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Genomic evaluation of body weight traits in a F_2 mixture of commercial broiler and native chicken

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Genetic improvement of body weight (BW) traits has received major consideration in the poultry industry due to their economic and environmental implications. With the rapid implementation of genomic selection (GS) in the poultry industry and a decrease in the cost of genotyping, genomic prediction (GP) is a feasible way to increase productivity. Moreover, a pre-selection of SNPs could represent a reasonable option to speed up GP. We used 312 F_2 broiler chicken genotyped with 60K Illumina Beadchip to investigate the effect of reduced SNP densities on accuracy and bias of prediction using single-step genomic BLUP (ssGBLUP) for BW at 2-4 weeks of age (488 chickens). To investigate the effect of reduced SNP densities by varying minor allele frequency (MAF), SNPs were grouped into five subgroups with MAF of 0.05-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.4 and 0.4-0.5. The accuracy and bias of genomic predictions from different MAF bins were compared to that using a standard array of 60k SNP genotypes and the traditional BLUP method. Our study showed that using a subset of common SNPs genotypes may increase accuracy of genomic predictions compared to using all SNPs, specifically in the studied F2 population with a limited number of genotyped/ phenotyped individuals.

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KEY WORDs: SNP / genomic prediction / phylogenetic tree / reciprocal crosses

The uncertainty concerning the true genetic merit of breeding animals is the most important limitation in breeding programs. Investments in breeding programs are therefore often related to trait measurement, genetic evaluation methodology, and technologies to improve reproductive performance. Having a good measurement and more accurate genetic evaluation methodology could result in better identification of genetically superior animals, which leads to more accurate selection and greater genetic gain.

Genomic selection (GS) – Meuwissen *et al*. [2001] and the availability of high-density SNP panel creates an extraordinary opportunity to dissect the genetic basis of complex traits, especially for difficult or expensive-to-measure and/or low-heritability traits. Several studies have used single-step Genomic Best Linear Unbiased Prediction – ssGBLUP. [Legarra *et al*. 2009, Salek Ardestani *et al*. 2021] to estimate Genomic Breeding Values (GEBV) for livestock. The ssGBLUP combines the pedigree-based relationship matrix (**A**) with the genomic relationship matrix (**G**) into a hybrid matrix (**H**), which consequently could increase the accuracy, and the method reduces the prediction bias of GEBVs when compared to those generated from multi-step genomic predictions [Aguilar *et al*. 2011, Chen *et al*. 2011, Christensen *et a*l. 2012, Simeone *et al.* 2012, Li *et al.* 2014, Song *et al*. 2017].

Theoretically, higher density SNP panels increase the likelihood that any quantitative traits loci (QTL) are in linkage disequilibrium (LD) with SNPs [Meuwissen *et al*. 2016]. Also using a high density SNP panel can lead to a relevant statistical and computational issue. Moreover, genotyping animals by medium to high density SNP panels will be costly in many livestock and poultry breeding programs. So, preselection of SNPs may provide a reasonable compromise between accuracy of results, the number of independent variables to be considered, computing requirements and genotyping cost [Meuwissen and Goddard 2010, Druet *et al.* 2014, MacLeod *et al*. 2014].

In the current study, genomic breeding values were estimated using ssGBLUP methodology for body weight at 2-4 weeks of age on a set of 312 F_2 broiler chicken using whole SNP data and 5 different subsets of SNPs with MAF bins of 0.05-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.4 and 0.4-0.5. Also, GEBVs were compared with BVs estimated from a traditional BLUP method.

Material and methods

Experimental population

The F1 population was generated by applying reciprocal crosses between a commercial fast-growing broiler strain (Arian line, A) and a slow-growing indigenous population (Urmia Iranian native chickens, N). Each F1 male, resulting from a reciprocal cross, mated with four to eight females from the other families. Finally, a total of 488

F_2 chickens from eight half-sib families were generated in five different hatches. Day-old F_2 chickens were weighed and reared on the floor for 7 days under 24h light and a brooding temperature of 33°C. This temperature was decreased to 30°C on day 7. On day 8, birds were weighed and moved to individual cages with a temperature of 30°C, which was gradually decreased to reach a final temperature of 22°C, and a 22h light and 2h dark cycle throughout the experimental period. Chickens did not receive vaccines during the rearing period. Feed and water were provided *ad libitum*.

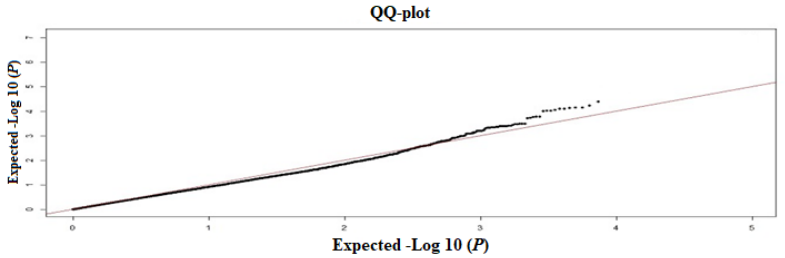
Genotyping and Population structure

DNA was extracted from 312 blood samples by the standard salting-out procedure. All samples were genotyped at Aarhus University, Denmark, using the Illumina Chicken 60K BeadChip provided by Cobb Vantress (312 chickens with specific

Supplementary Table 1. Distribution of SNPs before and after quality control and the average distance between adjacent SNPs on each chromosome.

Chromosome	No. of SNP Markers after quality control	No. of SNP in chip	Average distance (kb)
1	7546	8303	26.5
2	5762	6355	26.7
3	4340	4739	26.3
4	3553	3872	26.5
5	2303	2542	27.1
6	1815	1995	19.6
7	1907	2089	20.1
8	1502	1636	20.1
9	1269	1366	18.8
10	1378	1553	16.1
11	1329	1531	16.4
12	1356	1559	14.4
13	1251	1371	14.6
14	1081	1179	14.3
15	1094	1222	11.8
16	20	24	21.7
17	898	994	11.8
18	930	1048	11.9
19	878	973	11.3
20	1587	1815	8.8
21	805	901	8.5
22	313	432	12.6
23	631	724	9.3
24	763	853	8.5
25	177	211	11.5
26	685	776	7.4
27	518	576	9.4
28	582	708	7.6
29	118	142	7.7
30	4	7	6.9
Z	1984	2842	37.5
Total	48379	54338	15.8

genotype and 176 chickens without genotypes). Quality control was performed using PLINK (v1.9) – Chang *et al*. [2015] and Purcell *et al*. [2007]. SNPs with a MAF threshold below 5% and SNPs with a call rate below 95% were removed. The Hardy-Weinberg equilibrium threshold of 1×10^{-6} was also applied. Moreover, samples with high missing genotype rates (<99.9%) were discarded. After quality control, the final dataset contains 48,379 SNPs and 308 birds, including 170 male and 138 female. The number of SNPs before and after quality control and the average distance between adjacent SNPs on each chromosome, determined using synbreed [Wimmer *et al*. 2012], are given in Supplementary Table 1. The normality of the data after quality control was checked and confirmed using QQ-plot in R (Supplementary Fig. 1).



Supplementary Figure 1. Quantile-Quantile plot representation obtained from 48379 studied SNPs for the body weight trait.

To study the relationship between allele frequencies and predictive abilities, 48,379 SNPs were grouped into 5 subsets with MAF bins of 0.05-0.1 (6,731 SNPs), 0.1-0.2 (8,884 SNPs), 0.2-0.3 (10,148 SNPs), 0.3-0.4 (11,128 SNPs) and 0.4-0.5 (11,488 SNPs) using PLINK (v1.09) – Chang *et al.* 2015 and Purcell *et al*. [2007].

The population structure was evaluated by multi-dimensional scaling (MDS) using PLINK (v1.09) – Chang *et al*. [2015]. Independent SNPs were obtained for all autosomes using the independence-pairwise option, with a window size of 30 SNPs, a step of five SNPs and an r^2 threshold of 0.2, as suggested by Wang *et al.* [2009]. Then, independent SNPs were used to estimate the pairwise identity-by-state (IBS) relationship between all individuals [Liu *et al*. [2015]. MDS components were obtained using the MDS-plot option based on the IBS matrix [Sun *et al*. 2013]. Cluster analysis was conducted for all genotypes based on genetic distance according to the neighbour joining method using agglomerative clustering and Tassel software [Luo *et al.* 2020, Bradbury *et al.* 2007].

Statistical analyses

Model 1 was used to estimate breeding values of each animal using the AIREMLF90 (v1.61) module from the Blupf90 program [Misztal *et al*. 2002]:

$$\boldsymbol{y = 1\mu + Xb + Za + e}$$

where: $\boldsymbol{y}$ – the vector of raw phenotypes; $\boldsymbol{\mu}$ – the overall mean; $\boldsymbol{X}$ – the incidence matrix relating fixed effects of sex-hatch-year to phenotypes; $\mathbf{b}$ – the vector of fixed

effects; **Z** – the incidence matrix relating phenotypes to additive genetic effects; **a** is the vector of additive genetic effects assumed to be distributed as ~ N (**0**, **A**σ_a^2), where **A** is the pedigree-based relationship matrix, σ_a^2 is the variance of additive genetic effects and **e** is the vector of random residual effects *as* ~N (**0**, **I**σ_e^2), where **I** is the identity matrix, and σ_e^2 is the residual variance. Adjusted phenotypes were calculated as the sum of the animals' EBV and residual values [Lourenco *et al*. 2020].

Model 2 was used to estimate single-step genomic breeding values using AIREMLF90 (v1.61) – Misztal *et al*. [2014] with 48,379 SNPs or a different subset of SNPs with MAF bins of 0.05-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.4 and 0.4-0.5:

$$\boldsymbol{y = 1\mu + Xb + Zg + e}$$

where **y**, **μ**, **X**, **b**, and **e** are the same as Model 1, **Z** is the incidence matrix for random additive genetic effects; **g** is a vector of random additive genetic effects assumed to be distributed as ~N(0, **H**), where **H** is a combination of genomic relationship matrix (**G**) and pedigree-based relationship matrix (**A**). The inverse of the **H** matrix used in this study was created as:

$$H^{-1} = A^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & t(\alpha G + \beta A_{22})^{-1} - \omega A_{22}{}^{-1} \end{bmatrix}$$

where A_{22} is the subset of the **A** matrix related to genotyped animals, t and ω are the scaling factors, which both were set equal to one as the default option in AIREMLF90 (v1.61) – Misztal *et al*. [2014]. To avoid singularity problems and improve predictions, the blending factors of α and β were set at 0.95 and 0.05, respectively [VanRaden 2007, Lourenco *et al*. 2014, Salek Ardestani *et al.* 2021].

The accuracy was calculated as the correlation between breeding values (GEBVs/EBVs) and adjusted phenotypes of birds in the validation population. The standard error of prediction accuracy was calculated using the following equation [Salek Ardestani *et al*. 2021]:

$$\text{Standard error} = \frac{1 - \text{accuracy}^2}{\sqrt{\text{number of individuals} - 1}}$$

The accuracy improvement was calculated using the following equation [Salek Ardestani *et al*. 2021]:

$$\text{Improvement accuracy} = \left(\frac{\text{accuracy of GEBV} - \text{accuracy of EBV}}{\text{accuracy of EBV}}\right) \times 100$$

The bias of prediction was calculated as the regression coefficients (r) of GEBVs on the adjusted phenotype using the *lm* function in R 4.0.2 (R Core Team. 2013).

Cross validations for model assessment

To assess predictive performance of different prediction models, we used the 5-fold cross-validation (CV) method. Out of all 308 birds, 40 birds were randomly selected as the validation population and the other (268) birds were considered as the reference population. This was done in 5 replications. GEBVs in the validation set

were estimated using the ssGBLUP method and different SNP densities. Furthermore, traditional breeding values were estimated using the BLUP method for different age groups. The accuracy and bias of GEBVs/EBVs were used to compare the predictive ability of different scenarios.

Results and discussion

Summary statistics and population structure

Traits, the mean and standard deviation, coefficient of variation, and the minimum and maximum values of BW at weeks 2 to 4 are given in Table 1. To explore the genetic population structure, we performed MDS and neighbor-joining tree using 48,379 SNPs in the crossbreed population (Fig. 1 and 2). Our findings revealed the existence of eight subgroups in the studied population. The kinship matrix was used to correct population stratification.

Table 1. Descriptive statistics of body weight traits in F2 chickens

Trait	Mean	SD	CV	Minimum	Maximum
BW2	92.3	18.8	20.35	41.20	135
BW3	218.8	61.2	27.96	68.55	325
BW4	419.1	102.4	24.45	157.30	651

BW2, BW3, BW4 – body weight at 2, 3 at 4 weeks of age, respectively; SD – standard deviation; CV – coefficient of variation.

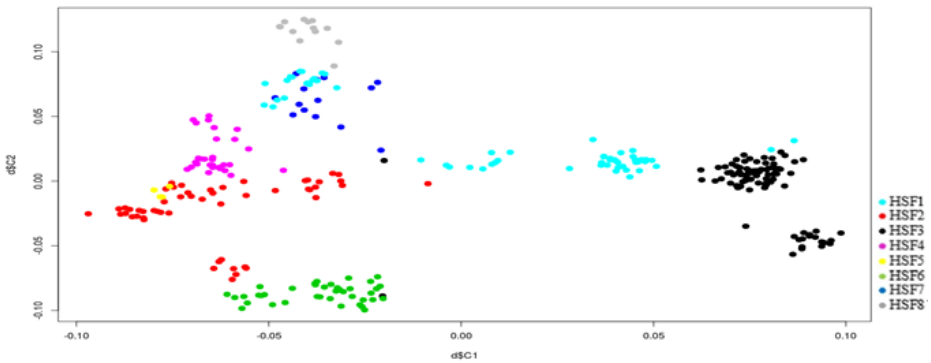


Fig. 1. Population structure identification with multidimensional scaling analysis. Fullsib families are shown in the same color (HSF = half-sibling family).

Predictive ability

The accuracy of EBV (GEBV) for BW at 2 to 4 weeks of age were 0.166 (0.264), 0.054 (0.173), and 0.215 (0.216), respectively (Tab. 2). The highest and lowest accuracy improvement in ssGBLUP over BLUP were observed for 3 (220.37%) and

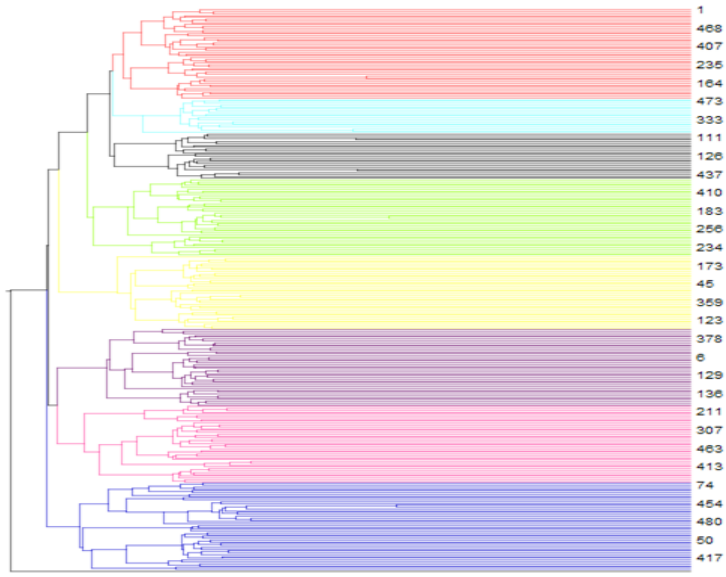


Fig. 2. Genetic relationships among 8 chicken groups constructed using a neighbor-joining phylogenetic tree from shared allele distance, based on 48,379 single nucleotide polymorphisms (SNPs).

Table 2. Accuracy and bias of BLUP and ssGBLUP predictions for broiler body weight in different weeks using 5-fold cross-validation method

Weeks	Accuracy / BLUP	Accuracy / ssGBLUP	Improvement accuracy% / ssGBLUP	Regression coefficient / ssGBLUP
2	0.166 (0.042)	0.264 (0.044)	59.03	1.3
3	0.054 (0.045)	0.173 (0.043)	220.37	0.89
4	0.215 (0.043)	0.216 (0.043)	0.46	0.74

4 (0.46%) weeks of age, respectively. The lowest bias of genomic predictions (0.89) using the ssGBLUP model was observed for BW at 3 weeks of age (Tab. 2).

The accuracy of genomic prediction for each trait based on different SNP subsets is shown in Figure 3. We used the ssGBLUP scenario (60k) and traditional BLUP here as the benchmark.

For BW at week 2, the highest accuracy (0.273) and the lowest bias of estimates (r =1.08) were observed for MAF bin 0.1-0.2, which resulted in 5.42% improvement compared to using all SNPs (Tab. 3). However, for BW at 3 weeks of age, using MAF bin of 0.4-0.5 resulted in the highest accuracy improvement (16.6%) and the lowest bias of estimates (r =0.9) – Table 4. For BW at 4 weeks of age, MAF bins of 0.3-0.4 (0.234) and 0.4-0.5 (0.229) showed the highest accuracy of prediction, respectively (Tab. 5). Figures 3 shows a comparison between the accuracy of the evaluation of each subgroup of markers and the accuracy of the evaluation of information concerning all markers in weeks 2 to 4, respectively. The average ssGBLUP (60k) and BLUP accuracy

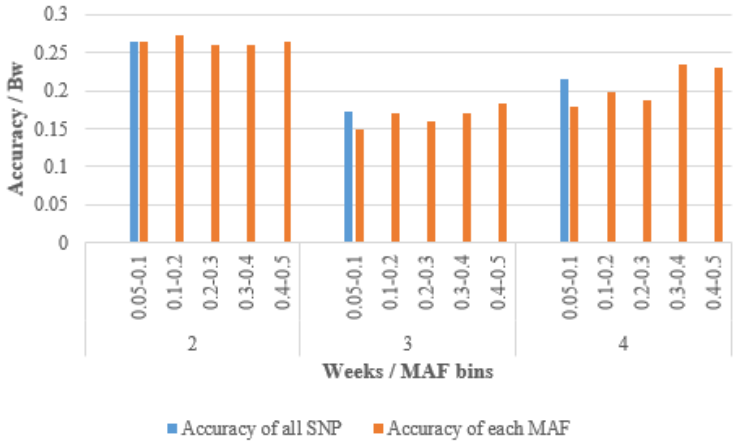


Fig. 3. Compare the accuracy of each MAF subgroup with the accuracy of information about all markers in the second to fourth weeks.

Table 3. Accuracy and bias of genomic prediction of body weight traits using different MAF bins at two weeks of age

MAF	Accuracy / ssGBLUP	Improvement accuracy% / ssGBLUP	Improvements for each MAF %	Regression coefficient / ssGBLUP
0.05-0.1	0.265 (0.042)	59.63	0.6	1.32
0.1-0.2	0.273 (0.041)	64.45	5.42	1.08
0.2-0.3	0.259 (0.042)	56.02	-3.01	1.8
0.3-0.4	0.259 (0.042)	56.02	-3.01	1.6
0.4-0.5	0.265 (0.042)	59.63	0.6	1.6

Table 4. Accuracy and bias of genomic prediction of body weight traits using different MAF bins at three weeks of age

MAF	Accuracy / ssGBLUP	Improvement accuracy% / ssGBLUP	Improvements for each MAF %	Regression coefficient / ssGBLUP
0.05-0.1	0.149 (0.044)	175.92	-44.45	0.81
0.1-0.2	0.170 (0.044)	214.81	-5.56	0.92
0.2-0.3	0.159 (0.044)	194.44	-25.93	0.86
0.3-0.4	0.170 (0.044)	214.81	-5.56	0.86
0.4-0.5	0.182 (0.043)	237.03	16.66	0.90

Table 5. Accuracy and bias of genomic prediction of body weight traits using different MAF bins at four weeks of age

MAF	Accuracy / ssGBLUP	Improvement accuracy% / ssGBLUP	Improvements for each MAF %	Regression coefficient / ssGBLUP
0.05-0.1	0.179 (0.043)	-16.74	-17.2	0.64
0.1-0.2	0.199 (0.043)	-7.44	-7.9	0.73
0.2-0.3	0.188 (0.043)	-12.55	-13.01	0.70
0.3-0.4	0.234 (0.043)	8.83	8.37	0.77
0.4-0.5	0.229 (0.042)	6.51	6.05	0.79

across all the traits were 0.217 and 0.145, respectively. The average accuracy based on the SNPs with MAF bin of 0.3-0.4 and 0.4-0.5 across all the traits was slightly increased relative to ssGBLUP (60k) – 0.221 and 0.225, respectively. However, using the ssGBLUP method and a subset of SNPs with MAF bins of 0.05-0.1, 0.1-0.2 or 0.2-0.3, resulted in a slightly lower average prediction accuracy across traits compared to ssGBLUP (60k) – 0.197, 0.214 and 0.202, respectively (Fig. 4). Figure 5 confirmed the MAF 0.4-0.5 advantage in different weeks.

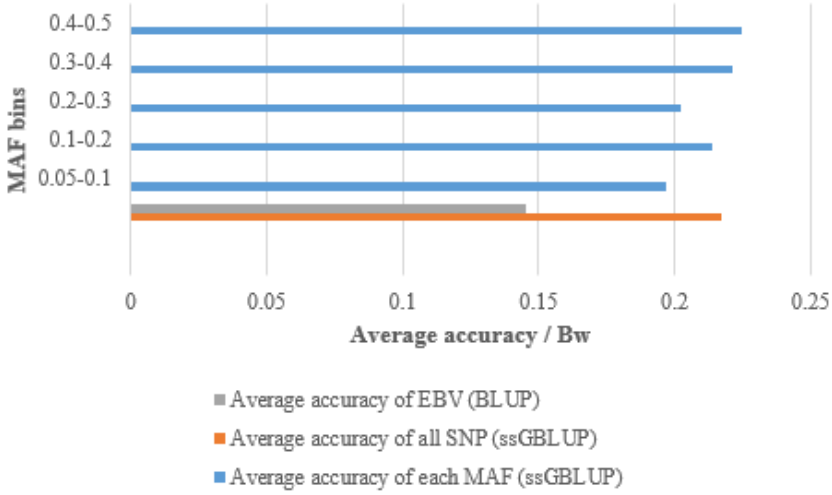


Fig. 4. Compare the average accuracy across all traits of each MAF subgroup with the accuracy of information about all markers.

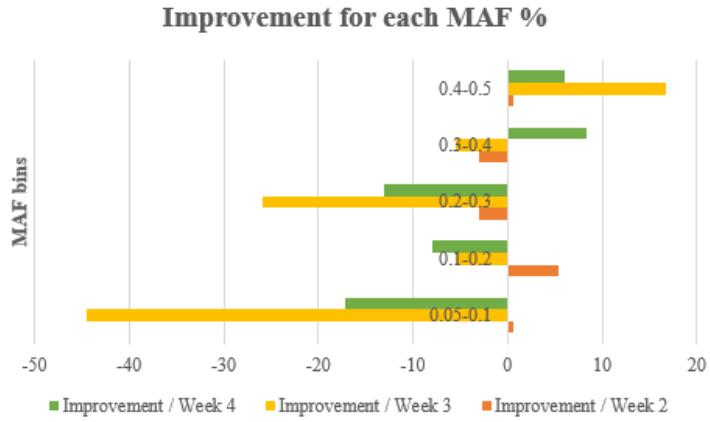


Fig. 5. Improvement for each MAF in the second to fourth weeks.

Obtaining an accurate and unbiased genomic prediction can be a profitable strategy for genetic improvement of economic traits in livestock and poultry industries [Mrode *et al*. 2019]. Our studies provided some valuable insights into applying genomic selection with low-density markers in an F_2 cross broiler population. It is generally expected that a high proportion of genetic diversity may be explained by the high-density panels used, but given that most of the SNPs in the high-density SNP panel are in linkage disequilibrium (LD) with causal mutations, increasing the number of markers may not result in a significant accuracy improvement in genomic evaluation of a population with a single-breed reference population [Su *et al.* 2012, Zhang *et al.* 2018). Also, using a high density SNP panel can lead to a relevant statistical and computational issue. Moreover, genotyping animals by medium to high density SNP panels will be costly in many livestock and poultry breeding programs. So, pre-selection and using a subset of SNPs may provide a reasonable compromise between accuracy of results, the number of independent variables to be considered, computing requirements and genotyping cost [Meuwissen and Goddard 2010, Druet *et al*. 2014, MacLeod *et al.* 2014]. In the present study, we investigated the effect of reduced SNP densities by varying minor allele frequency for BW at 2-4 weeks of age in a small F2 chicken population. The results showed that the use of SNPs with MAF bin of 0.4-0.5 can result in a slight improvement of accuracy of prediction compared to those generated from all genotype data or using traditional BLUP (Fig. 4 and 5). Consistently with our results, several studies showed that using the subset of SNPs can provide even better results than using all SNP information [Habier *et al.* 2009, Rolf *et al*. 2010, Wellmann *et al.* 2013, Ogawa *et al*. 2014, Li *et al.* 2018, Salvian *et al.* 2020].

Here we used the ssGBLUP using a 60k SNP array and traditional BLUP as the benchmark. As expected, using a combination of pedigree and genomic information resulted in more accurate estimates of genetic merit compared to using pedigree information alone. Generally, ssGBLUP generated on average higher prediction accuracy than traditional BLUP even when a subset of SNPs were used (Fig. 4). In agreement with current results, Salek Ardestani *et al*. [2021] found the highest prediction accuracy using ssGBLUP in comparison with the BLUP, GBLUP, BayesC, and BayesCπ methods for the medium-size genotyped Canadian pig population. Silva *et al*. [2016] showed the higher accuracy when ssGBLUP was used compared to using the BayesCπ and GBLUP methods for residual feed intake and feed conversion ratio traits in Nelore cattle. Yan *et al*. [2017] reported a lower bias of estimates and higher accuracy of predictions using ssGBLUP compared to traditional BLUP for a pure line of laying hens.

Due to the small reference population size used in the current study and the architecture of the BW traits, which is polygenic [Clark *et al.* 2011], the rate of improvement over BLUP was not noticeable. Given the relatively low to moderate heritability of BW at different weeks of age [Mignon-Grasteau *et al*. 1999, Adeyinka *et al.* 2006, Mebratie *et al.* 2017], a large number of records in the reference population

is required to achieve high GEBV accuracy [Goddard and Hayes. 2009, Bermann *et al.* 2021]. In addition, the presence of false positive errors in real data can also be responsible for small accuracy improvement compared to BLUP [VanRaden *et al.* 2017]. Besides, when a small effective population is selected over a long period of time, most of the genetic variance can be explained by the genetic variance of SNPs due to the relationship between individuals [VanRaden *et al*. 2009] and therefore, significant gains in prediction accuracy will not be achieved [MacLeod *et al*. 2014]. In consistence with the current results, for BW traits in a Yorkshire population of 592 pigs Song *et al.* [2019] reported a small accuracy improvement (1%) using ssGBLUP compared to BLUP, which could be explained by the small number of animals with genotype and phenotype information and a low pedigree depth. They also showed accuracy improvement by increasing the reference population size [Song *et al*. 2019]. Lourenco *et al*. [2014] also reported 3% higher accuracy of prediction for ssGBLUP compared to BLUP for fat percentage in a relatively small population of dairy cows with genotype.

In the current study the improvement in accuracy of genomic prediction using ssGBLUP compared to BLUP was noticeable at 2 and 3 weeks of age (59% and 220%, respectively), which could be due to the higher genetic correlation of adjusted phenotypes and GEBVs than EBVs for these age groups. Generally, the stronger the genetic correlation between GEBVs and the adjusted phenotypes, the greater the accuracy of genomic prediction. The degree of genetic correlation between the adjusted phenotype and EBVs for BW at 3 and 2 weeks of age were increased by 0.119 and 0.098 using ssGBLUP compared to the BLUP method. However, small improvement was observed for BW at 4 weeks of age, which could be due to the relatively small increase in genetic correlation between adjusted phenotypes and EBVs using ssGBLUP over BLUP (0.001). Based on the current results, implementation of genomic evaluation based on the ssGBLUP method using whole SNPs for BW at two weeks of age can result in more accurate results in populations with a similar structure.

Conclusion

The body weight trait is one of the main breeding objectives in chicken breeding, but research focusing on the best age to implement genomic breeding values is limited. In the current study we investigated the accuracy and bias of genomic prediction across different age groups, 2-4 weeks of age in the F_2 broiler population using the 5-fold cross-validation method based on the ssGBLUP method. Moreover, a different subset of SNPs varying in minor allele frequency were used for genomic predictions using the ssGBLUP method. Generally, SNPs with MAF bin of 0.4-0.5 had a higher predictive ability compared to other MAF bins for most of the age groups. However, one of the limitations of the current study is that a small population size was used for genomic prediction and so further studies are needed to confirm the current results.

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Data Availability: Derived data supporting the findings of this study are available from the corresponding author on request.

Conflict of interest: The authors declare that there is no conflict of interest regarding the publication of this article.

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