ANIMAL GENETICS AND GENOMICS

Investigating the persistence of accuracy of genomic predictions over time in broilers

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Abstract

Accuracy of genomic predictions is an important component of the selection response. The objectives of this research were: 1) to investigate trends for prediction accuracies over time in a broiler population of accumulated phenotypes, genotypes, and pedigrees and 2) to test if data from distant generations are useful to maintain prediction accuracies in selection candidates. The data contained 820K phenotypes for a growth trait (GT), 200K for two feed efficiency traits (FE1 and FE2), and 42K for a carcass yield trait (CY). The pedigree included 1,252,619 birds hatched over 7 years, of which 154,318 from the last 4 years were genotyped. Training populations were constructed adding 1 year of data sequentially, persistency of accuracy over time was evaluated using predictions from birds hatched in the three generations following or in the years after the training populations. In the first generation, before genotypes became available for the training populations (first 3 years of data), accuracies remained almost stable with successive additions of phenotypes and pedigree to the accumulated dataset. The inclusion of 1 year of genotypes in addition to 4 years of phenotypes and pedigree in the training population led to increases in accuracy of 54% for GT, 76% for FE1, 110% for CY, and 38% for FE2; on average, 74% of the increase was due to genomics. Prediction accuracies declined faster without than with genomic information in the training populations. When genotypes were unavailable, the average decline in prediction accuracy across traits was 41% from the first to the second generation of validation, and 51% from the second to the third generation of validation. When genotypes were available, the average decline across traits was 14% from the first to the second generation of validation, and 3% from the second to the third generation of validation. Prediction accuracies in the last three generations were the same when the training population included 5 or 2 years of data, and a decrease of ~7% was observed when the training population included only 1 year of data. Training sets including genomic information provided an increase in accuracy and persistence of genomic predictions compared with training sets without genomic data. The two most recent years of pedigree, phenotypic, and genomic data were sufficient to maintain prediction accuracies in selection candidates. Similar conclusions were obtained using validation populations per year.

Key words: independent chromosome segments, linear regression method, persistence of accuracy, prediction accuracy, single-step GBLUP

Abbreviations

A	pedigree relationship matrix
CY	carcass yield trait
FE1	feed efficiency trait one
FE2	feed efficiency trait two
G	genomic relationship matrix
GT	growth trait
L	length of the genome
LR	linear regression
N_e	effective population size
SNP	single nucleotide polymorphisms

Introduction

Accuracy of genomic predictions is an important parameter in animal breeding programs because of its direct relationship with selection response. This parameter is a function of the proportion of the genetic variance captured by single nucleotide polymorphisms (SNP) and the accuracy of SNP effect estimates, which depends on the amount and distribution of phenotypic and genotypic data available, the genetic architecture and the heritability of the trait, and the statistical method used (Dekkers, 2007; Goddard, 2009).

The decay in accuracy of predictions over time in initial genomic selection studies using stochastic simulations was small. Meuwissen et al. (2001) found that the prediction accuracy for a trait with major genes, in the absence of artificial selection, decreased from 0.84 to 0.72 after five generations without phenotyping the genotyped animals. Muir (2007), also using a stochastic simulation, concluded that accuracy of genomic selection in breeding programs decays faster for traits under selection.

Using simulated data from layers, Wolc et al. (2015) reported that after 3 years of selection, the prediction accuracy remained almost stable, decaying from 0.77 to 0.73 when the breeding program included new animals with genotypes and phenotypes every generation. Conversely, the accuracy declined from 0.77 to 0.34, when no new animals with phenotypes were included, and the attained selection response was smaller. In the same study, results obtained using real data from approximately 2,700 genotyped animals were consistent with those of the simulation; however, the accuracy was lower.

Genomic selection acts on independent chromosome segments (VanRaden, 2008; Goddard, 2009) and on clusters of chromosome segments (Pocrnic et al., 2019). The number of independent chromosome segments segregating in a finite population can be estimated as $4N_eL$ (Stam, 1980), where N_e is the effective population size and L is the length of the genome in Morgans. Equivalently, the number of independent chromosome segments can be estimated as the number of the largest eigenvalues explaining 98% of the variation in the genomic relationship matrix (**G**; Pocrnic et al., 2016a). Assuming $L = 30$ Morgans, Pocrnic et al. (2016b) estimated the number of independent chromosome segments in a broiler population to be approximately 5.5K, when N_e was 44.

Based on the findings of Pocrnic et al. (2016b), we hypothesized that the accuracy of genomic predictions in a broiler population under selection would be high, with a small decay over time if predictions are based on at least 5.5K genotyped animals with high individual prediction accuracies, that is, if the data are large enough to estimate accurately the effect of the independent chromosome segments segregating in the population. Chromosome segments are high linkage disequilibrium regions with low recombination rate (Muir, 2007);

therefore, the persistence of genomic prediction accuracies should be high in a breeding program under the assumption of an additive model even with strong selection on traits of interest. Bradford et al. (2017) demonstrated that accuracy of genomic predictions declines marginally under intensive selection. In their study, the accuracy of predictions in animals from the generation of validation was similar using training populations with genotyped animals from the previous or distant generations (up to 5 generations back).

In the absence of inbreeding, the relatedness and potential contributions of ancestors of an animal, based on pedigree relationships, decline 50% for each generation traced back in the pedigree. Therefore, very distant ancestors have small or even negative effects on the accuracy of predictions of the youngest animals (Lourenco et al., 2014). The decline of relatedness and potential contributions based on genomic relationships will depend on the method used to compute **G**. Thus, it is of interest to study the contribution of genotypes, pedigree, and phenotypes from distant generations to the accuracy of genomic predictions in selection candidates.

One of the most commonly used methods for estimating the accuracy of genomic predictions is a cross-validation test called predictive ability. Predictive ability refers to the correlation between genomic predictions and phenotypes adjusted for fixed and random effects other than additive genetic and residual effects (Legarra et al., 2008). According to Legarra and Reverter (2018), the statistic of this method is sensitive to incorrect heritabilities, structure of systematic effects, and pre-correction of phenotypes and may yield biased results if these are incorrect. Legarra and Reverter (2018) proposed a semi-parametric method based on linear regression (LR) that relies on the comparison of successive evaluations based on partial and whole data. The statistic of this method does not require pre-correction of phenotypes and may yield better estimates of prediction accuracies. Thus, the objectives of this research were: 1) to investigate trends for prediction accuracies over time in a broiler population of accumulated phenotypes, genotypes, and pedigrees, using the LR method and 2) to test if data from distant generations are useful to maintain prediction accuracies in selection candidates.

Materials and Methods

Animal care and use committee approval were not needed because data were obtained from preexisting databases.

Data and variance components

The dataset used in this research study was provided by Cobb-Vantress Inc. (Siloam Springs, AR). The pedigree included 1,252,619 purebred broilers hatched over 7 years. A total of 154,329 birds were genotyped with a 60K SNP panel. Depending on the trait, birds were selected for genotyping randomly or based on phenotypes. Quality control on genotypes was performed using PREGSF90 software (Misztal et al., 2014a) and excluded duplicated genotypes, birds, and SNP with call rate <0.90, SNP with minor allele frequency <0.05 or with departure from Hardy–Weinberg equilibrium (difference between the observed and expected heterozygous frequency) > 0.15. Parent-progeny pairs were tested for Mendelian conflicts (discrepant homozygous SNP); SNP were removed if the conflict rate was >10% (from the total of pairs evaluated), progenies were eliminated if the conflict rate was >1% (as percentage of all SNP). Monomorphic SNP, with

unknown position or located at sex chromosomes were also discarded. After quality control, 44,448 autosomal markers for 154,318 birds were kept for the analyses. All genotyped animals belonged to the four most recent years in the dataset. The whole dataset contained 820,110 phenotypes for a growth trait (GT), 200,093 phenotypes for the first feed efficiency trait 1 (FE1), 42,895 phenotypes for a carcass yield trait (CY), and 203,060 phenotypes for the second feed efficiency trait (FE2). The GT and CY phenotypes were recorded at 35 d of age, and the FE1 and FE2 phenotypes were measured during a 1-week period after 35 d of age.

Variance components were estimated using the average information restricted maximum likelihood algorithm implemented in the AIREMLF90 software (Misztal et al., 2014a). The analysis to estimate variance components was performed using the four-trait traditional pedigree-based animal model described in Lourenco et al. (2015) including all available pedigree and phenotypic data. The statistical model included sex and generation-hatch interaction as fixed effects, and the direct additive genetic and residual as random effects for all the traits but for GT, which also included the maternal permanent environmental random effect. The heritabilities for the four traits ranged from 0.20 to 0.55, the genetic correlations ranged from −0.15 to 0.31, and the phenotypic correlations ranged from −0.01 to 0.43.

Statistical analyses and computations

Genomic estimated breeding values were obtained with a four-trait animal model using a single-step genomic best linear unbiased prediction procedure (ssGBLUP; Aguilar et al., 2010) and the algorithm for proven and young (APY; Misztal et al., 2014b). Computations were performed with the software BLUP90IOD2OMP1 (Misztal et al., 2014a). The construction of the genomic relationship matrix G was based on VanRaden (2008). Matrix G was blended with 5% of the block of the pedigree relationship matrix A corresponding to genotyped animals (A_{22}) to avoid singularity problems. The rescaling of G to match A_{22} involved diagonals and off-diagonals (Chen et al., 2011). To implement APY, the eigenvalue decomposition of G was done to determine the number of the largest eigenvalues explaining 98% of the variation. Based on this, a core set of 5,173 genotyped animals was randomly selected.

Training and validation populations

The effect of increasing or decreasing the size of the training population on prediction accuracies was evaluated using a 7-year accumulated poultry dataset split according to year of hatch.

In the first scenario, increasing the size of the training population, the objective was to investigate the evolution of prediction accuracy over time using yearly accumulated phenotype, genotype, and pedigree data. Thus, the initial training population was progressively increased by adding 1 year of data at a time. For example, the first training population included all animals with phenotypes hatched in the first year, the second training population included all animals with phenotypes hatched in the first 2 years, and so on until the sixth training population, which included all animals with phenotypes in the first 6 years.

The first 3 years of data did not include genotyped animals; thus, only the last 4 years of data contributed with genotyped animals to the training populations. This data structure permitted the evaluation of the impact of including genomic information in training populations on accuracies of predictions of validation animals. When the training population included up to the first 3 years of data (no genomic information), validation was done on animals with phenotypes and pedigree, whereas for the training populations with genotyped animals, validation was done on animals with phenotypes, pedigree, and genotypes in the accumulated datasets.

The validation populations were constructed using two approaches: 1) animals hatched in the three generations after the most recent generation of the training population, that is, the progeny (P), grand progeny (GP), and great grand progeny (GGP) of animals from the most recent generation in the training population and 2) animals hatched during the years after the most recent year in the training population; hence, these validation populations included animals hatched only in 1 year. For example, if the training population included animals hatched in the first 3 years, there were four validation populations, formed by animals hatched in the fourth, fifth, sixth, and seventh year. The validation populations were defined by generations and by years to have an estimate of accuracy of predictions for separated generations and for overlapped generations (validation by years). The phenotypes of animals and their contemporaries in the validation populations were removed from the analyses. Also, siblings of birds in validation populations were removed from training populations, genotypes (when available) were kept in validation animals in all the analyses.

In the second scenario, decreasing the size of the training population, the objective was to test if the data from distant generations helped to avoid a decrease in prediction accuracy in selection candidates. The training population with 5 years of data was progressively reduced by removing the oldest animals. For example, when the training population was reduced from 5 to 4 years of data, data from the first year were removed from the training population. When the second year of data was removed, the training population was left with 3 years of data (i.e., data from years 3 to 5). This process continued until only the last year of data was kept in the training population (data from year five). The validation populations in this case were always formed by animals hatched in the three generations after the last year of the training population (i.e., after the fifth year of data). The number of animals in the training populations is presented in Table 1. The number of animals in the validation populations is presented in Table 2 by generation, and in Table 3 by year.

Table 1. Number of animals with phenotypic records in the training populations

Training population Years	Trait[1]			
Accumulated data	GT	FE1	CY	FE2
1	104,993	24,059	5,830	24,753
1–2	224,193	52,590	12,613	53,861
1–3	342,282	82,214	18,214	83,940
1–4	464,088	111,521	23,915	113,487
1–5	596,956	141,521	30,381	143,823
1–6	711,252	171,232	36,749	173,905
Removal of old data				
1–5	596,956	141,521	30,381	143,823
2–5	491,963	117,462	24,551	119,070
3–5	372,763	88,931	17,768	89,962
4–5	254,674	59,307	12,167	59,883
5	132,868	30,000	6,466	30,336

[1]GT, growth trait; FE1, feed efficiency trait one; CY, carcass yield trait; FE2, feed efficiency trait two.

Table 2. Number of animals in the validation populations by generation

Training population Years	Validation population[1]	Trait[2]			
		GT	FE1	CY	FE2
1	P	90,673	21,341	4,927	21,797
	GP	101,843	25,416	5,134	25,853
	GGP	111,953	26,824	5,008	27,081
1–2	P	95,485	23,730	4,150	24,134
	GP	106,400	25,024	4,893	25,245
	GGP	102,146	25,264	5,150	25,511
1–3	P	98,337	22,715	4,289	22,909
	GP	99,476	23,776	4,857	24,021
	GGP	103,909	24,028	5,161	24,298
1–4	P	37,823	27,628	6,286	27,925
	GP	30,473	22,888	4,760	23,157
	GGP	31,607	22,086	4,768	22,346
1–5	P	78,663	58,084	12,731	58,748
	GP	31,594	22,021	4,509	22,280
	GGP	17,489	12,651	2,921	12,759

[1]P, progeny; GP, grand progeny; GGP, great grand progeny.
[2]GT, growth trait; FE1, feed efficiency trait one; CY, carcass yield trait; FE2, feed efficiency trait two.

Table 3. Number of animals in the validation populations by year[1]

Year of validation	Trait[2]			
	GT	FE1	CY	FE2
2	119,200	28,531	6,783	29,108
3	118,089	29,624	5,601	30,079
4	33,343	24,856	5,652	25,066
5	39,068	28,695	6,442	29,022
6	39,859	29,633	6,341	30,003
7	41,019	28,769	5,948	29,063

[1]The number of animals presented corresponds to the smallest training population including 1 year of data, when the training population included 2 years of data, the first year of validation was year 3 in the table. The same logic applies to the successive and larger training populations.
[2]GT, growth trait; FE1, feed efficiency trait one; CY, carcass yield trait; FE2, feed efficiency trait two.

values was well estimated in all cases, and it was more precise as the amount of information (heritability) increased, proving that the LR method can provide accurate estimates of accuracy even with wrong heritabilities because accuracies are invariant to shift and scaling. In their study, the real heritability was either 0.10 or 0.30 and the assumed wrong heritabilities were deviate 0.05 upwards or downwards. In our study, we estimated genetic parameters using a pedigree-based model, though the heritability estimated using the genomic information can be different from the pedigree-based estimated, it is a good approximation.

Results and Discussion

Effect of increasing the size of the training population

The trends for the accuracy of estimated breeding values for GT, FE1, CY, and FE2 in the validation populations per generation and per year are shown in Figures 1 and 2, respectively. Accumulation of phenotypes and genotypes over time increased accuracy. A trait with lower heritability would require a larger number of phenotypes to achieve a similar level of accuracy and persistency of accuracy as a trait with higher heritability. For instance, FE1 and FE2 were half as heritable as CY, but number of FE1 and FE2 phenotypes were five times larger than the number of CY phenotypes; thus, the accuracy and persistency of accuracy attained by these traits was similar. Another factor influencing the accuracy attained is the structure of information, for CY, most birds were genotyped and with phenotypes.

When genotypes were not available for animals in the training populations (first 3 years of data), prediction accuracies in the validation populations were either nearly stable or their increase was small (ranging from not increase up to 15% of increase) even as pedigrees and phenotypes accumulated over time (Figures 1 and 2). As an illustration, the accuracy for GT in the progeny was 0.27, 0.26, and 0.31 when the training population included 1, 2, and 3 years of data, respectively. In contrast, when genotyped birds were available in the training populations, prediction accuracies in the validation populations had an important increase in all traits. Prediction accuracies in the progeny increased by 54% (0.31 vs. 0.48) for GT, 76% (0.35 vs. 0.61) for FE1, 110% (0.30 vs. 0.63) for CY, and 38% (0.47 vs. 0.65) for FE2 when the training population included 4 rather than 3 years of data (Figure 1). As
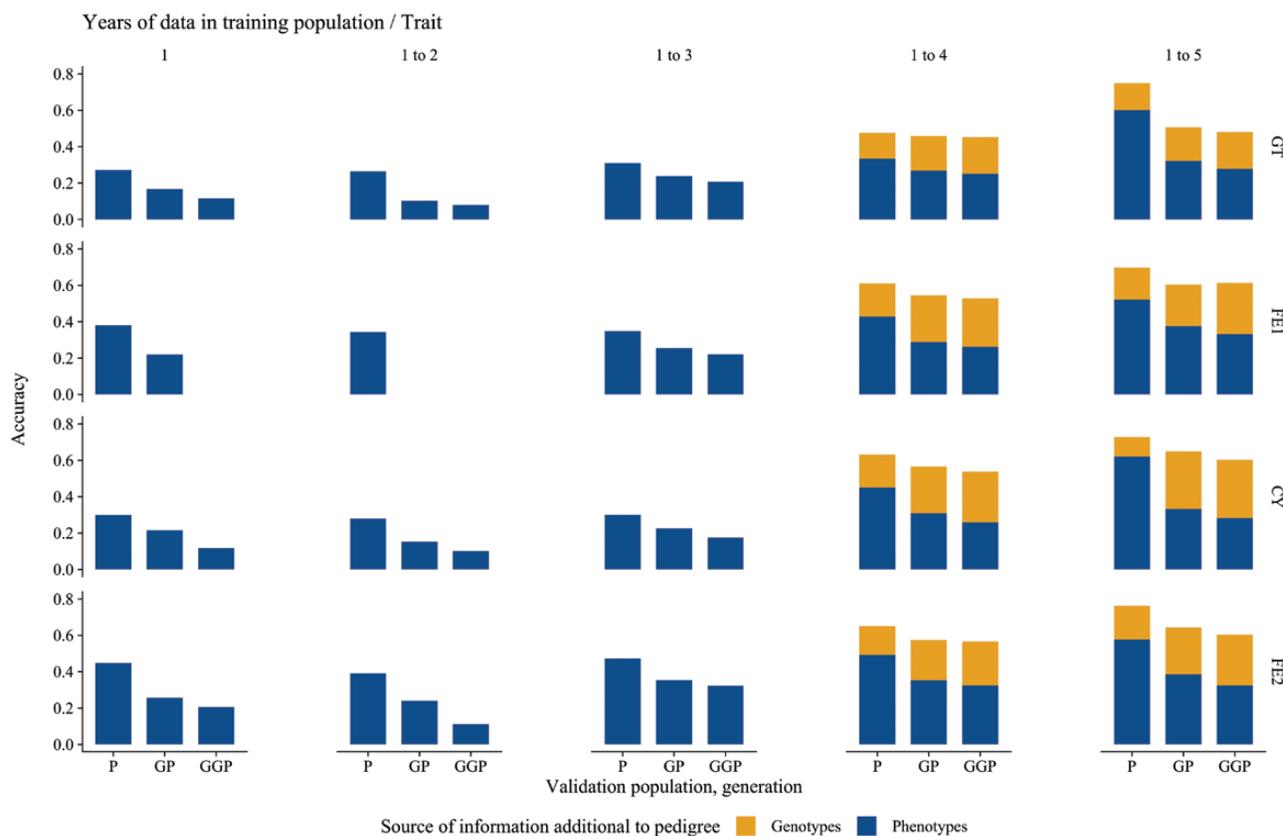
Accuracy of genomic predictions

Validation of genomic estimated breeding values was done by the LR method, which may provide more accurate estimates of prediction accuracies than the predictive ability method because it does not depend on the adjustments present in the predictive ability formula (Legarra and Reverter, 2018). In the LR method, statistics for validation individuals are computed by comparing estimated breeding values obtained using the whole dataset ($\hat{u}_w$) with estimated breeding values obtained using a partial dataset ($\hat{u}_p$). In the latter, phenotypes of validation individuals are removed from the analyses. Thus, both methods yield estimates of the correlation between estimated and "true" breeding values. The accuracies of estimated breeding values using the LR method ($\widehat{Acc}_{LR}$) were calculated as follows:

$$\widehat{Acc}_{LR} = \sqrt{\frac{cov(\hat{u}_w, \hat{u}_p)}{(1 - \bar{F})\sigma_a^2}},$$

where $cov(\hat{u}_w, \hat{u}_p)$ is the covariance between estimated breeding values obtained with the whole dataset and estimated breeding values obtained with the partial dataset, $\bar{F}$ is the average inbreeding coefficient in the validation population, and σ_a^2 is the additive genetic variance of the population.

Macedo et al. (2020b) used simulation to assess the performance of the statistics of the LR method when the evaluation model used either overestimated or underestimated heritabilities, and when the evaluation model did not account for environmental trends. The accuracy of estimated breeding

Figure 1. Trends for prediction accuracies of estimated breeding values in P, GP, and GGP of broilers in different training populations of accumulated pedigree, phenotypic, and genomic data for GT, FE1, CY, and FE2. Prediction accuracies were nearly stable with the accumulation of pedigree and phenotypes over time. The addition of genomic information generated an increase in prediction accuracy.

expected, the greatest increase in accuracy was observed for the trait with the greatest heritability. Across traits, on average, 74% of the increased accuracy was due to the inclusion of genotypes and the remaining 26% was due to the inclusion of more phenotypes and pedigrees (Figure 1).

A similar trend was observed for validation per year. The accuracy in the validation animals hatched 1 year after the training population increased by 72% (0.29 vs. 0.50) for GT, 78% (0.32 vs. 0.58) for FE1, 116% (0.29 vs. 0.59) for CY, and 39% (0.46 vs. 0.64) for FE2 when the training population included 4 instead of 3 years of data (Figure 2). The maximum accuracy attained per traits was greater in the validation per generation than in the validation per year. The maximum accuracy for the validation per generation(year) was 0.75(0.55) for GT, 0.70(0.67) for FE1, 0.73(0.67) for CY, and 0.76(0.66) for FE2.

The benefits of including genomic information on prediction accuracies have been reported across several species and traits. Wolc et al. (2011) indicated an average increase ~17% for predictions of 16 traits in layers. Lourenco et al. (2015) estimated an increase of ~50% in accuracy of predictions for growth and efficiency-related traits in broilers. Vallejo et al. (2017) stated that genomic information doubled the accuracy of predictions for disease resistance in rainbow trout. Garcia et al. (2018) found that genomic information increased accuracy up to 36% for predictions of residual carcass weight in channel catfish. In dual purpose cattle, Cesarani et al. (2020) found an increase of 37% in accuracy for predictions of milkability. Macedo et al. (2020a) reported an increase in accuracy of ~33% for predictions of milk production in a sheep population. Bermann et al. (2020) reported an increase of 15% in accuracy of predictions for mortality in broilers.

Increases in accuracy are attributed to a more precise estimation of Mendelian sampling terms (Hayes et al., 2009; Cole and VanRaden, 2011). The magnitude of the increase in accuracy of genomic predictions depends on the number, distribution, and contribution of genotypes and phenotypes, as well as on the selection intensity on traits (Lourenco et al., 2015). In our study, the increase in accuracy by inclusion of genotypes was greater than in most previous studies, which can be explained by the large number of phenotypes and genotypes available in this broiler population.

Accuracies in the validation populations declined faster without genotyped birds than with genotyped birds in the training populations (first 3 years of data), suggesting that the effects of independent chromosome segments were estimated with more precision in the latter case. According to Bastiaansen et al. (2012), pedigree relationships are not able to predict the random segregation of independent chromosome segments to the next generations, whereas this segregation can be traced by markers. Therefore, the proportion of the genetic variance explained by linkage disequilibrium with markers decays less than the proportion of the genetic variance explained by family structure. When individuals in the training and validation populations are related, they will share more chromosome segments, minimizing the loss of accuracy from training to validation populations; furthermore, if the data is large enough to accurately estimate the effect of the independent chromosome segments segregating in the population, the persistence will be high across several generations.

When no genotyped birds were included in the training populations, the average decrease in accuracy of estimated breeding values across traits and training populations was 41% from progeny to grand progeny, 60% from progeny to great grand
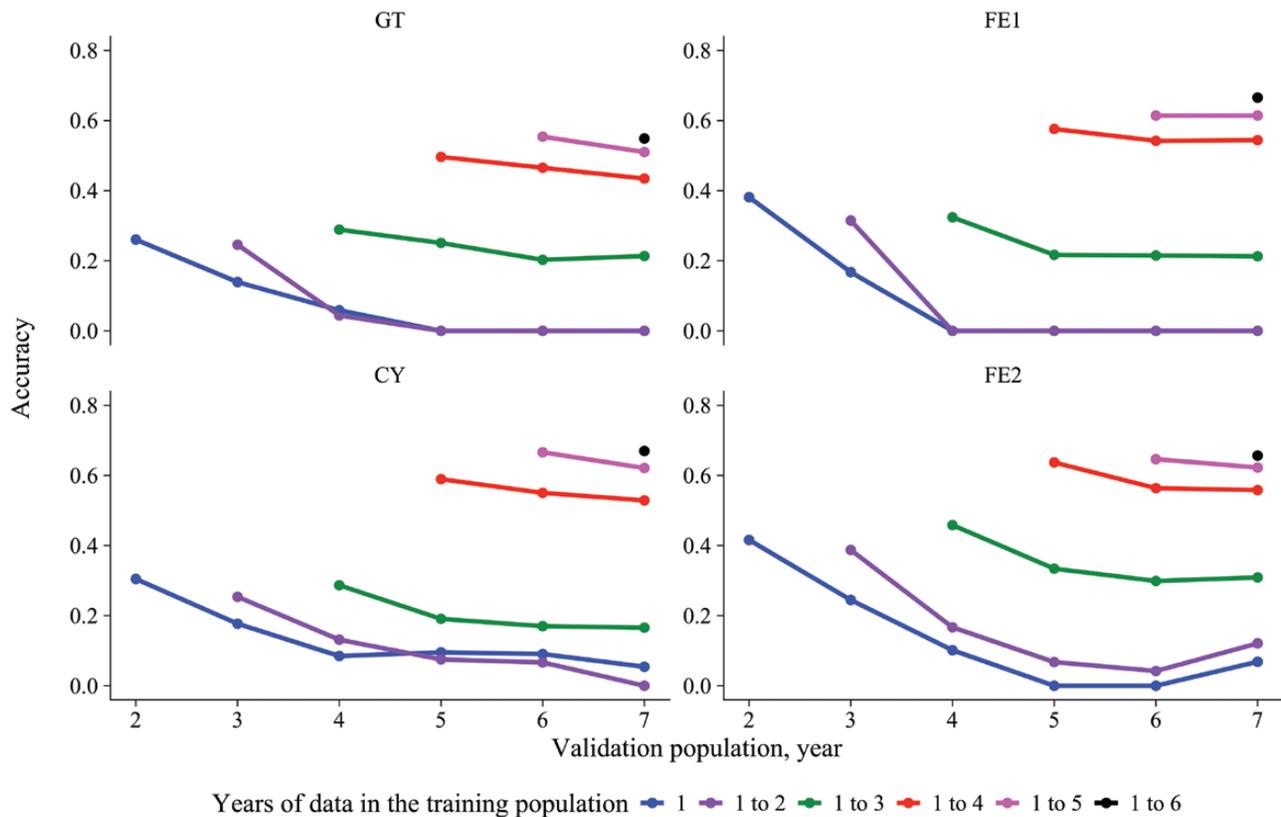
Figure 2. Trends for prediction accuracies of estimated breeding values of broilers hatched during successive years after the last year included in different training populations of accumulated pedigree, phenotypic, and genomic data for GT, FE1, CY, and FE2. Prediction accuracies were nearly stable with the accumulation of pedigree and phenotypes over time. The addition of genomic information generated an increase in prediction accuracy.

progeny, and 51% from grand progeny to great grand progeny. Conversely, the accuracy of estimated breeding values declined by 14% from progeny to grand progeny, 17% from progeny to great grand progeny, and only 3% from grand progeny to great grand progeny when training populations included genotyped birds (Figure 1). Habier et al. (2007) reported similar results when comparing several methods of estimation of breeding values. In their study, the persistence of accuracies of genomic-based methods was always greater than that of pedigree-based methods.

Our results agreed with the expectation of a 50% decay in pedigree relationships every generation. Genomic relationships are expected to decline at a slower rate (Wolc et al., 2011), which was confirmed by the higher persistence of genomic prediction accuracies. The decrease in accuracy across traits when training populations included genotyped birds was important from progeny to grand progeny; however, this decline was marginal from grand progeny to great grand progeny. Thus, the advantage of using genomic information increased as breeding values from more distant validation generations were predicted. Wolc et al. (2011) also reported higher persistence of accuracies of estimated breeding values from genomic evaluations than from genetic evaluations, as well as a larger decrease in accuracy in the first generation and smaller losses in subsequent generations.

The decay of accuracy over generations was similar when the training population included 1 or 2 years of genomic information (Figure 1). Thus, although the decrease in accuracy was smaller when genomic information was used, it is important to highlight the need for continuing phenotyping animals to minimize accuracy decay (Sonesson and Meuwissen, 2009).

The persistence of accuracy of genomic estimated breeding values had a similar trend when validation was done by year. When no genotyped birds were included in the training populations (first 3 years of data), the average decline in accuracy across traits and training populations was 46% from the first to the second year of validation, 79% from the first to the third year of validation, and 67% from the second to the third year of validation. Further, the persistence of the accuracy of genomic estimated breeding values was greater when training populations included genotyped birds. In this case, on average, the accuracy decreased by 8% from the first to the second year of validation and 10% from the first to the third year of validation (Figure 2).

Figure 3 shows trends for accuracies of estimated breeding values for GT, FE1, CY, and FE2 from broilers hatched the year after the last year included in various training populations. Although data accumulation over years resulted in an increase in accuracy, the addition of the last year of data (year six) to the training population did not increase the accuracy for GT, CY, and FE2.

Considering that the formula for the accuracy based on the LR method contains the additive genetic variance in the validation population, a possible explanation would be a decline in the heritability (genetic variance) of the trait that was not accounted for by the formula (Legarra and Reverter, 2018). Selection would reduce genetic variances and heritabilities as shown analytically by Bulmer (1971) and through simulations by Bijma (2012) and Gorjanc et al. (2015). Recent studies using real data reported a reduction in genetic variances and heritabilities as a result of selection (Bulmer effect) and drift (Hidalgo et al., 2020; Macedo et al., 2021; Tsuruta et al., 2021).
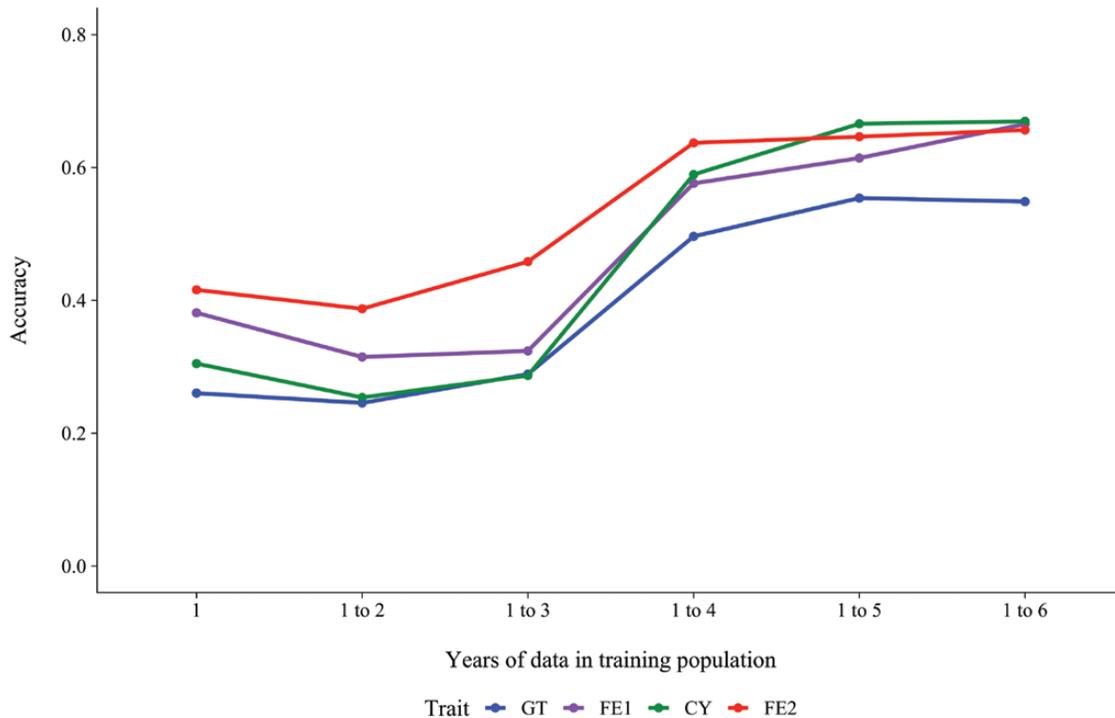
Figure 3. Trends for prediction accuracies of estimated breeding values of broilers hatched the year after the last year included in different training populations of accumulated pedigree, phenotypic and genomic data for GT, FE1, CY, and FE2. Overall, the accumulation of data increased prediction accuracy, although after accumulating data for 5 years, adding one more year of data did not increase accuracy in GT, CY, and FE2.

It would be useful to have theoretical formulas for accuracies of estimated breeding values of animals hatched in the generation following the last generation in the training population as well as in subsequent generations based on parameters such as population size, effective population size, number of animals with genotypes and phenotypes, breeding structure, and genetic parameters. In theory, one would expect to have similar theoretical accuracies for traits with similar parameters, an increase in prediction accuracy and persistence as data accumulates over time, and a consistent decline in prediction accuracy from progeny to grand progeny and succeeding generations without collection of additional phenotypes. However, the outcomes of this study defied such expectations because when the training population included 5 years of data, the accuracy of estimated breeding values was the same across traits for progeny (GT vs. FE2; Figure 1), and it was greater for great grand progeny and great grand progeny for traits with fewer data and lower heritability (FE1 and FE2) than for a trait with more data and higher heritability (GT; Figure 1). A possible explanation to the greater accuracy attained by traits with smaller heritabilities was reported by Weng et al. (2016), in their study, the low-heritable traits required less training generations of data than high-heritable traits to reach the maximum accuracy.

Further, within traits, accuracies of estimated breeding values were the same in grand progeny and great grand progeny for several training populations (Figure 1). Thus, the expected decline in prediction accuracy was not consistent in this broiler population. These outcomes can be explained by selection intensity and by changes in genetic parameters over time.

Lourenco et al. (2015) looked at accuracies of genomic predictions obtained with genotypes of males, females, and both

males and females in a broiler population. Prediction accuracies were strongly dependent on selection intensity within sexes, which means that accuracies of estimated breeding values for strongly selected traits in males were reduced when the training population included genotypes of both sexes. Hence, prediction accuracies provided insights into selection practices.

Hidalgo et al. (2020) found that genetic parameters based on pedigrees and phenotypes differed from parameters based on phenotypes, pedigrees, and genomic information. If heritabilities decline over time, accuracies computed by LR method using previous estimates of heritability will be underestimated. Also, if genetic correlations change, correlated responses will change accordingly. Therefore, a realistic theory for accuracy and persistence of genomic predictions would have to include the effects of selection and to account for changes in genetic parameters. An additional complication would be the need to account for epistatic changes if they occurred at a faster rate with genomic selection due to a greater genetic gain than without genomic selection. According to Forneris et al. (2017), epistatic interactions can change the additive genetic variance available for selection, affecting the selection response. Complex genetic architectures (involving epistasis) can reduce the value of old data, requiring the update of the evaluation model as genomic selection proceeds.

Effect of decreasing the size of training population

Figure 4 shows trends for accuracies of genomic estimated breeding values for GT, FE1, CY, and FE2 in the last three generations of validation when data from distant generations were removed. The accuracy of genomic predictions in the last three generations was the same as when the training population included 5 or 2 years of data. A marginal decrease in accuracy of genomic estimated breeding values was observed when training
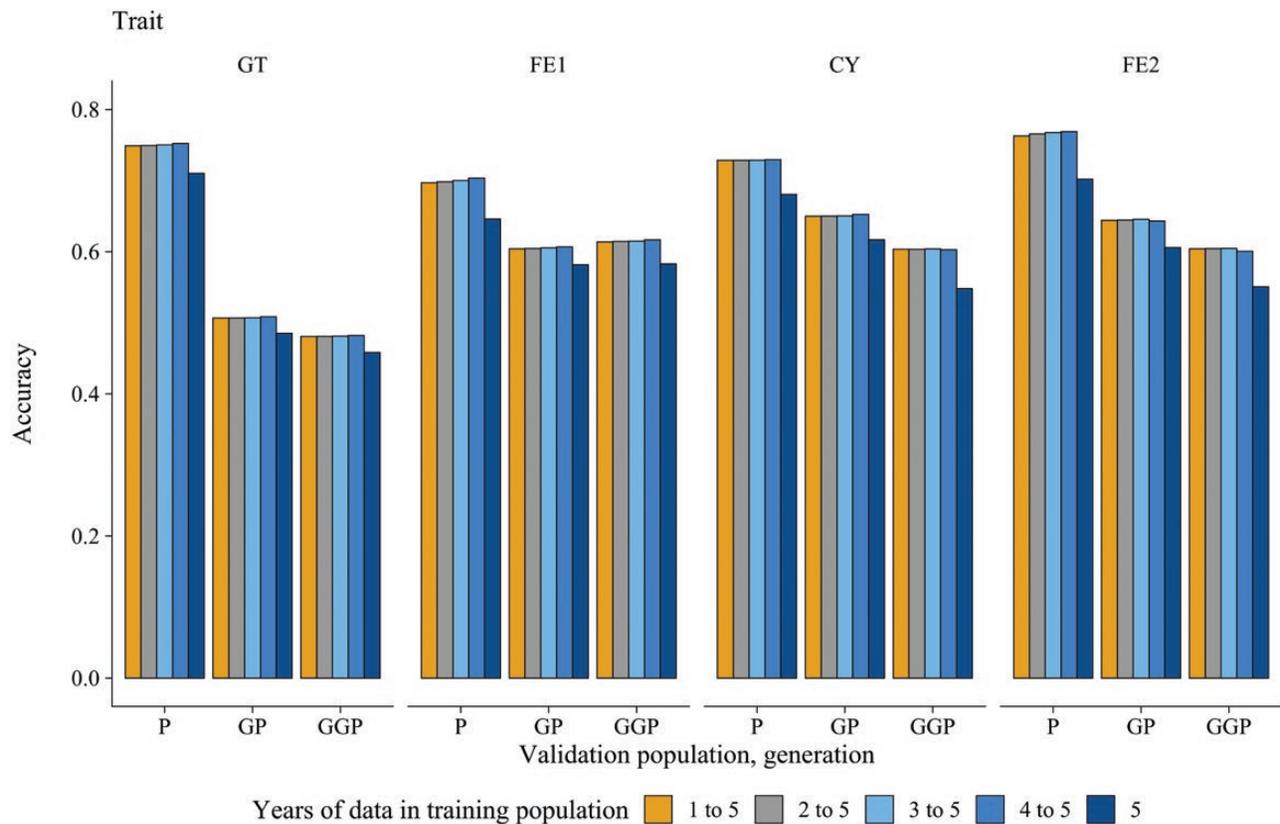
Figure 4. Prediction accuracies of estimated breeding values in P, GP, and GGP of broilers in different training populations of accumulated pedigree, phenotypic, and genomic data for GT, FE1, CY, and FE2. Validation populations included three generations after the fifth year of data. Prediction accuracies were the same with either 5 or 2 years of data in the training population. A marginal decay in prediction accuracy was observed when the training population included only the last year of data.

populations only included data from the nearest year to the three generations included in the validation populations (i.e., data from the fifth year). For instance, accuracies in the progeny decreased from 0.75 to 0.71 for GT, from 0.70 to 0.65 for FE1, from 0.73 to 0.68 for CY, and from 0.76 to 0.70 for FE2. Across traits, on average, the accuracy of genomic predictions declined 7% for progeny, 5% for grand progeny, and 7% for great grand progeny when the training population include 1 rather than 2 years of data. These results indicate that the 2 years of pedigree, phenotypic, and genomic data closest to the selection candidates are enough to maintain the accuracy of genomic estimated breeding values. However, additional research is needed to assess the decay in accuracy when more years of information are eliminated, including genotypes. The high persistence of accuracy of genomic predictions obtained in this research study is explained by the large amount of data available in recent relatives of the selection candidates, smaller populations may need more years/ generations of data depending on the size of the population.

Similar results were reported by Lourenco et al. (2014), where no decrease in accuracy of genomic estimated breeding values was observed for final score in US Holsteins after removing two or three generations (12–17 years) of phenotypes and pedigrees. This was also true for evaluations of reproductive traits in pigs after removing up to five generations (15 years) of phenotypes and pedigrees. The conclusions of Lourenco et al. (2014) agree with our findings that retaining two or three generations of phenotypes are enough to maintain the accuracy of genomic estimate breeding values. An additional advantage is a decrease in computing cost due to reductions in the size of datasets.

In a simulation study by Bastiaansen et al. (2012), the decay in accuracy of genomic predictions was steeper in the first generation of validation, with marginal reduction from the second to the tenth generation of validation. These results agreed with our results (Figures 1 and 2); however, the same authors indicated similar reduction in the accuracy of genomic predictions across generations using either a deep (five generations) or a shallow (one generation of data) training population of the same size. Those results were not in agreement with ours because the reduction in accuracy of genomic predictions, in our study, was only present with the shallower training population (most recent year of data; Figure 1). A key difference in our study was that the deeper training populations were of greater size, providing more information. In addition, possible explanations for this discrepancy can be the genetic architecture simulated in the study of Bastiaansen et al (2012), which included either from 3 to 4 or from 30 to 300 quantitative trait loci and only 10% of the quantitative trait loci explained 90% of the genetic variance; and the size of the training population, always composed of 500 individuals.

Conclusions

Training populations in this broiler population that included genomic information yielded increases in accuracy and persistence of genomic estimated breeding values about twice as large as training populations without genomic data. There was a general decline in accuracy when predicting the performance of distant relatives from training populations such as grand

progeny and great grand progeny, and this decline was larger for grand progeny than for great grand progeny. Accuracies were greater when the most recent data were incorporated into the analysis. The most recent 2 years of pedigree, phenotypic, and genomic data produced persistent accuracies of estimated breeding values for selection candidates in the three generations following the training population.

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Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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