping (without imputation).  
 773 Results are shown for egg weight and for the 67 G1 breeders according to the number of  
 774 SNPs on low density SNP chip for both methodologies.