L28 Genomic Prediction in Laying Hens

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Summary
In layers, selection in males has to be made at a time when only parent average or full-sib-based breeding values are available. Thus, distinguishing between full-sibs is not possible with classical breeding value approaches. The availability of genomic data and the methodological idea of genomic selection has revolutionized the field of animal breeding in the last years since prediction of individual breeding values is therefore possible also for young individuals without own or progeny observations. In this study, we addressed the question if and how genomic selection can be applied in breeding programs of laying hens and what are the opportunities of this methodology in layer breeding schemes illustrated with real data results. We used around 930 individuals that were genotyped with a high density SNP chip comprising around 580K SNPs and had accurate conventional breeding values for egg shell strength, laying rate, feed intake and egg weight. Using a five-fold cross-validation, predictive ability of a genomic BLUP model was between 0.61 and 0.73 depending on trait. In a realistic forward prediction scheme, predictive ability was lower (0.37 – 0.64) since in that case training set individuals have less accurate conventional breeding values. When applying directional selection within full-sib male groups based on genomic breeding values instead of selecting randomly, a clearly higher genetic gain could be achieved. In conclusion, genomic prediction provides a valuable tool to enhance selection accuracy in breeding programs of laying hens.

Keywords Laying Hens, Genomic Prediction, GBLUP

Introduction
The idea of genomic selection (Meuwissen et al., 2001) has revolutionized the field of animal breeding, at most dairy cattle breeding programs, in the last years. The idea behind genomic selection is that, if dense enough marker sets are available, each of the quantitative trait loci (QTL) influencing a complex trait will be in adequate linkage disequilibrium with at least one marker and the markers all together, thus, can reflect the whole genetic variance caused by all QTL. In contrast to classical marker assisted selection approaches, SNP effects are estimated simultaneously in one model as a basis for genomic selection and the final genomic breeding value of an individual is the sum of all marker effects without any significance testing step on marker effects beforehand. To estimate marker effects accurately a so called "training set" is needed which consists of individuals that are genotyped and have reliable observations (may be raw phenotypes, conventional estimated breeding values, daughter yield deviations, etc.). Once marker effects have been estimated, genomic breeding values can be calculated for any

further genotyped individual without any phenotypic observation. Accuracy of genomic prediction is in many cases considerably higher than the accuracy of classical parent average breeding values which makes accurate selection of candidates possible very early in life. In dairy cattle, large enough marker sets to establish genomic prediction as a part of practical breeding programs have been available since around six years. Training sets with thousands to ten thousands of bulls (e.g. EuroGenomics (David et al., 2010)) are available nowadays. In chicken, some first studies regarding genomic prediction have been published in the last three years in broilers (e.g. Chen et al., 2011; Wang et al., 2013; Morota et al., 2014) and in layers (e.g. Wolc et al., 2011a; Wolc et al., 2013a; Wolc et al., 2013b). Analyses in layers include a real long term selection experiment (e.g. Wolc et al., 2013c) where two sublines were created by selecting one subset of a line based on conventional breeding values and the other subset based on genomic breeding values over a period of three years. At the end of the experiment, the genomically selected subline had made higher genetic progress in most of the 16 observed traits. Results on usefulness and accuracy of genomic prediction presented so far in layers have been based on a single nucleotide polymorphism (SNP) panel comprising 42K SNPs (e.g. Wolc et al., 2013c). Individuals used in this study are all genotyped with a high density SNP array (Kranis et al., 2013) consisting of 580K SNPs. The aim of this study was to assess opportunities of including genomic prediction into breeding programs of laying hens by studying different traits and prediction scenarios.

Material and Methods

Genomic data and individual information

Within the "Synbreed – Synergistic Plant and Animal Breeding" project a wide range of individuals from different chicken breeds and lines were genotyped with the Affymetrix Axiom® Genome-Wide Chicken Genotyping Array that comprises around 580K SNPs. Among this panel of individuals, there were around 980 individuals (males and females) from a commercial brown layer line from five different generations which built the basis for the following analyses.

All individuals that had a genotyping rate of less than 97% or parent-offspring conflicts on many SNPs were discarded. Filter criteria per SNP included a call rate of less than 97%, minor allele frequency of less than 0.5%, unknown location and locations on sex chromosomes or unassigned linkage groups. Missing SNP data were imputed using the software BEAGLE (Browning & Browning, 2007). The final number of SNPs for the following analyses was 335'605 while the final number of individuals was 973 (see Table 1 for more details).

Table 1: Overview over individuals used for the genomic prediction analyses.

	Generation 1	Generation 2	Generation 3	Generation 4	Generation 5
Male	84	60	66	115	95
Female	0	0	0	517	0

Phenotypes and conventional breeding values

For a two-step genomic approach, pedigree based breeding values had to be estimated first. Routinely collected observations from a set of around 48'000 hens from 6 generations were available to estimate conventional breeding values (EBVs) for genotyped individuals. The following single trait animal model was used:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wa} + \mathbf{e} \quad [1]$$

where $\mathbf{y}$ is a vector of raw phenotypes for one of the traits described below, $\mathbf{X}$ is a design matrix for fixed effects and $\mathbf{b}$ is a vector of fixed effects, which included generation, farm, battery and tier level, $\mathbf{W}$ is a design matrix relating phenotypes to random effects, $\mathbf{a}$ is a vector of random effects, i.e. breeding values, and $\mathbf{e}$ is a vector of random residual error terms. Breeding values were assumed to be distributed $N(0, \mathbf{A}\sigma_a^2)$ and residual terms were assumed to be distributed $N(0, \mathbf{I}\sigma_e^2)$.

A broad range of phenotypes were available including laying performance parameters and egg quality parameters. In this paper, results will be presented for the traits egg shell strength which was measured as the force in Newton that was necessary to break the shell, laying rate expressed in percentage of days where a hen laid an egg within a defined time frame, egg weight in grams and daily feed intake in grams. As laying rate was not normally distributed, it was transformed with an arcsine transformation before using it in the model.

Accuracy of conventional breeding values derived with mixed model theory for genotyped males was 0.93 on average over individuals and traits, while it was 0.83 for the available genotyped hens. To study the influence of the quasi-phenotype (EBVs or deregressed proofs (DRPs)) used for genomic prediction in the second step of the two-step approach, EBVs were also deregressed following Garrick et al. (2009).

Genomic prediction methodology

For predicting genomic breeding values, a genomic relationship matrix ($\mathbf{G}$) was calculated first following VanRaden (2007) using the following formula:

$$\mathbf{G} = \frac{\mathbf{ZZ}'}{\sum_{i=1}^{\#SNPs} 2(p_i(1-p_i))}$$

where

$$\mathbf{Z} = \mathbf{M} - \mathbf{P}$$

and $\mathbf{M}$ is a marker matrix of dimensions individuals x SNPs with genotypes coded 0, 1 and 2 and $\mathbf{P}$ is a matrix of dimension individuals x SNPs whose entries are $2p_i$ in the i-th column and p_i is the allele frequency for the second allele for SNP_i.

The following genomic BLUP (GBLUP) model was then used for genomic prediction:

$$\mathbf{y}^* = \mathbf{K\beta} + \mathbf{Zg} + \boldsymbol{\epsilon}$$

where $\mathbf{y}^*$ is a vector of EBVs or DRPs of a specific trait, respectively, $\mathbf{K}$ is a design matrix for fixed effects and $\boldsymbol{\beta}$ is a vector of fixed effects, $\mathbf{Z}$ is a design matrix relating EBVs/DRPs to random effects, $\mathbf{g}$ is a vector of random genomic effects, i.e. genomic breeding values (GBVs), and $\boldsymbol{\epsilon}$ is a vector of random residual error terms. Genomic breeding values were assumed to be distributed $N(0, \mathbf{G}\sigma_g^2)$ and residual terms were assumed to be distributed $N(0, \mathbf{I}\sigma_\epsilon^2)$ when $\mathbf{y}^*$ consisted of EBVs and $N(0, \mathbf{R}\sigma_\epsilon^2)$ when $\mathbf{y}^*$ comprised DRPs. $\mathbf{R}$ is a diagonal matrix with weights reflecting the reliability structure of the DRPs so that

$$\mathbf{R}_{ii} = \frac{c + h^2 \frac{1 - r_{DRPi}^2}{r_{DRPi}^2}}{1 - h^2}$$

where h^2 is the heritability of the observed trait, r_{DRPi}^2 is the reliability of the DRP of individual i and c is a parameter reflecting the proportion of genetic variance that cannot be explained by the available marker set. Due to results from previous studies (data not shown) we set $c = 0.1$ for all traits. Variance components were estimated using ASReml 3.0 (Gilmour et al., 2009).

Validation schemes

To assess the usefulness of genomic prediction in this laying hen population, different approaches were used:

First, to obtain an overall assessment of the accuracy of prediction, we performed a random five-fold cross-validation i.e. data was split into five equally sized folds, genomic breeding values of individuals of each of the folds were predicted once (assuming EBVs/DRPs to be not available) using the other folds as the training set, accuracy of prediction was measured in all these runs and averaged over all folds at the end. The random splitting procedure was replicated 20 times. The predictive ability of the model was assessed by calculating the correlation between observed (EBVs/DRPs) and predicted (GBVs) values for the individuals in the validation set as well as by determining the average theoretical accuracy based on mixed model theory and the prediction error variance (PEV). The theoretical accuracy for a specific individual j is defined as

$$r_{MMEj} = \sqrt{1 - \frac{PEV_j}{\mathbf{G}_{jj}\sigma_g^2}}$$

Since specific combinations (e.g. individuals in the prediction set may be progenies of individuals in the training set) may lead to an overestimation of predictive ability when the aim is to predict individuals from the youngest generation, we also performed a forward prediction exercise. For this, we split the available data into individuals from generation 1 to 4 which built the training set and individuals from generation 5 which built the validation set. The predictive ability was measured as $r_{EBVs,GBVs}$.

In layer breeding, the bottleneck regarding accurate selection is the fact that full sib males cannot be distinguished at the time point of selection within conventional breeding programs since no progeny information is available for them at that time. Having genomic breeding values for these selection candidates at hand would overcome this problem. Thus, we also studied the possibilities of genomic prediction for directional selection within full-sib groups. As within the genotyped males, no larger full-sib groups were available, we used the ~ 500 genotyped hens from generation 4 to act as a proxy for the selection situation described above. Among these hens, 12 full sib groups with at least 10 members could be identified. These large full sib groups were then used as the validation set while all other available individuals from generation 1 to 4 built the training set. Afterwards the average EBV of two randomly selected individuals out of a full-sib group was compared to the average EBV of the two individuals with the highest predicted genomic breeding values.

As the number of SNPs genotyped is a matter of costs, as a last exercise the number of SNPs for calculating the **G** matrix was reduced to 200'000, 100'000, 50'000, 25'000, 10'000, 5'000 and 2'500 SNPs to study if lower density SNP chips could also be used and how accuracy of prediction changes. For this scenario, a five-fold cross-validation with all individuals from generation 1 to 4 was performed using **G** matrices built with one of the reduced SNP sets. Predictive ability was again measured as $r_{EBVs,GBVs}$.

Results

Five-fold cross-validation

Table 2 shows the results from the five-fold random cross-validation scheme. Given the relatively small training set (~ 778 individuals) results from the five-fold cross-validation looked quite promising with predictive abilities up to 0.73. Empirically assessed predictive abilities and theoretically derived accuracies were always higher when EBVs were used as quasi-phenotypes compared to the use of DRPs. Prediction worked best for egg shell strength while it worked worst for laying rate. The regression coefficient of observed values (EBVs or DRPs, respectively) on predicted values was close to one which is a signal that there is only little bias. Theoretically derived accuracies were always higher than empirical values and were always > 0.7 regardless if EBVs or DRPs were used as quasi-phenotypes.

Table 2: Empirical predictive ability (correlation between observations (OBS) and predicted GBVs), regression of observed on predicted values ($b_{OBS|GBVs}$) and theoretical accuracy of prediction (r_{MME}) assessed by a random five-fold cross-validation for different traits and different quasi-phenotypes used as observations. Means and standard deviations over the 20 replicates are shown.

Trait	Quasi-Phenotpye	$r_{OBS,GBVs}$	$b_{OBS\|GBVs}$	r_{MME}
Egg Shell Strength	EBV	0.734±0.007	0.994±0.061	0.789±0.002
	DRP	0.657±0.008	0.971±0.075	0.770±0.003
Feed Intake	EBV	0.670±0.009	0.972±0.096	0.792±0.002
	DRP	0.585±0.011	0.947±0.114	0.771±0.002
Laying Rate	EBV	0.611±0.009	0.954±0.110	0.757±0.003
	DRP	0.485±0.011	0.894±0.133	0.725±0.003
Egg Weight	EBV	0.711±0.009	0.978±0.089	0.811±0.002
	DRP	0.667±0.010	0.965±0.010	0.801±0.002

Forward prediction

In most of real applications of genomic prediction the aim is to predict more accurate breeding values of the youngest individuals than it is possible with conventional schemes. We thus also studied different forward prediction scenarios (Table 3). For the first scenario all individuals from generation 5 were predicted using all other individuals from generation 1 to 4 as training set which worked out quite well for all studied traits. However, in reality at the time of selection, no progeny information is available for the sires of the validation individuals and thus the conventional breeding values of the training set individuals are less accurate than assumed before. Therefore, for both forward prediction scenarios described in the following, training set individuals were assumed to have observations with information at the fictive time point of selection of the validation set while for the assessment of the prediction ability in the validation set all available information was used. As can be seen with $r_{EBVs,GBVs\_real}$, predictive ability of the genomic model is considerably lower for all traits. Since data from females will not be created regularly in a practical genomic selection scheme we were also interested in studying the prediction ability if only males from generation 1 to 4 were used as training set. Predictive abilities from this scenario ($r_{EBVs,GBVs\_real\_nodams}$) are similar to those one where female genotypes were included ($r_{EBVs,GBVs\_real}$) with a maximal decrease of 0.059 in the trait egg weight.

Table 3: Predictive ability of GBLUP in a forward prediction scheme. Individuals from generation 5 built the validation set, while all other individuals built the training set for calculating $r_{EBVs,GBVs}$ and $r_{EBVs,GBVs\_real}$ and all other male individuals built the training set for calculating $r_{EBVs,GBVs\_real\_nodams}$. For calculation of $r_{EBVs,GBVs\_real}$ and $r_{EBVs,GBVs\_real\_nodams}$ training set individuals were assumed to have no progeny information available.

Trait	$r_{EBVs,GBVs}$	$r_{EBVs,GBVs\_real}$	$r_{EBVs,GBVs\_real\_nodams}$
Egg Shell Strength	0.769	0.688	0.638
Feed Intake	0.650	0.390	0.374
Laying Rate	0.611	0.500	0.447
Egg weight	0.782	0.597	0.538

Selecting within full-sib groups is an important starting point for possible application of genomic prediction in layers. Figure 1 and Table 4 show results from studying the question on how better directional selection based on genomic breeding values works compared to random selection. From Figure 1 it can clearly be seen that directional selection works not perfect, but as the size of the training set is relatively small and predictive ability of the model is not 1 this is also not expected. Nevertheless, on average, genetic gain could be increased per generation (Table 4) when applying directional selection to select e.g. two individuals out of a full sib group instead of randomly choosing two individuals.

Table 4: Advantage of using directional selection within full sib groups (12 groups with ≥10 individuals) instead of random selection of two individuals out of each group expressed by the average difference between average EBV in the case of directional selection and random selection over all full sib groups studied.

Trait	Absolute difference	Difference expressed as % of σ_a
Egg Shell Strength	9.64	21%
Laying Rate	0.37	6%
Feed Intake	0.93	12%

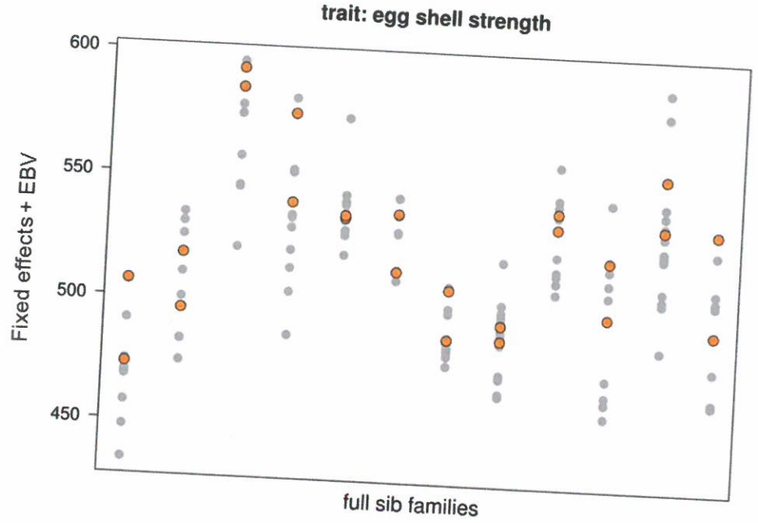

Figure 1: Selection within full sib families for the trait Egg Shell Strength. The two individuals with the highest predicted GBVs within family are marked with orange color.

Results from studying different SNP subsets show that predictive ability decreases considerably only when a really low number of SNPs is used, i.e. less than 10'000 (Figure 2). This trend could be observed for all traits studied and shows that available SNP number is high enough and even denser SNP chips will probably not lead to large increases in predictive ability as well as the slight reduction of the number of SNPs will not lead to a sharp decrease.

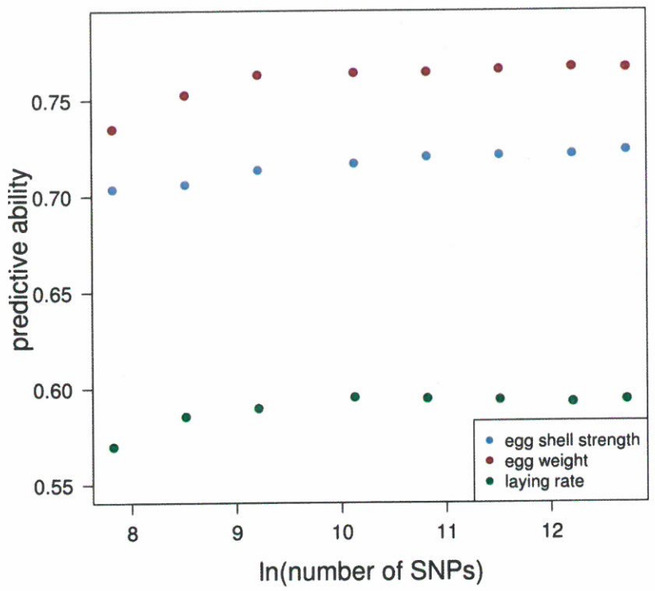

Figure 2: Predictive ability ($r_{EBVs,GBVs}$) when using different SNP subsets with different number of markers for three different traits.

Discussion

The results of this study show that genomic prediction provides an effective tool for enhancing selection response and especially for applying directional selection within full-sib families.

The size of the training set in our study is relatively small compared to other studies in other species e.g. dairy cattle (see e.g. Pryce and Daetwyler, 2012) or also in laying hens (e.g. Wolc et al., 2011b). Nevertheless, absolute values of predictive abilities are quite promising and relatively high which may in large parts be caused by the fact that individuals from a commercial breeding program in laying hens are very closely related. Close relationships favor high accuracy of genomic prediction (e.g. Clark et al., 2012). Apart from this, training set size will automatically grow when new generations have to be regularly genotyped in case genomic selection will be applied in praxis. Thus, predictive abilities reported here can be assumed to be rather the lower limit of what can be obtained in a practical application. Furthermore, predictive ability measured as the correlation between observations (EBVs or DRPs) and GBVs may not be equal to the correlation of true breeding values (TBVs) and GBVs which is mainly of interest in a breeding scheme. As TBVs are not available in real data, one can approximate $r_{GBVs,TBVs}$ by dividing $r_{EBVs,TBVs}$ by the average accuracy of EBVs in the validation set (Hayes et al., 2009) or the square root of the genomic heritability of the trait which would result in higher values than the values shown in the tables. However, this relation between $r_{GBVs,TBVs}$ and $r_{EBVs,GBVs}$ just holds if there is no covariance between the errors of EBVs and GBVs (see Amer and Banos, 2010). This topic has to be studied further in real data.

From a methodological point of view, other models could be applied on the available data. In this study, only BLUP based models were applied. In genomic prediction, different Bayesian methods are also popular (e.g. Bayes A or B; Meuwissen et al., 2001), but in most studies no considerable difference in accuracies have been observed up to now in real data of different species and in different traits. Wolc et al. (2011a) and Wolc et al. (2011b) did not find any significant difference between two Bayesian methods and genomic BLUP models regarding accuracy of prediction and the persistency of these accuracies over time in laying hens. A further methodological important development is a single step prediction model (e.g. Legarra et al., 2009) that can use genotypic and pedigree data simultaneously and genomic enhanced breeding values (GEBV) are calculated directly. The model for such a single step BLUP itself is the same as [1] with the difference that the inverse of the covariance matrix between individuals is modeled as

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}$$ (e.g. Christensen and Lund, 2010)

where $\mathbf{A}$ is a pedigree based relationship matrix, $\mathbf{A}_{22}$ is the part of the pedigree-based relationship matrix comprising genotyped individuals and $\mathbf{G}$ is a genomic relationship matrix for all genotyped individuals. In chickens, single step BLUP has already been applied successfully on broiler data sets (e.g. Chen et al., 2011).

In conclusion, genomic prediction provides a valuable tool to enhance selection accuracy in breeding programs of laying hens and can provide new opportunities even with relatively small training sets and relatively low number of SNPs. Genomic prediction will especially allow more precise selection within full-sib groups which will lead to a higher genetic gain due to higher selection accuracy and possible shortening of the generation interval.

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