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Comparison of accuracy of genomic evaluation of body weight and average daily gain using different SNP densities in the F2 population of broiler chickens

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This study evaluated the accuracy and bias of estimated breeding values (EBV) using pedigree-based BLUP (PBLUP) and single-step genomic BLUP (ssGBLUP). Genomic evaluations for body weight (BW) and average daily gain (ADG) were compared using either all SNPs or a subset with minor allele frequency (MAF) 0.4-0.5. Data included 312 F2 broilers genotyped with a 60K Illumina BeadChip and 176 non-genotyped birds (total 488). The effect of reduced SNP density on prediction accuracy and bias for BW and ADG at 2-4 weeks of age was assessed using ssGBLUP. To examine the effect of reducing SNP density by changing minor allele frequency, SNPs with allele frequencies of 0.4-0.5 were isolated. The accuracy and bias of genomic predictions from the 0.4-0.5 MAF SNP subset were compared with those obtained using the standard 60K SNP array and traditional BLUP. Our study showed that using low-coverage genotype data would be a cost-effective approach for genomic prediction in crossbred chickens even with a small population size (less than 500).

KEY WORDS: crossbreeding / genomic selection / local chicken population / single-step genomic BLUP

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The uncertainty about true genetic merit of breeding animals is the most important limitation in a breeding program. 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 the genetically superior animals, which leads to more accurate selection and enhanced genetic gain. Genomic selection (GS) and the availability of high-density SNP panels create an extraordinary opportunity to dissect the genetic basis of complex traits, especially for difficult or expensive to measure and/or low-heritability traits [Meuwissen *et al*. 2001]. Several studies have used single-step Genomic Best Linear Unbiased Prediction - ssGBLUP [Legarra *et al*. 2009, Salek Ardestani *et al*. 2021] to predict Genomic Breeding Values (GEBV) for livestock. The ssGBLUP combines the pedigree-based relationship matrix (**A**) and the genomic relationship matrix (**G**) into a hybrid matrix (**H**) to increase the accuracy and reduce 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 al*. 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]. However, the use of high density (HD) SNP panels to generate a **G** matrix has not made significant improvements in the accuracy of the estimates [Misztal *et al*. 2013]. Using high density SNP panel can also lead to a relevant statistical and computational issue. Moreover, genotyping animals by medium to high density SNP panels will be costly in livestock and poultry breeding programs. So, preselection of SNPs may provide a reasonable compromise between the accuracy of results, number of independent variables to be considered, computing requirements and genotyping cost [Meuwissen and Goddard 2010, Druet *et al*. 2014, Macleod *et al*. 2014].

The objective of this study is to predict genomic breeding values (GEBV) using the ssGBLUP methodology for BW and ADG at 2-4 weeks of age on a set of 312 F_2 broiler chicken by using whole SNPs data and subset of SNPs with MAF bin 0.4-0.5. Also, GEBVs were compared with BVs estimated from a traditional BLUP method.

Material and methods

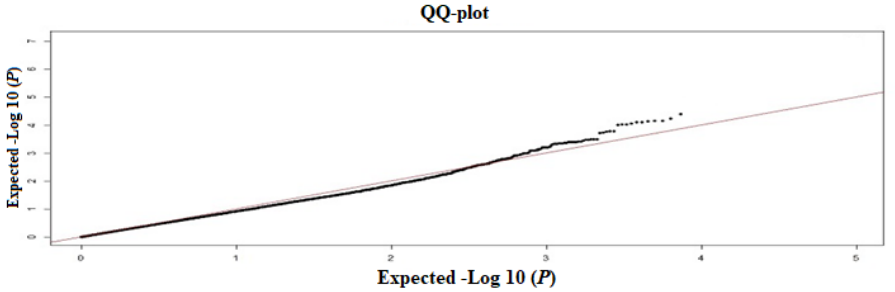
Experimental population

The F1 population was generated by applying reciprocal crosses between a commercial fast-growing broiler strain (Arian line, A) and Urmia Iranian native chicken population (N). Each F1 male, resulted from a reciprocal cross, mated with 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. To examine the changes in BW and ADG of chickens in different weeks, day-old F_2 chickens were weighed and reared on the floor for 7 days under 24 h 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 22 h light and 2 h dark cycle throughout the experimental period. Feed and water were provided freely.

Genotyping and population structure

DNA was extracted from 312 blood samples using 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 genotype and 176 chickens without genotype). Quality control was performed by using PLINK (v1.9) [Purcell *et al*. 2007, Chang *et al*. 2015]. SNPs with a MAF threshold less than 5% and SNPs with call rate less than 95% were removed. Hardy-Weinberg equilibrium threshold of 1×10^{-6} was also applied. Samples with high missing genotype rates (<99.9%) were discarded. After quality control, the final dataset contained 48,379 SNPs and 308 birds, including 170 male and 138 female. Number of SNPs before and after quality control and the average distance between adjacent SNPs on each chromosome, determined by using synbreed [Wimmer *et al*. 2012], were shown 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 Fig. 1. Quantile-Quantile plot representation obtained from 48379 studied SNP for the body weight trait.

To study the relationship between allele frequency and predictive abilities, SNPs with allele frequency of 0.4-0.5 (11,488 SNPs) were isolated using PLINK (v1.09) – Purcell *et al*. [2007] and Chang *et al*. [2015].

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 30-SNP window, five-SNP step and an r^2 threshold of 0.2, following Wang *et al.* [2009]. Then, independent SNPs were used to estimate the pairwise identity-by-state (IBS) relationship between all individuals as in 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].

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

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

Statistical analyses

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

$$\boldsymbol{y = 1\mu + Xb + Za + e} \quad \textbf{(1)}$$

where **y** is the vector of raw phenotype, **μ** is the overall mean, **X** is the incidence matrix relating fixed effects of sex–hatch–year to phenotypes, **b** is the vector of fixed effects, **Z** is the incidence matrix relating phenotypes to additive genetic effects, **a** is the vector of additive genetic effects assumed to be distributed as $\sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, 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* $\sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$, where ***I*** is the identity matrix, and σ_e^2 is the residual variance. Adjusted phenotypes were calculated as 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 subset of SNPs with MAF bin 0.4-0.5:

$$\boldsymbol{y = 1\mu + Xb + Zg + e} \quad \textbf{(2)}$$

where **y**, **μ**, **X**, **b**, and **e** are the same as Model 1, **Z** is a design matrix for the 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:

$$\mathbf{H^{-1}} = \mathbf{A^{-1}} + \begin{bmatrix} 0 & 0 \\ 0 & t(\alpha\mathbf{G} + \beta A_{22})^{-1} - \omega {A_{22}}^{-1} \end{bmatrix} \quad \textbf{(3)}$$

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 equal to 0.95 and 0.05, respectively [VanRaden 2007, Lourenco *et al.* 2014, Salek Ardestani 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 equation described by Salek Ardestani [2021]:

$$\text{Standard error} = \frac{1 - \text{accuracy}^2}{\sqrt{\text{number of individuals} - 1}} \quad \textbf{(4)}$$

The accuracy improvement was calculated according to Salek Ardestani *et al.* [2021]:

$$\text{Improvement accuracy} = \left(\frac{\text{accuracy of GEBV} - \text{accuracy of EBV}}{\text{accuracy of EBV}}\right) \times 100 \quad \textbf{(5)}$$

Two criteria of accuracy and regression coefficient of GEBV were used to compare the predictive ability of different prediction methods in BW and ADG traits. The bias of prediction was calculated as the regression coefficients (r) of GEBVs on adjusted phenotype using *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 5-fold cross-validation (CV) method. Out of all 308 birds, 40 birds were randomly selected as validation population and the remaining (268 birds) were considered as reference population. This was done in 5 replications. GEBVs in the validation set

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

Results and discussion

Summary statistics and population structure

Basic characteristics of BW and ADG at weeks 2 to 4 (mean and standard deviation, coefficient of variation, and the minimum and maximum values) are listed in Table 1. To explore the genetic population structure, we performed MDS and neighbour-joining tree using 48379 SNPs in 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 the Average daily gain (ADG) and Body weight (BW) traits in F2 chickens

Trait (g)	Mean	SD	CV	Min	Max
BW2[1]	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
ADG1[2]	18.03	6.64	36.80	0.864	30.90
ADG2	28.70	7.82	27.23	7.460	58.92
ADG3	38.70	10.71	27.67	5.813	72.95

[1]Body weight.
[2]Average Daily Gain.

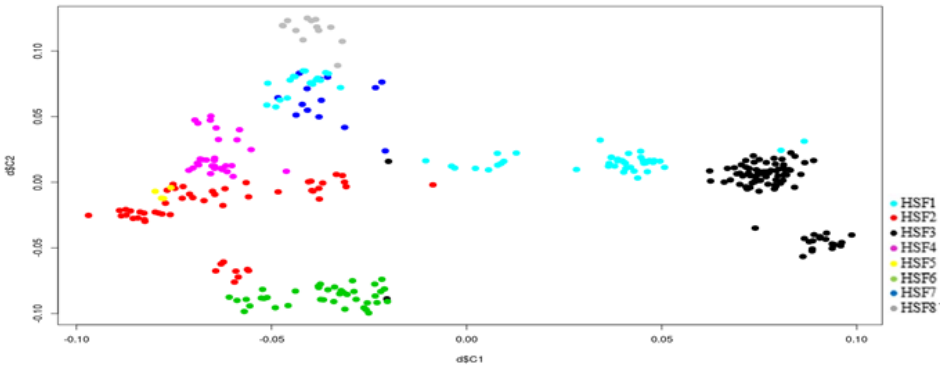


Fig. 1. Population structure identification with multidimensional scaling analysis. Fullsib families are shown in the same color (HSF = half-sibling family).

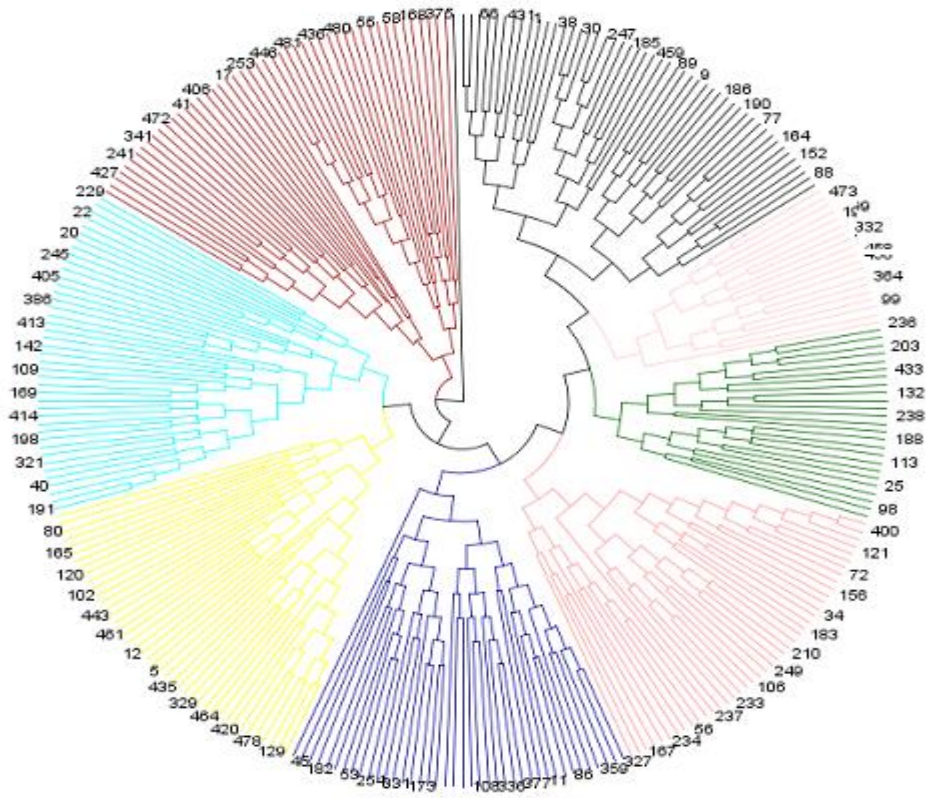


Fig. 2. Genetic relationships among 8 chicken groups constructed using a neighbor-joining phylogenetic tree from shared allele distance, based on 48,379 single nucleotide polymorphisms (SNPs).

Predictive ability

The accuracy of EBV (GEBV) for BW at 2 to 4 weeks of age was 0.166 (0.264), 0.054 (0.173), 0.215 (0.216) – Asadollahi *et al*. [2022], and for ADG at 2 to 4 weeks of age were 0.102 (0.104), 0.155 (0.161) and 0.094 (0.096), respectively (Fig. 3). The highest and lowest accuracy improvements of ssGBLUP over BLUP for ADG were observed at weeks 3 (3.87%) and 2 (1.96%), respectively, while for BW they were at weeks 3 (220.37%) and 4 (0.45%). The lowest bias of genomic predictions (0.91 and 0.89) using ssGBLUP model was observed for ADG and BW at 3 weeks of age, respectively (Tab. 2).

The accuracy of genomic prediction for each trait based on the information of all SNPs and SNPs with MAF 0.4-0.5 were shown in Figure 4. We used the scenario ssGBLUP (60k) and traditional BLUP here as the benchmark. The accuracy of genomic evaluation using markers with MAF 0.4-0.5 for BW traits in the second, third, and

Table 2. Comparison of accuracy and bias of BLUP and ssGBLUP prediction for Bw and ADG traits in F2 chickens at the age of two, three and four weeks

Traits	Weeks	Accuracy/ BLUP	Accuracy/ ssGBLUP	Improvement accuracy%/ ssGBLUP	Regression coefficient/ ssGBLUP
ADG	2	0.102 ± 0.044	0.104 ± 0.044	1.96	0.75
Bw	2	0.166 ± 0.042	0.264 ± 0.044	59.03	1.28
ADG	3	0.155 ± 0.044	0.161 ± 0.044	3.87	0.91
Bw	3	0.054 ± 0.045	0.173 ± 0.043	220.37	0.89
ADG	4	0.094 ± 0.044	0.096 ± 0.044	2.12	1.49
Bw	4	0.215 ± 0.043	0.220 ± 0.043	0.45	0.71

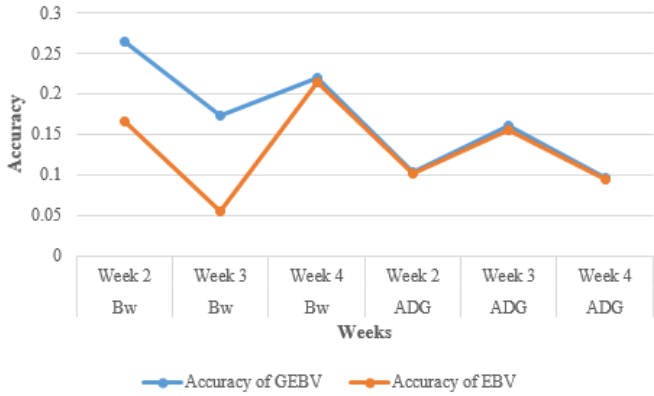


Fig. 3. Comparison of PBLUP and ssGBLUP accuracy in the second, third, and fourth weeks for the average daily gain (ADG) and Body weight (Bw) traits.

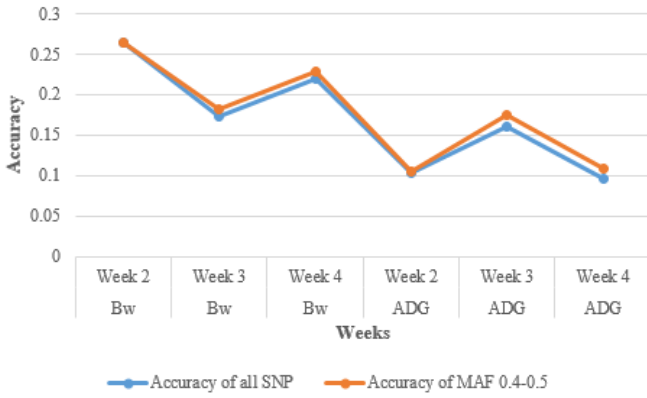


Fig. 4. Comparison of genomic prediction accuracy of body weight (Bw) and Avrage Daily Gain (ADG) traits in broilers using information of all SNPs and markers with MAF 0.4-0.5 in the second, third, and fourth weeks.

fourth weeks was 0.265, 0.182, and 0.229, respectively [Asadollahi *et al*. 2022]. For ADG traits, the corresponding accuracies were 0.105, 0.174, and 0.108. For ssGBLUP, the average accuracy of genomic prediction using markers with MAF 0.4-0.5 showed improvement over using all SNPs in weeks 2-4. For BW traits, the improvements were 0.6%, 16.66%, and 6.05%, and for ADG traits, 0.98%, 8.38%, and 12.77%, respectively. The lowest bias of genomic predictions (1.02 and 0.90) using ssGBLUP model and with markers in the 0.4-0.5 MAF bin was observed for ADG and BW at 3 weeks of age, respectively (Tab. 3). Figure 4 compares the evaluation accuracy of markers in the 0.4-0.5 MAF bin with that obtained using all markers across different weeks. Comparison of genomic prediction improvement using all SNPs versus SNPs with MAF 0.4-0.5 confirmed the superior performance of the 0.4-0.5 MAF subset across different weeks (Fig. 5). Standard error values and improvement of genomic prediction for each trait in each week were presented in Table 2 and 3.

Obtaining an accurate and unbiased genomic prediction method can be a profitable

Table 3. Comparison of accuracy and bias of genomic prediction of Bw and ADG traits in F2 chickens using markers with allelic frequency 0.4-0.5 (MAF 0.4-0.5)

Traits	Weeks	Accuracy/ ssGBLUP	Improvement accuracy%/ ssGBLUP	Improvement for MAF 0.4-0.5%	Regression coefficient
ADG	2	0.105 ± 0.044	2.94	0.98	0.81
Bw	2	0.265 ± 0.042	59.63	0.6	1.6
ADG	3	0.174 ± 0.043	12.25	8.38	1.02
Bw	3	0.182 ± 0.043	237.03	16.66	0.90
ADG	4	0.108 ± 0.044	14.89	12.77	1.23
Bw	4	0.229 ± 0.042	6.51	6.05	0.79

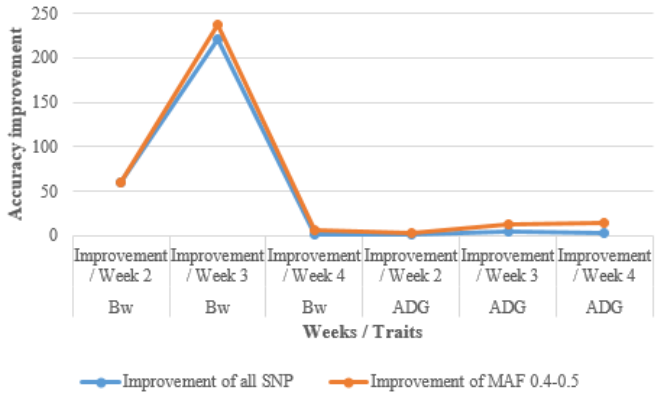


Fig. 5. Genetic improvement of markers with MAF 0.4-0.5 compared to the information of all SNPs in the second, third and fourth weeks.

strategy for genetic improvement of economic traits in livestock and poultry industries [Mrode *et al*. 2019]. Our studies provided valuable insights into applying genomic selection with low-density markers in F_2 cross broiler population. It is generally expected that a high proportion of genetic diversity may be explained by using high-density panels but given that most of the SNPs in high-density SNP panel are in linkage disequilibrium (LD) with causal mutations, increasing the number of markers may not result in significant accuracy improvement in genomic evaluation of population with single-breed reference population [Su *et al.* 2012, Zhang *et al*. 2018]. Also, using 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, 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 (MAF) 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 0.4-0.5 in both traits BW and ADG can result in slight improvement of accuracy of prediction compared to those generated from all genotype data or using traditional BLUP (Fig. 4, 5). Consistent with our results, several studies showed that using the subset of SNPs can provide even better results than using of all SNPs 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].

We used the ssGBLUP using a 60k SSNP 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 was used (Fig. 3, 4). In agreement with current results, Salek Ardestani *et al*. [2021] found the highest prediction accuracy using ssGBLUP in comparison with BLUP, GBLUP, BayesC, and BayesCπ methods for the medium-size genotyped Canadian pig population. Silva *et al.* [2016] showed a higher accuracy when ssGBLUP was used compared to using BayesCπ and GBLUP methods for residual feed intake and feed conversion ratio traits in Nelore cattle. Yan *et al*. [2017] reported 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 and ADG traits, which are polygenic [Clark *et al.* 2011], the rate of improvement over BLUP was not noticeable. Given the relatively low to moderate heritability of these traits at different weeks of age [Mignon-Grasteau *et al.* 1999, Adeyinka *et al*. 2006, Mebratie *et al*. 2017], the large number of records in the reference population are 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]. Consistent with the current results, for growth 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 low pedigree depth. They also showed accuracy improvement by increasing 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 in both BW and ADG traits for 3 weeks of age (220.37 and 3.87%, respectively), which could be due 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.

In both traits, the degree of genetic correlation between adjusted phenotype and EBVs at different ages were increased using ssGBLUP compared to BLUP method. However, small improvement was observed for BW at 4 weeks of age and ADG at 2 and 4 weeks of age which could be due to the relatively minor increase in genetic correlation between adjusted phenotypes and EBVs using ssGBLUP over BLUP. Based on the current results, implementation of genomic evaluation based on ssGBLUP method using whole SNPs for BW at two and three weeks of age and for ADG at three weeks of age can result in more accurate results in populations with similar structure.

Conclusion

Although traits related to growth are of the main breeding objectives in chicken breeding, 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 5-fold cross-validation method based on the ssGBLUP method. Moreover, the subset of SNPs with MAF 0.4-0.5 was used for genomic predictions using ssGBLUP method. Generally, SNPs with MAF 0.4-0.5 had higher predictive ability compared to 100% information of SNPs, and three weeks was the best time to perform genomic evaluations in growth traits. 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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Conflict of interest

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

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