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Accounting for genetic architecture for body weight improves accuracy of predicting breeding values in a commercial line of broilers

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Abstract

BLUP (best linear unbiased prediction) is the standard for predicting breeding values, where different assumptions can be made on variance–covariance structure, which may influence predictive ability. Herein, we compare accuracy of prediction of four derived-BLUP models: (a) a pedigree relationship matrix (PBLUP), (b) a genomic relationship matrix (GBLUP), (c) a weighted genomic relationship matrix (WGBLUP) and (d) a relationship matrix based on genomic features that consisted of only a subset of SNP selected on a priori information (GFBLUP). We phenotyped a commercial population of broilers for body weight (BW) in five successive weeks and genotyped them using a 50k SNP array. We compared predictive ability of univariate models using conservative cross-validation method, where each full-sib group was divided into two folds. Results from cross-validation showed, with WGBLUP model, a gain in accuracy from 2% to 7% compared with GBLUP model. Splitting the additive genetic matrix into two matrices, based on significance level of SNP (G_f: estimated with only set of SNP selected on significance level, G_r: estimated with the remaining SNP), led to a gain in accuracy from 1% to 70%, depending on the proportion of SNP used to define G_f. Thus, information from GWAS in models improves predictive ability of breeding values for BW in broilers. Increasing the power of detection of SNP effects, by acquiring more data or improving methods for GWAS, will help improve predictive ability.

1 | BACKGROUND

In animal breeding, it is needed to estimate breeding values to select the future reproducers. Best linear unbiased prediction (BLUP) model that was conceptualized by Henderson (Henderson, 1963, 1975), made possible to predict breeding values for each candidate for selection. Originally, models' variance–covariance structure was described by a pedigree relationship matrix (PBLUP). Wide implementation of PBLUP was possible in the 90's thanks to the development of computation methods that could easily and rapidly solve complex mixed-model equations integrating large pedigree relationship matrices (Golden et al., 1991; Meuwissen & Luo, 1992; Tier, 1990).

Haley and Visscher (1998) suggested describing the variance–covariance structure with a genomic relationship matrix. This matrix was later conceptualized by Meuwissen, Hayes, and Goddard (2001), which led to the genomic best linear unbiased prediction (GBLUP) model.

The classical GBLUP model assumes that additive genetic variance is homogeneous across the genome. However, many gene mapping studies have shown that some genomic regions contribute more to genetic variance than others (Chicken QTL Database, 2017; Hu et al., 2013), with differences depending on traits and/or populations.

In order to define a model based on the genetic architecture of individual traits, Zhang et al. (2010) proposed a variation of the GBLUP model, where prior information on genetic architecture of the traits was used to assign a discrete variance to each SNP when defining a genomic relationship matrix. Because different genomic regions affect different traits, a different genomic relationship matrix is needed for each trait. In this model, the genetic variance–covariance was described by a weighted genomic relationship matrix (WGBLUP) rather than by the standard GBLUP matrix, where each SNP was weighted equally. Zhang et al. (2010) showed that WGBLUP model performs better than GBLUP because it increases the prediction accuracy of estimated breeding values (EBV) from 3% to 10% relative to GBLUP. The expected improvement in accuracy is high with WGBLUP for traits deviating more from an infinitesimal model. So, gain in predictive ability is expected for traits controlled by few large QTL.

Sørensen, Edwards, and Jensen (2014) proposed another model that considers the genetic variance across the genome and evaluated the collective effects of sets of SNP (GFBLUP, Genomic Feature BLUP). In this model, genetic markers were split into two or more components based on a priori genetic information, such as identified QTLs, gene ontology (GO) or pathway enrichment. Specifically, sets of SNP, which are expected to be in strong linkage disequilibrium (LD) with the QTL, are included in the first genomic matrix, which is called a genomic feature matrix ($\mathbf{G}_f$). The remaining SNP are assigned to a second matrix, called the residual genomic matrix ($\mathbf{G}_r$). This model was found to improve predictive ability relative to the standard GBLUP models for humans, fruit flies, dairy cattle and pigs (Fang et al., 2017; Rohde et al., 2018; Sarup et al., 2016). The improvement in predictive ability depends on the number of causal variants represented by the set of SNP defined by a given genomic feature and thus on the ability to identify such variants.

The genetic improvement in a breeding programme is proportional to the accuracy of predicted breeding values. Therefore, it is important to optimize genomic models used in genetic evaluations to maximize genetic improvement. Even, if models, such as WGBLUP and GFBLUP, might lead to an increase in predictive ability, it could be quite challenging to implement it into current breeding programmes in broilers. Indeed, the estimation of SNP effects is time consuming whereas, with the short interval of generation, evaluation should be done in a short time. It might increase this need for investment in genotyping also, since usually in broilers only a proportion of the selection candidates are genotyped.

In this study, various ways to define the genomic variance–covariance structure in a commercial line of broilers were tested. The aim of our study was to evaluate the benefits of having prior information on SNP effects in the definition of the covariance matrix describing additive genetic relationships among birds to improve the accuracy of predicted breeding values. We compared predictive accuracy of four best linear, unbiased prediction models with differently defined variance–covariance structure of the additive genetic effect: (a) a PBLUP, (b) a genomic relationship matrix (GBLUP), (c) a WGBLUP and a genomic relationship matrix with genomic features (GFBLUP).

2 | MATERIALS AND METHODS

2.1 | Birds

Our population of birds consisted of both sexes obtained from a commercial line of broilers, raised in a commercial environment. Their parents were raised in a bio-secure environment where selection was done on the relatives of birds in our study. Pedigree covered 23 selection rounds (SR), which corresponds to when a decision of selection was done, back to when the line was formed and included birds from both the commercial and bio-secure environments (Chu, Bastiaansen, et al., 2019; Chu, Madsen, et al., 2019; Mebratie et al., 2019). However, the phenotypes and genotypes used in this study were only commercially reared birds and were focussed on 12 SR. Therefore, the only information on the parents was the pedigree information. All birds were both phenotyped and genotyped.

2.2 | Phenotypes

Body weight (BW) was recorded once per week for five successive weeks (W1–W5) after hatching. For two SR (SR17 and SR18), BW was recorded only until Week 4; for remaining, SR birds were recorded until Week 5. We analysed 10 traits relative to BW for each of the 5 weeks by sex (m = male, f = female): BW1f, BW1m, BW2f, BW2m, BW3f, BW3m, BW4f, BW4m, BW5f and BW5m. We phenotyped approximately 17,000 birds in total and provide descriptive statistics of the analysed traits in Table 1.

2.3 | Genotypes

All birds were genotyped with a custom Illumina 60k array (Illumina) and covered chromosomes GGA1 to GGA28, GGA33, Linkage group LGE64, and a group of SNP that did not have chromosome positions assigned.

TABLE 1 Descriptive statistics (number of observations, *N*; mean and standard deviation, *SD*) for body weight (BW) in grams for week 1 to 5 for females (F) and males (M)

	BW1		BW2		BW3		BW4		BW5	
	F	M	F	M	F	M	F	M	F	M
N	8,280	7,950	8,900	8,547	8,768	8,338	8,582	8,139	7,819	7,371
Mean	153.86	154.76	392.49	402.69	761.57	809.97	1,131.06	1,243.04	1,549.84	1,735.12
SD	21.55	21.95	61.54	63.44	117.81	131.42	190.20	218.24	248.92	303.26

In total, 18,270 birds were genotyped for 55,792 SNP. We performed quality control using Plink (Purcell et al., 2007) software with the following procedure: (a) SNP with a call rate less than 90% were removed (13 SNP); (b) Individuals with a call rate less than 99% were removed (482 individuals); (c) SNP with a call rate <99.9% were removed (4,249 SNP); (d) SNP with a minor allele frequencies <0.01 were excluded (4,914 SNP) and (e) SNP deviating from Hardy–Weinberg equilibrium based on F_{st} (Wright, 1922) were removed (114 SNP). Finally, genotype data included 46,502 SNP and 18,096 individuals.

2.4 | GWAS

For GFBLUP and WGBLUP models, individual SNP effects must be estimated. Therefore, for each SNP (1–46,502), we ran an SNP-by-SNP regression using this model for each of the 10 traits with univariate analysis:

$$\mathbf{y} = \mathbf{Xb} + \beta_1 \times \mathbf{SNP_{ia}} + \beta_2 \times \mathbf{SNP_{id}} + \mathbf{Zu} + \mathbf{Wm} + \mathbf{Wc} + \mathbf{e} \quad (1)$$

where **y** is a vector of phenotypic observations and **b** is vector of fixed effects. Fixed effects included the interaction selection rounds by hatch (11–12 classes), the interaction selection rounds by hatch of dam (83 classes) and age of dam at hatching (28 levels). β_1 is the effect for $\mathbf{SNP_{ia}}$ of the individual examined, and β_2 is the effect of $\mathbf{SNP_{id}}$ for each dam. $\mathbf{SNP_{ia}}$ and $\mathbf{SNP_{id}}$ are vectors of SNP for the *i*-th SNP genotype indicator variable coded as 0, 1 or 2 for both an individual and its dam. Matrices of **X**, **Z** and **W** are incidence matrices. Vectors **u**, **m**, **c** and **e** represent the direct additive genetic effect, maternal genetic effect, permanent environmental maternal effect and residual, respectively. Vectors **u** and **m** are the vectors of genomic values for direct additive genetic effects and maternal additive genetic effects captured by SNP on different chromosomes, leaving out the chromosome carrying $\mathbf{snp_i}$. To avoid redundancy, each time that a chromosome was excluded, we estimated variances of **u** and **m** using the AIREML module implemented in DMU (Madsen & Jensen, 2013). We assumed that the random effects and residuals were independent, normally distributed variables described as follows: $\mathbf{u} \sim N(0, \mathbf{G}\sigma^2_u)$, $\mathbf{m} \sim N(0, \mathbf{G}\sigma^2_m)$ and $\mathbf{e} \sim N(0, \mathbf{I}\,\sigma^2_e)$. We corrected all *p*-values by a Bonferroni procedure. We set the genome-wide significance threshold at $p < (0.05/46{,}502)$.

2.5 | Variance components estimation and prediction of breeding values

The manner in which we specified the variance–covariance structure was the only difference between the four models we examined (PBLUP, GBLUP, WGBLUP and GFBLUP). The general model we used was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wm} + \mathbf{Wc} + \mathbf{e} \quad (2)$$

where **y** is a vector of phenotypic observations and **b** is vector of fixed effects. Matrices of **X**, **Z** and **W** were incidence matrices. Vectors **u**, **m**, **c** and **e** were the direct additive genetic effect, maternal genetic effect, permanent environmental maternal effect and residual, respectively. We assumed that the maternal genetic effects, permanent environmental maternal effects and residuals were independent, normally distributed variables described as follows: $\mathbf{m} \sim N(0, \mathbf{A_d}\sigma^2_m)$, $\mathbf{c} \sim N(0, \mathbf{I_d}\sigma^2_c)$ and $\mathbf{e} \sim N(0, \mathbf{I}\sigma^2_e)$, where $\mathbf{A_d}$ is a pedigree relationship matrix for dams, and $\mathbf{I_d}$ and **I** are identity matrices of dimensions, number of dams and number of observations, respectively. We compared four different assumptions regarding direct additive genetic effects and compared various assumptions on the covariance structure of **u**, described in the following sections. We assumed direct and maternal additive genetic effects to be independent of one another.

For each variance–covariance structure we tested, we estimated variance components (VC) using the full dataset because, for GFBLUP, the additive genetic variance was split into two components. Therefore, the only way to know the variance explained by each of the components was to estimate VC for each proportion tested. This means that for each of the following models (below), we estimated VCs using the corresponding variance–covariance structure and then used them to predict breeding values.

2.5.1 | PBLUP

For the PBLUP model, we used a pedigree relationship matrix to describe variance–covariance structure. We assumed that variables for direct genetic effects were normally distributed, described as $\mathbf{u} \sim N(0, \mathbf{A}\sigma^2_u)$, where $\mathbf{A}$ is a pedigree relationship matrix for individuals.

2.5.2 | GBLUP

For all SNP, we described the variance–covariance structure with a genomic relationship matrix. Therefore, we assumed that variables describing the direct genetic effects were normally distributed, described as $\mathbf{u} \sim N(0, \mathbf{G}\sigma^2_u)$, with $\mathbf{G}=\mathbf{MDM}'$ and $d_{ii} = \frac{1}{\sum 2p_iq_i}$, where $\mathbf{M}$ is the matrix of cantered marker genotypes, and p and q are the allele frequencies of the i-th SNP (VanRaden, 2008).

2.5.3 | WGBLUP

We used a WGBLUP to describe variance–covariance structure. We determined weights based on individual SNP effects estimated in the GWAS. Therefore, we assumed that variables describing the direct genetic effect were independent and normally distributed, described as $\mathbf{u} \sim N(0, \mathbf{G}\sigma^2_u)$, with $\mathbf{G}=\mathbf{MDM}'$ and, $d_{ii} = \frac{\hat{\beta}^2_{1i}/\overline{\beta 1}}{\sum 2p_iq_i}$ where $\overline{\beta_1} = \frac{\sum 2p_iq_i \times \hat{\beta}^2_{1i}}{\sum 2p_iq_i}$ (Su et al., 2014) We estimated the SNP effect β_1 using Model 1.

2.5.4 | GFBLUP

For the GFBLUP matrix, we split the direct genetic effects into two components, one based on the genomic feature matrix ($\mathbf{G}_f$) and one based on the residual genomic matrix ($\mathbf{G}_r$). Therefore, $\mathbf{u} = \mathbf{f} + \mathbf{r}$ where $\mathbf{f} \sim N(0, \mathbf{G}_f\sigma^2_{gf})$, $\mathbf{G_f} = \mathbf{M_f D_f M_f'}$ with $d_{f_{ii}} = \frac{1}{\sum 2p_iq_i}$and $\mathbf{r} \sim N(0, \mathbf{G_r}\sigma^2_{gr})$ where $\mathbf{G_r} = \mathbf{M_r D_r M_r'} d_{rii} = \frac{1}{\sum 2p_iq_i}$, where $\mathbf{M_f}$ is the matrix of cantered marker genotypes included in the genomic feature matrix, and $\mathbf{M_r}$ is the matrix of cantered marker genotypes included in the residual genomic matrix. We assigned SNP to $\mathbf{M_f}$ or $\mathbf{M_r}$ based on results of our GWAS. For this, we ranked SNP based on their degree of significance and compared various proportions of SNP to be included in $\mathbf{G}_f$. We compared 13 different cut-off levels for SNP. For each proportion, we included the most genome widely significant SNP in $\mathbf{G}_f$. The proportions we compared were 0.1%, 0.2%, 0.3%, 0.4%, 0.5%, 1%, 2%, 3%, 4%, 5%, 10%, 15% and 20% of SNP.

To examine if the genetic variance explained by the 20% of the most significant SNP was due to chance, we sampled randomly 9,300 SNP 10 times. Then genetic variance explained by those 20% of SNP was estimated.

If a VC in a model converged to zero, we removed the corresponding genetic effect from the model. For all cases, this situation only occurred for σ^2_{gr}.

2.6 | Cross-validation

In order to compare models, we applied a two-fold cross-validation. For this, we first split the phenotypic data into two equal groups. Then, within each selection round, we randomly assigned animals to a group. Thus, we obtained three datasets, the full dataset and two reduced datasets. Then, we conducted a GWAS on both cross-validation groups. That is, we used the reduced datasets to estimate effects of SNP. For each genetic variance–covariance structure we tested, we estimated the VC on the full dataset, using AIREML software implemented in DMU. Therefore, for each trait we computed VC once for the PBLUB model, once for GBLUP model, twice for the WGBLUP model and 26 times for the GFBLUP model. For the WGBLUP and GFBLUP models, we used SNP information (weight or a set of significant SNP) to compare one group with another relative to estimated VC and breeding values. Thus, we used results from our GWAS for Group 1 to build a relationship matrix defining the variance–covariance structure of Group 2 and vice versa. We compared model accuracies using the correlation between the corrected phenotype (y_c) for fixed effects and the predicted breeding value based on the reduced dataset, divided by the square root of heritability: $(\text{Accuracy} = \text{cor}(\text{EBVr}, y_c)/\sqrt{h^2})$. In order to compare traits on the same basis, we used the heritability that we estimated with a PBLUP model on the full dataset. We assumed these estimates of heritability to be more accurate than heritability estimated with the GBLUP model because we observed some missing heritability with the GBLUP model (Table 2). We estimated inflation (often called "bias" in animal breeding literature) in predicted breeding values from the slope of the regression of the phenotype corrected for fixed effects on the predicted breeding value. Inflation values can be either positive or negative. Predictive accuracies and inflation values presented in this paper depict overall accuracies and inflation values across cross-validation groups. We computed standard errors of those estimates using formulas presented in the Appendix S1 of Chu, et al. (2019); Chu, et al. (2019).

We chose this two-fold cross-validation strategy to ensure that we had conservative criteria to compare models. Having close relatives in the training population ensured a high accuracy for PBLUP and GBLUP models. Therefore, further increases in model accuracy were more difficult to achieve. Secondly, we wanted to ensure that frequencies of markers and

TABLE 2 Estimated SNP effects relative to body weight (BW), by week (1–5 weeks) and sex (F = female, M = male)

(a)

	Group 1	Group 2	Group 1 & Group 2	Total	Male & Female
BW1					
F	67	99	61	105	93
M	98	2	0	100	
BW2					
F	122	75	69	128	120
M	156	39	31	164	
BW3					
F	18	54	16	56	42
M	70	70	47	93	
BW4					
F	2	17	2	17	1
M	1	0	0	1	
BW5					
F	0	1	0	1	0
M	0	2	0	2	

(b)

	Number of SNP the initial week	Number of SNP the next week	Number of SNP in common
BW1-BW2			
F	105	128	92
M	100	164	100
BW2-BW3			
F	128	56	54
M	164	93	88
BW3-BW4			
F	56	17	17
M	93	1	1
BW4-BW5			
F	17	1	0
M	1	2	0

Note: (a) Number of SNP reaching Bonferroni corrected significance level (p <.01) for each cross-validation group (Group 1 and Group 2), number of SNP common to both cross-validation groups (Groups 1 & 2 combined), total number of SNP, by trait (Total) and number of SNP common to both sexes. (b) Number of SNP reaching Bonferroni corrected significance level (p <.01) from a given week of age to the next.

QTL were not influenced by selection or genetic drift during the experiment. This approach is in contrast to the often-used forward prediction methods used to assess the accuracy of predicted breeding values for individuals without its phenotype. However, this criterion is not relevant for assessing the accuracy of predicted breeding values in broilers because genotypes and phenotypes are available before sexual maturity. Therefore, selection criteria in genomic broiler-breeding programmes always include information from an individual's own phenotype and pedigree/genomic data on its relatives, including contemporary close relatives.

We performed all statistical analysis using the DMU software package (Madsen & Jensen, 2013).

3 | RESULTS

3.1 | Summary of the data

Our single trait analyses focussed on BW of a commercial population of broilers measured at five successive weeks of age (for both sexes) (Table 1).

Fewer individuals were phenotyped for BW5 (body weight of 5-week-olds) than for the other traits we examined. For all samples, mean BW was higher for males than for females. This difference was significant for all traits ($p < .05$).

3.2 | Genetic architecture of body weight by age

SNP effects were estimated using single marker regression analysis for each reduced dataset. Significant SNP we identified are summarized in Table 2. Details on individual SNP were omitted because our focus was on determining the accuracy of predictive breeding values.

Spearman's correlation between SNP's effects estimated in the two cross-validation groups was on average 0.3. We identified several SNP reaching high levels of significance for BW1 and BW2, whereas we identified few highly significant SNP for BW4 and BW5 (Table 2a). Moreover, Table 2a shows that males and females at the same age shared a large proportion of common, highly significant SNP affecting BW. Even so, we observed some differences (different SNP or different levels of significance for sets of SNP) between sexes.

Table 2b shows that the genetic architecture of BW changed as chicks aged. More than 65% of the SNP identified as highly significant in females at Week 2 were the same as the SNP identified as highly significant in Week 1, whereas only 30% of SNP identified as highly significant in females at Week 4 were identified as highly significant in Week 3 were the same. So, as chicks aged, genetic architecture of successive BW became more different from each other's.

3.3 | Impact of genomic information on genetic parameters

The genetic parameters we estimated (with PBLUP and GBLUP models) with the full dataset for each trait are presented in Table 3.

Based on the PBLUP model, estimates of heritability (h^2) in BW ranged from 0.19 to 0.31, with a standard error between 0.04 and 0.05. Based on the GBLUP model, estimates of heritability (h^2) in BW ranged from 0.16 to 0.27 with standard errors of 0.02. For all data, our estimates of heritability were lower with the GBLUP model than when estimated with the PBLUP model.

Estimates of total variance were higher for males than for females for both models, and this difference became bigger as chicks aged. In the GBLUP model, heritability tended to be higher in females than in males as chicks aged, whereas we found no difference in heritability between sexes using the PBLUP model.

Maternal heritability (m^2) ranged from 0.02 to 0.07 in the PBLUP model and from 0.02 to 0.08 in the GBLUP model. Estimates of heritability of maternal effects declined over time in both models. Moreover, heritability of maternal

TABLE 3 Estimates of genetic parameters for body weight, by age (week 1–5) and sex (F = female, M = male) estimated with PBLUP and GBLUP models

	PBLUP				GBLUP			
	h^2	m^2	c^2	σ^2_p	h^2	m^2	c^2	σ^2_p
BW1								
F	0.20	0.034	0.095	307	0.18	0.041	0.096	305
M	0.19	0.075	0.065	315	0.16	0.078	0.070	312
BW2								
F	0.27	0.025	0.064	2,838	0.20	0.020	0.078	2,776
M	0.27	0.028	0.066	3,075	0.20	0.037	0.079	3,030
BW3								
F	0.26	0.024	0.048	9,531	0.21	0.023	0.060	9,406
M	0.26	0.021	0.064	11,966	0.18	0.032	0.081	11,799
BW4								
F	0.30	0.021	0.038	23,314	0.24	0.020	0.046	22,917
M	0.31	0.017	0.046	31,637	0.20	0.035	0.066	31,056
BW5								
F	0.31	0.018	0.038	48,033	0.27	0.021	0.041	47,542
M	0.29	0.019	0.030	68,369	0.23	0.029	0.04	67,931
Standard error range	0.04–0.05	0.015–0.024	0.015–0.020		0.02	0.012–0.021	0.012–0.018	

Abbreviations: c^2, permanent environmental maternal effect expressed as part of the total phenotypic variance (σ^2_p), h^2, the direct heritability; m^2, maternal heritability.

effects tended to be higher in males than in females and to decline less quickly over time. Although heritability of direct additive genetic effects tended to increase by age of the chicks, maternal heritability declined as the chicks aged.

3.4 | Integration of genomic information of traits into the evaluation models

We predicted breeding values using PBLUP and GBLUP models to compared models where relationships were either based on pedigree or on genomic information. In the PBLUP model, variance–covariance structure was described by a pedigree relationship matrix, whereas in the GBLUP model, variance–covariance structure was described by a genomic relationship matrix. We made predictions for both folds and by using VC estimated from the full dataset for both models. The accuracy of a predicted breeding value for an individual chick without phenotypic information is not equivalent to accuracies of prediction obtained in broiler breeding programmes because, with broilers, phenotypes are obtained prior to sexual maturity, whereas predictions for breeding value are used as conservative criteria for comparing models.

Tables 4a,b show mean predictive accuracies of breeding values for individual chicks with masked phenotypes and the inflations of these estimates for each trait for all models (PBLUP, GBLUP, WGBLUP and GFBLUP).

This section is focussed on accuracies of prediction and inflations of the EBV obtained with PBLUP and GBLUP models. Detailed results from WGBLUP and GFBLUP models are presented below.

Based on PBLUP models, accuracies of prediction ranged from 0.50 to 0.59, with a mean of 0.53 (Table 4a). Inflation ranged from 1.01 to 1.49 (Table 4b). Inflations of breeding values were highest for BW at week 1 (BW1).

With the GBLUP model, accuracies of prediction ranged from 0.53 to 0.67 (Table 4a), with a mean of 0.60. Inflations were low and ranged from 0.97 to 1.09 (Table 4b).

Thus, genomic information contributed to higher accuracies of breeding values, providing an observed gain of accuracy from 2% (BW1m) to 24% (BW5f). Gains in accuracy were less in males than in females for younger age classes (i.e., Week 1 [BW1] to Week 3 [BW3] after hatching). For BW1, inflations of the estimates were significantly lower in the PBLUP model than in the GBLUP model.

3.5 | Integration of genetic architecture of traits into the evaluation models

3.5.1 | WGBLUP model

WGBLUP model was the first model we used to integrate the genetic architecture of traits into an evaluation model. In a WGBLUP model, variance–covariance structure can be described by a WGBLUP, so in this study, we weighted each SNP individually based on our GWAS results. This means that we computed 20 weighted genomic matrices, one per trait and cross-validation group. We made subsequent predictions for both reduced datasets, using VC estimated from the full dataset. Accuracies of prediction and inflation of predicted breeding values are presented in Tables 4a,b.

Using the WGBLUP model, accuracies of prediction ranged from 0.52 to 0.66 (Table 4a), with a mean accuracy of 0.61. With this model, inflations ranged from 0.69 to 0.77 (Table 4b). Our use of a WGBLUP, rather than a classic genomic relationship matrix, increased our predictive ability. We observed gains in accuracy for BW in age class BW2 (BW 2 weeks after hatching) for females and males (+6% and +7%, respectively) and for BW3 for females and males (+2% and +4%, respectively). These increases in accuracy were only significant for chick at the second week after hatching (BW2). For the other traits, gains in accuracy ranged from −2% to 0%. Nonetheless, we observed an important inflation of the EBV.

3.5.2 | GFBLUP model

GFBLUP model was the second model we used to integrate the genetic architecture of traits into an evaluation model. In this model, we described the variance–covariance structure with two genomic relationship matrices. The first matrix ($\mathbf{G}_f$) was built using SNP showing the highest levels of significance of effect on a given trait, whereas the second matrix ($\mathbf{G}_r$) was built using the remaining SNP. We added various proportions of SNP, those with the highest $-\log_{10}(p)$ values, in the genomic feature matrix ($\mathbf{G}_f$). Table 5 provides accuracies of prediction and inflation of predicted breeding values, for each trait and proportions of SNP in $\mathbf{G}_f$.

Based on our GFBLUP model, the best accuracies of prediction ranged from 0.59 to 0.96 (Table 4a). With this model, inflations ranged from 0.62 to 1.21 (Table 4b).

Maximum gain of accuracy ranged from 1% (BW1f) to 70% (BW3m), but we observed no improvements in accuracy of predicted breeding values for weight of week-old males (BW1m) and for 4-week-old females (BW4f) (Table 4a). High gain in accuracy was often associated with a higher inflation of breeding values.

Overall accuracies were higher when the number of SNP in the genomic feature comprised between 0.1% and 0.5% of the most significant SNP or between 10% and 20% of all SNP (Table 5a). The proportion of SNP in the $\mathbf{G}_f$ matrix exhibiting the highest accuracies depended on the specific trait.

The proportion of total genetic variance explained by the $\mathbf{G}_f$ matrix ranged from 11% to 100%.

TABLE 4 Accuracy and inflation for estimated breeding values for body weight (BW) by age (week 1 to 5) and sex (F = female, M = male) with PBLUP, GBLUP and WGBLUP models, Accuracy (a) is the correlation between phenotypes corrected for fixed effects and predicted breeding values (reduced dataset) divided by the square root of heritability estimated with the PBLUP model. Inflation (b) is the slope of the regression for the corrected phenotype based on estimated breeding values

(a)

	BW1		BW2		BW3		BW4		BW5	
Model	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**
PBLUP	0.59 (0.02)	0.59 (0.02)	0.54 (0.02)	0.52 (0.03)	0.54 (0.02)	0.52 (0.02)	0.51 (0.02)	0.51 (0.02)	0.50 (0.02)	0.50 (0.02)
GBLUP	0.67 (0.03)	0.60 (0.02)	0.62 (0.02)	0.58 (0.03)	0.63 (0.02)	0.56 (0.02)	0.60 (0.03)	0.53 (0.02)	0.62 (0.03)	0.57 (0.02)
WBLUP	0.66 (0.03)	0.60 (0.02)	0.66 (0.02)	0.62 (0.03)	0.64 (0.02)	0.58 (0.02)	0.60 (0.03)	0.52 (0.02)	0.61 (0.03)	0.56 (0.02)
GFBLUP	0.68 (0.03)	0.59 (0.02)	0.67 (0.02)	0.62 (0.02)	0.65 (0.02)	0.95 (0.03)	0.60 (0.02)	0.68 (0.02)	0.96 (0.03)	0.81 (0.03)

(b)

	BW1		BW2		BW3		BW4		BW5	
Model	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**
PBLUP	1.32 (0.05)	1.49 (0.06)	1.04 (0.04)	1.12 (0.04)	1.05 (0.04)	1.08 (0.04)	1.01 (0.04)	1.03 (0.04)	1.02 (0.04)	1.03 (0.04)
GBLUP	1.09 (0.04)	1.08 (0.04)	0.99 (0.03)	1.03 (0.04)	1.00 (0.03)	1.03 (0.04)	0.98 (0.03)	1.03 (0.04)	0.99 (0.03)	0.97 (0.04)
WBLUP	0.72 (0.03)	0.69 (0.03)	0.76 (0.02)	0.76 (0.02)	0.73 (0.02)	0.72 (0.03)	0.71 (0.02)	0.70 (0.03)	0.74 (0.02)	0.69 (0.03)
GFBLUP	1.00 (0.03)	0.89 (0.04)	0.93 (0.03)	0.98 (0.03)	0.96 (0.03)	1.23 (0.02)	0.89 (0.03)	0.91 (0.02)	1.17 (0.02)	1.21 (0.03)

Note: Standard errors are shown inside parentheses. For the GFBLUP model, only accuracy results are presented that correspond to the highest correlations among all proportions of SNP tested.

TABLE 5 Accuracy and inflation for estimated breeding values obtained with the GFBLUP model, by proportion (Prop) of most significant SNP included in the genomic feature matrix ($\mathbf{G}_f$)

(a)													
Propin G_f	**0.1**	**0.2**	**0.3**	**0.4**	**0.5**	**1**	**2**	**3**	**4**	**5**	**10**	**15**	**20**
BW1													
F	0.64	0.65	0.66	**0.68**	NC	0.61	0.60	0.60	0.60	0.61	0.63	0.63	0.64
M	0.59	**0.58**	0.55	0.54	0.54	0.53	0.53	0.53	0.52	0.56	0.57	0.59	NC
BW2													
F	NC	NC	NC	**0.67**	NC	0.61	0.60	0.61	0.61	0.61	0.62	0.62	0.62
M	0.62	0.62	**0.62**	0.62	0.61	0.59	0.58	0.57	0.58	0.57	0.57	0.57	0.58
BW3													
F	0.62	0.63	0.64	0.64	**0.65**	0.59	0.59	0.59	0.59	0.59	0.59	0.60	0.61
M	0.56	0.56	0.57	0.58	0.58	0.54	0.54	0.54	0.63	0.79	0.87	0.92	**0.95**
BW4													
F	0.57	0.57	0.58	0.58	**0.60**	0.57	0.56	0.56	0.56	0.56	0.56	0.57	0.58
M	0.48	0.48	0.48	0.49	0.49	0.48	0.48	0.48	0.48	0.48	0.63	0.66	**0.68**
BW5													
F	0.58	0.58	0.58	0.55	0.56	0.57	0.57	0.57	0.58	0.58	0.59	0.77	**0.96**
M	0.76	0.76	0.77	0.79	**0.81**	0.73	0.71	0.71	0.70	0.71	0.70	0.73	0.74
(b)													
Propin Gf	**0.1**	**0.2**	**0.3**	**0.4**	**0.5**	**1**	**2**	**3**	**4**	**5**	**10**	**15**	**20**
BW1													
F	0.87	0.89	0.95	**1.00**	NC	0.75	0.68	0.66	0.64	0.64	0.65	0.66	0.69
M	0.89	**0.87**	0.83	0.79	0.67	0.61	0.59	0.59	0.58	0.61	0.63	0.66	NC
BW2													
F	NC	NC	NC	**0.93**	NC	0.76	0.70	0.69	0.68	0.68	0.69	0.71	0.72
M	0.96	0.96	**0.98**	0.95	0.93	0.78	0.72	0.69	0.69	0.67	0.68	0.69	0.71
BW3													
F	0.86	0.88	0.92	0.93	**0.96**	0.76	0.70	0.68	0.66	0.66	0.66	0.68	0.70
M	0.82	0.87	0.92	0.99	0.99	0.72	0.66	0.64	0.79	1.02	1.12	1.18	**1.23**
BW4													
F	0.78	0.79	0.82	0.83	**0.89**	0.73	0.68	0.66	0.66	0.66	0.65	0.66	0.68
M	0.73	0.75	0.78	0.82	0.82	0.67	0.64	0.64	0.63	0.63	0.83	0.88	**0.91**
BW5													
F	0.76	0.77	0.78	0.69	0.76	0.73	0.71	0.70	0.69	0.69	0.70	0.92	**1.17**
M	1.09	1.09	1.12	1.18	**1.21**	1.00	0.94	0.92	0.89	0.89	0.86	0.89	0.92

Note: Accuracy (a) is the correlation between phenotypes corrected for fixed effects and predicted breeding values (reduced dataset) divided by the square root of heritability estimated with the PBLUB model. Inflation (b) is the slope of the regression for the corrected phenotype based on estimated breeding values. Top row corresponds to the percentage of SNP included in the genomic feature matrix, based on level of significance. The remaining SNP have been set into the residual genomic matrix.

4 | DISCUSSION

4.1 | Genetic parameters for BW

Our heritability estimates for BW were in the lower range of estimates reported in the published literature, where BW heritability is between 0.21 and 0.64 (Mignon-Grasteau et al., 1999, Gaya et al., 2006, Mebratie et al., 2017). The lower estimates we found might be explained by the fact that the broiler line we studied was selected for BW over many generations. Moreover, as age chicks aged, heritability estimates (h^2) of weight tended to increase. In our study, heritability estimates tended to be higher in females than in males.

Heritability estimates tended to be lower with our GBLUP model than with our PBLUP model. We believe that applying genetic markers to describe population structure was insufficient for capturing all additive genetic variance in this population. Adding an extra additive genetic effect based on a pedigree relationship matrix into the GBLUP model may help overcome missing heritability difficulties by modelling residual additive genetic variances.

Again, our heritability of maternal effects (m^2) occurred at the lower range of estimates reported in the published literature. For example, Koerhuis and Thompson (1997) reported maternal heritability ranging from 0.01 to 0.17 depending on models and lines examined. Mignon-Grasteau et al. (1999) reported similar estimates of maternal heritability. Depending on age at measurement, maternal heritability ranged from 0.08 to 0.24, maternal heritability declined with age and maternal genetic effects ceased for females sooner than for males. As chicks aged, maternal effects declined and this decline was more rapid for females than for males, as it is in our study. Moreover, Hartmann et al. (2003) showed that maternal genes related to egg quality (yolk and albumen quality) had a larger effect on offspring BW at hatching than did additive genetic effects of genes inherent to the offspring itself. This finding suggests that some QTL related to BW identified in young chicks may in fact be maternal QTL affecting other traits or QTL having pleiotropic effects on both direct and maternal effects on BW.

4.2 | Impact of integrating genomic information in prediction models

Adding genomic information to evaluation models provides better predictive ability of breeding values for birds without own records. Our improvements in predictive ability were quite small relative to improvements obtained by Chen et al. (2011), wherein predictive ability for BW improved by 50% for broilers. The relatively small gain in predictive ability observed in our study is due to the conservative cross-validation strategy applied in this study. The inherent increased accuracy of our approach is because every individual in the validation population had half of its siblings in the training population. Therefore, breeding values estimated with PBLUP tended to be already highly accurate. Nevertheless, even if gain in accuracy was small for some traits, adding genomic information into the evaluation model affected the animals selected.

4.3 | Input from SNP effects in genetic evaluation models

4.3.1 | SNP effects estimation

To maximize the predictive ability of evaluation models incorporating genetic architecture of traits, estimation of SNP effects should be accurate. Fragomeni et al. (2017) showed, in a simulation study, that when covariance–variance structure is defined by a WGBLUP, using the true SNP effects over the estimated effects let to a gain in accuracy of 41%. The higher predictive ability of GFBLUP model relies as well on one's ability to accurately estimate SNP effects to differentiate the SNP describing causal mutations from other, non-causal SNP (Sarup et al., 2016; Zhang et al., 2016).

In our study, each SNP effect was estimated SNP by SNP. In doing so, we did not consider LD between SNP. This approach could have led us to placing more weight than reasonable on specific genomic regions because the estimated effect of one SNP could be have been partially due to SNP in high LD. This over-consideration of some genomic regions might explain the inflation of breeding values observed with WGBLUP and the large standard error observed with GFBLUP model. A joint estimation of SNP effects, using for example Bayesian variable selection methods, might help to estimate more realistic SNP effects.

4.3.2 | WGBLUP model

Gain in predictive ability using WGBLUP has been observed in various farmed species such as pig and cattle (Su et al., 2014; Tiezzi & Maltecca, 2015; Veroneze et al., 2016). The improvement of predictive ability depends on weighting strategies as it has been showed in simulation studies (Karaman et al., 2018; Zhang et al., 2016) and in real data studies (Tiezzi & Maltecca, 2015). Some authors showed that considering SNP windows or/and using Bayesian methods to estimate SNP variances led to higher predictive ability (Karaman et al., 2018; Su et al., 2014; Teissier et al., 2018; Zhang et al., 2016).

The superiority, in term of predictive ability, of evaluation models using a WGBLUP over the ones classical genomic matrix depends also on the genetic architecture of the traits analysed. Indeed, WGBLUP model performs better for genetic traits that differed strongly from the polygenic model (Zhang et al., 2010). Tiezzi and Maltecca (2015) reported gain in accuracy while using a WGBLUP approach only for a trait affected by a QTL with large effect, whereas no gain was observed for the other traits influenced by QTL with smaller effects. Thus, we expect that a gain in accuracy would be observed for traits controlled by some large QTLs. We observed indeed gain in predictive ability for traits influenced by several highly significant SNP. But for BW of week-old chicks, we observed no gain in accuracy, whereas we found few highly significant SNP affecting this trait. This lack of gain in accuracy could be due to the fact that the BW of 1-week-old chicks might not be regulated by the same genes that regulate BW of two- and 3-week-old chicks, or at least that the effects of the genes involved are not as high at earlier stages of growth than they are at later stages. Few highly significant

SNP were found for later traits, and so no gain in accuracy was observed for those traits. Previous selection pressures may have been primarily focussed on BW of older chicks and thus QTLs affecting birds at this age might more likely have been fixed by selection.

The WGBLUP model led to an increase in accuracy of EBV, but it also lead to a negative inflation (deflation) of breeding values compare to the one observed in the GBLUP model This increase in inflation might be explained by differences in scale between the two genomic matrices. Here, the largest difference between the average diagonals of the two matrices (classic genomic matrix vs. weighted genomic matrix) was of 0.042 with a median at 0.030, which could have been due to the way we computed SNP weights. We suspect that a better estimate of the SNP's effect might help reduce this inflation value and thus increase predictive accuracy.

4.3.3 | GFBLUP models

In a simulation study, Sarup et al. (2016) obtained a gain of accuracy of 36% for the best-case scenario wherein all causal mutations were used in the $\mathbf{G}_f$ matrix and were assumed to be known such that the G matrix was not "diluted" by anonymous SNP with no effects. Therefore, the high accuracy we found with the large proportion of SNP we included in our $\mathbf{G}_f$ matrix (BW3m, BW4m and BW5f) and found for BW5m seem overly optimistic to us, although we cannot explain our highly positive results. Random samples of 20% of SNP (10 samplings) showed fewer predictive accuracies than the samples obtained for our 20% of more significant SNP for BW3m and BW4m (0.31 for both vs. 0.48 and 0.53, respectively), suggesting a real effect of those SNP on those specific traits. Predictive accuracies for the other traits obtained with a random sampling of 20% of SNP were similar to the predictive accuracy we obtained when using the top 20% most significant SNP. In any case, it seems that 20% of SNP was sufficient to explain all genomic variance in the population we studied. The effective number of SNP (estimate based on LD) was 13,732 SNP. Therefore, we conclude that 20% of SNP (~9,300 SNP) should be sufficient for determining the effective number of SNP needed to describe the LD in this population. This 20% estimate aligns with an Ilska et al. (2014) study demonstrating that the SNP density used for genomic evaluations has a small effect on accuracy of prediction of breeding values for BW in broilers.

The performance of genomic feature models relies on their ability to differentiate SNP linked to causal mutations from non-informative SNP. When more non-informative SNP are added to a genomic feature matrix (G_f), the predictive ability declines (Sarup et al., 2016). In contrast, a sufficient number of informative SNP (i.e. SNP describing causal mutations) should be added to this G_f matrix. In fact, Sarup et al. (2016) showed that to reach the highest degree of predictive ability, at least 10% of the genetic variance should be explained by the variants included in the genomic feature matrix. In our study, at least 11% of the genetic variance was explained by the genomic feature matrix.

A GFBLUP model must consider the combined action of a specific set of SNP being evaluated. The SNP used in $\mathbf{G}_f$ matrices are supposed to be the SNP known to have an effect on the trait of concern. In our case, the selection of SNP was very simple because we only considered the most significant SNP. Thus, sometimes, depending on the genetic architecture of a specific trait, we might have included only one or two genomic regions in a $\mathbf{G}_f$ matrix. We could have employed different approaches, such as utilizing GO term. In that case, all the regions associated with a significant GO term could have been considered in the $\mathbf{G}_f$ matrix. For example, in a dairy cattle study, Fang et al. (2017) showed a significant increase in predictive accuracy for milk, fat and protein yields and mastitis when preselecting SNP based on GO for GFBLUP model. This approach could be a way to add prior biological information to the evaluation model to maximize an improvement in predictive accuracy. Another strategy could be to utilizing QTLs already reported in the literature.

4.4 | Implementation of such models in breeding programme

Because evaluation models that incorporate the genetic architecture of traits, such as GFBLUP and WGBLUP models, are useful for increasing predictive ability of breeding values in broilers, breeding companies could use these approaches to improve predictive ability. However, several barriers could limit implementation of such models in breeding programmes. One of the barriers is the selective genotyping strategy that is often done in breeding programme using genomic selection because of the large number of candidates. Integrating phenotypes of non-genotyped with weighted genomic matrix is possible with WssGBLUP (Wang et al., 2012) and lead to gain in accuracy (Liu et al., 2020; Teissier et al., 2018; Zhang et al., 2016). Such models might also help to reduce computation time, since it will estimate at the same time weight of the SNP within ssGBLUP. However, single-step approach might lead to a bias estimation of VC when selective genotyping is carried on (Wang et al., 2020). Moreover, a good representation of the QTL segregating in the population might be needed. Those two last arguments involve a change towards a random genotyping strategy should be done. Finally, it would be important for the poultry industry to determine for how many generations the SNP weights or the sets of SNP (G_f and G_r) could be used. In other words, how long would it take to break the LD between causal mutations and the set of SNP identified to be included in the genomic feature.

5 | CONCLUSION

Considering the genetic architecture of traits, improve the accuracy of predicting breeding values for traits influenced by highly significant SNP. To ensure that this gain in predictive ability can be exploited in commercial breeding programmes, conservative criteria for model comparisons should be used. An accurate estimate of SNP effects is needed to maximize gain in accuracy of prediction in models exploiting genetic architecture of traits. Use of GFBLUP showed less inflation of predicted breeding values relative to the WGBLUP model, but the predictive ability of the two methods was quite similar. The GFBLUP model requires determining the optimum set of SNP that should be included in a genomic feature matrix, whereas this criterion is not needed for the WGBLUP model. If enough data are available to a broiler-breeding programme to estimate SNP effects (and hence the genetic architecture of its breeding animals), the data could potentially be used to improve its breeding programme by increasing predictive ability when selecting for desired traits.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author with permission from Cobb-Vantress.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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