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Genetic parameters of egg defects and egg quality in layer chickens

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Abstract

Genetic parameters were estimated for egg defects, egg production, and egg quality traits. Eggs from 11,738 purebred brown-egg laying hens were classified as salable or as having one of the following defects: bloody, broken, calcium deposit, dirty, double yolk, misshapen, pee-wee, shell-less, and soft shelled. Egg quality included albumen height, egg weight, yolk weight, and puncture score. Body weight, age at sexual maturity, and egg production were also recorded. Heritability estimates of liability to defects using a threshold animal model were less than 0.1 for bloody and dirty; between 0.1 and 0.2 for pee-wee, broken, misshapen, soft shelled, and shell-less; and above 0.2 for calcium deposit and double yolk. Quality and production traits were more heritable, with estimates ranging from 0.29 (puncture score) to 0.74 (egg weight). High-producing hens had a lower frequency of egg defects. High egg weight and BW were associated with an increased frequency of double yolks, and to a lesser extent, with more shell quality defects. Estimates of genetic correlations among defect traits that were related to shell quality were positive and moderate to strong (0.24–0.73), suggesting that these could be grouped into one category or selection could be based on the trait with the highest heritability or that is easiest to measure. Selection against defective eggs would be more efficient by including egg defect traits in the selection criterion, along with egg production rate of salable eggs and egg quality traits.

Keywords

egg defect, egg quality, heritability, layer

Disciplines

Agriculture | Animal Sciences | Genetics and Genomics | Poultry or Avian Science

Comments

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Genetic parameters of egg defects and egg quality in layer chickens

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ABSTRACT Genetic parameters were estimated for egg defects, egg production, and egg quality traits. Eggs from 11,738 purebred brown-egg laying hens were classified as salable or as having one of the following defects: bloody, broken, calcium deposit, dirty, double yolk, misshapen, pee-wee, shell-less, and soft shelled. Egg quality included albumen height, egg weight, yolk weight, and puncture score. Body weight, age at sexual maturity, and egg production were also recorded. Heritability estimates of liability to defects using a threshold animal model were less than 0.1 for bloody and dirty; between 0.1 and 0.2 for pee-wee, broken, misshapen, soft shelled, and shell-less; and above 0.2 for calcium deposit and double yolk. Quality and production traits were more heritable, with estimates ranging from 0.29 (puncture score) to 0.74 (egg weight). High-producing hens had a lower frequency of egg defects. High egg weight and BW were associated with an increased frequency of double yolks, and to a lesser extent, with more shell quality defects. Estimates of genetic correlations among defect traits that were related to shell quality were positive and moderate to strong (0.24–0.73), suggesting that these could be grouped into one category or selection could be based on the trait with the highest heritability or that is easiest to measure. Selection against defective eggs would be more efficient by including egg defect traits in the selection criterion, along with egg production rate of salable eggs and egg quality traits.

Key words: egg defect, egg quality, heritability, layer

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INTRODUCTION

The frequency of egg defects has been reduced substantially in commercial crosses of layer chickens in the last decades as a result of intensive selection in pure lines, well-established crossing schemes, lighting control programs, and improved nutrition programs. Indirect selection against egg defects has been applied by selecting for normal (salable) egg production (i.e., only accounting for defect-free eggs in the definition of egg production), which is the most important economic trait in layers. No direct selection has been applied for specific external egg defects in the populations studied herein, but selection pressure was applied on shell quality using puncture score and other quality traits (albumen height, yolk weight, egg weight, shell color). Nevertheless, the incidence of downgraded eggs still represents an important source of economic loss for the egg industry due to product loss and need for further processing. Also, defects are still present in the pure line stocks, and selection against incidence of defective eggs in pure lines is expected to have a desirable effect on the performance of commercial crossbred stocks. Some of the egg defects may also be the unintended results of selection. For example, presence of pee-wee eggs may originate from intensive selection on sexual maturity and egg production (Poggenpoel and Duckitt, 1988), leading to a reduction in age at first egg and production by immature individuals. Machal et al. (2004) suggested that the incidence of double-yolked eggs was higher in strains with high production.

To infer if any further reduction in egg defects can be achieved through selection, the level of genetic variation for different defect types and their genetic correlations with other traits of economic importance, such as egg production and quality, must be established. However, because a single egg can take only 2 states, normal or defective, classical mixed linear models, for which normality is assumed, may not be adequate to

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Table 1. Summary statistics for egg defects, egg production, and egg quality traits in the studied population

Trait	Minimum	Mean	Maximum	SD
Percentage of bloody egg (BE)	0	0.05	33.33	0.55
Percentage of broken egg (BK)	0	0.68	57.14	2.16
Percentage of calcium deposits (CD)	0	1.23	43.59	3.13
Percentage of dirty egg (DE)	0	0.32	16.67	0.91
Percentage of double yolk (DY)	0	0.63	33.33	1.57
Percentage of salable eggs (EN)	0	96.14	100.00	6.63
Percentage of misshapen egg (ME)	0	0.33	25.00	1.09
Percentage of pee-wee (PW)	0	0.09	57.14	0.81
Percentage of shell-less (SL)	0	0.24	92.86	1.54
Percentage of soft shell (SS)	0	0.28	44.12	1.28
Total number of defective eggs (tdef)	0	3.203	59.000	5.078
Percentage of total defective eggs (pdef)	0	3.86	100.00	6.63
Albumen height (AH, mm)	3.35	7.52	11.99	1.05
Shell color (CO, Lab)	37.81	75.34	104.6	8.29
Egg production rate (PD, %)	28.16	83.69	102.2	10.56
Egg weight (EW, g)	38.18	57.66	78.73	4.86
Puncture score (PS, N)	1,213	1,453	1,656	59.95
Age at first egg (SM, d)	130.00	154.96	187.00	9.14
Yolk weight (YW, g)	9.43	15.17	19.43	1.16
BW (kg)	1.02	1.88	2.93	0.26

describe such traits and threshold models are recommended (Matos et al., 1997; Johanson et al., 2001). In threshold models, the observed binary response is assumed to reflect an underlying, unobserved continuous variable called liability (Gianola and Foulley, 1983), so that an egg shows a specific defect if the value of liability exceeds some threshold. On the other hand, when averaged over several eggs, the proportion of defects becomes more continuous and, thus, a standard linear mixed model can be used for routine evaluation.

Another aspect of increasing importance to egg producers is egg quality, especially shell quality, which determines not only product safety but also preserves the quality of the internal components of an egg. Poor shell quality limits product acceptability and compromises the quantity of processed egg products available from a given number of eggs.

Against this background, the objective of this study was to estimate heritability of liability of hens toward different types of egg defects, using a threshold model, and to estimate genetic relationships between egg defects and production and quality traits in a purebred layer line.

MATERIALS AND METHODS

Data on farm-recorded egg defects for a fully pedigreed purebred brown-egg experimental layer line over 5 generations were available. This comprised 1,031,045 single egg records from 11,738 hens. Eggs collected over on average 120-d production period were classified either as salable or as having one of the following defects: bloody egg (**BE**), broken egg (**BK**), egg with calcium deposit (**CD**), dirty egg (**DE**), double-yolk egg (**DY**), misshaped egg (**ME**), pee-wee egg (**PW**), shell-less egg (**SL**), soft-shelled egg (**SS**). If an egg had more than one defect, only the most severe abnormality was recorded. The age when the last egg was recorded ranged from 140 to 275 d (on average 256 d). For the same birds, data on the most important production and egg quality traits were also available. These included early egg production rate (**PD**, overall percentage of egg production up to 38 wk of age) and age at first egg (**SM**, d). At the age of 26 to 28 wk, 3 to 5 eggs were subjected to a detailed quality analysis. Data recorded here included egg weight (**EW**, g); egg color (**CO**), using a Minolta-Canon Chroma meter device that measures lightness (L) and hue (as a function of a red-green (a) and a yellow-blue (b) scale; shell quality measured as puncture score (a noninvasive deformation test averaged over 2 points of the shell; **PS**, N); albumen height (**AH**, mm); and yolk weight (**YW**, g). Adult BW was also evaluated. Pedigree was traced 2 generations back from the first generation with records. Summary statistics for all traits analyzed are in Table 1.

Genetic analysis of egg defect traits was undertaken with the following threshold animal model:

$$\boldsymbol{\eta} = \mathbf{X_1}\boldsymbol{\beta_1} + \mathbf{X_2}\boldsymbol{\beta_2} + \mathbf{X_3}\boldsymbol{\beta_3} + \mathbf{Z_1}\mathbf{a} + \mathbf{Z_2}\mathbf{p} + \mathbf{e},$$

where $\boldsymbol{\eta}$ is an n*1 vector of liabilities to laying defective eggs [the observation y_i takes the value 1 if η_i is larger than the fixed threshold (τ), and 0 otherwise], $\boldsymbol{\beta_1}$ is a p_1*1 vector of fixed effects of hatch within generation, $\boldsymbol{\beta_2}$ is a p_2*1 vector of fixed within-hatch quadratic regressions on age at sexual maturity, $\boldsymbol{\beta_3}$ is a p_3*1 vector of fixed within-hatch quadratic regressions on days in lay, **a** is a q*1 vector of random additive genetic effects, **p** is an r*1 vector of permanent environmental effects, **e** is an n*1 vector of random errors, and $\mathbf{X_1}$, $\mathbf{X_2}$, $\mathbf{X_3}$, $\mathbf{Z_1}$, and $\mathbf{Z_2}$ are incidence matrices for fixed and random effects, respectively. It was assumed that the threshold $\tau = 0$, $\mathbf{a} \sim$N(0, $\mathbf{A}\sigma_a^2$), $\mathbf{p} \sim$N(0, $\mathbf{I}\sigma_p^2$), $\mathbf{e} \sim$logistic(0, $\mathbf{I}$*3.29), where **A** is the q*q relationship matrix, σ_a^2 is the additive genetic variance for liability, σ_p^2 is the direct permanent environmental variance for liability, and **I** are respective identity matrices. Heritability (h^2) was defined as

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_p^2 + 3.29},$$

where 3.29 is the implicit residual variance on the underlying scale in the logistic distribution. The penalized quasi-likelihood approximation of the threshold model, as implemented in Asreml3 (Gilmour et al., 2008), was used to estimate variance components.

Production and egg quality traits were analyzed by a standard single trait linear animal model, with the fixed effect of hatch within generation. A multitrait linear model for production and for quality and defect traits, derived as the proportion of defective eggs produced by each female during the 120-d production period, was used for comparison.

Genetic relationships between traits were approximated by pooling correlations of estimated breeding value (**EBV**) computed within generations. Only the EBV of sires with at least 20 daughters and dams with own performance and at least 10 daughters (all together 676 EBV across generations) were used. Correlations were pooled by weighting by the number of EBV used within each generation. Correlations of EBV are expected to be of the same sign as corresponding genetic correlations but smaller in magnitude because of shrinkage of EBV toward the mean (Calo et al., 1973).

The software SelAction (Rutten et al., 2002) was used to predict the accuracy and responses to selection of selection indexes that include egg defects in addition to current index traits of egg production rate of salable eggs and egg quality traits. The relative economic weights per genetic standard deviation unit were chosen as −3 for each category of defects, 15 for EW, 23 for PS and YW, 20 for AH, and 40 for PD. The estimates of genetic parameters obtained from the analysis were used. A population of 100 males and 1,000 females, each producing 50 male and 50 female offspring with proportion selected of 0.01 in males and 0.1 in females was used to evaluate predicted responses to selection. Sources of information included parental EBV and records on 50 sisters and 450 half-sisters for male candidates and own performance, parental EBV, and records on 49 sisters and 450 half-sisters for female candidates.

RESULTS AND DISCUSSION

Changes in the percentage of different categories of eggs over the laying period up to 120 d of lay are shown in Figure 1. The frequency of pee-wee, double-yolked, and shell-less eggs tended to decrease with age, whereas the frequency of calcium deposits and misshapen eggs increased up to peak production and then gradually declined, similar to other reports (Van Middelkoop, 1973; Van Middelkoop and Siegel, 1976). The proportion of salable eggs increased with age. No clear trends were observed for other categories of defects. The effect of age on egg quality is well recognized in the literature (Ledur et al., 2002).

Proportion of Total Defects

The heritability estimate for the proportion of total egg defects (all categories of egg defects combined into a single proportion of defective eggs per hen) was 0.29 based on the linear model and 0.40 based on the threshold model. The correlation of EBV from these 2 models for sires with at least 20 daughters was 0.86, which suggests fairly good agreement in the ranking of animals. From the multitrait linear model analysis, the proportion of total egg defects was estimated to have a negative genetic correlation with egg number (−0.55) and puncture score (−0.18) and a positive correlation with egg weight (0.23), albumen height (0.17), and BW (0.49). The sign and magnitude of the estimates of phenotypic correlations were similar to those of the corresponding genetic correlations (Table 2).

External Quality Traits

Shell quality relates to the ability of eggshells to withstand external forces without cracking or breaking (De Ketelaere et al., 2002). Therefore, the proportion of cracked eggs is a function of both shell quality and the environment to which it was exposed. In this study, most defects that were recorded at the farm were related to shell quality. Of these, presence of calcium deposits had the highest estimate of heritability ($h^2 = 0.22$), whereas that of other types of shell quality defects ranged from 0.13 to 0.19 (Table 3). Heritability estimates for the frequency of cracked eggs from other studies ranged from 0 to 0.79, depending on the population, age of birds, and the model used (Brah et al., 1992; Wolc et al., 2005). Estimates of genetic correlations among defect traits that were related to shell quality (BK, CD, SL, SS) were positive and moderate to strong (Table 4), suggesting that these could be grouped into one category to improve distributional properties. Alternatively, selection can be based on the shell quality defect trait that is estimated to have the

Table 2. Estimates and SE of phenotypic (r_p) and genetic (r_g) correlations of the proportion of total egg defects with egg production and quality traits under a multitrait linear model[1]

Correlation	PD	SM	EW	PS	AH	CO	YW	BW
r_p	−0.68 ± 0.01	−0.01 ± 0.01	0.15 ± 0.01	−0.13 ± 0.01	0.08 ± 0.01	−0.08 ± 0.01	−0.02 ± 0.01	0.34 ± 0.02
r_g	−0.55 ± 0.04	0.02 ± 0.05	0.23 ± 0.05	−0.18 ± 0.06	0.17 ± 0.05	0.00 ± 0.05	0.00 ± 0.06	0.40 ± 0.06

[1] See Table 1 for trait name abbreviations.

highest heritability or that is easiest to measure, as correlated responses would be expected in the same direction for the other defect traits (Table 4). As BK is a trait routinely measured by the industry in egg-grading plants and is the main reason for under-grade eggs; it might be the best to use, in view of its importance and despite its quite low heritability ($h^2 = 0.13$). Broken eggs had a negative genetic correlation with puncture score (−0.26), which confirms the suitability of this trait as an indicator of shell quality. It was positively correlated with BW and shell color. Although no estimates of genetic correlations were available, Abdallah et al. (1993) reported phenotypic correlations of the percentage of cracked eggs with percentage of shell, shell weight per unit surface area, specific gravity, and shell weight are high and negative but positive with egg weight. Unpublished results obtained from a different population than that studied herein also showed a negative genetic correlation of cracked eggs, as measured using an acoustic egg test device, with egg weight

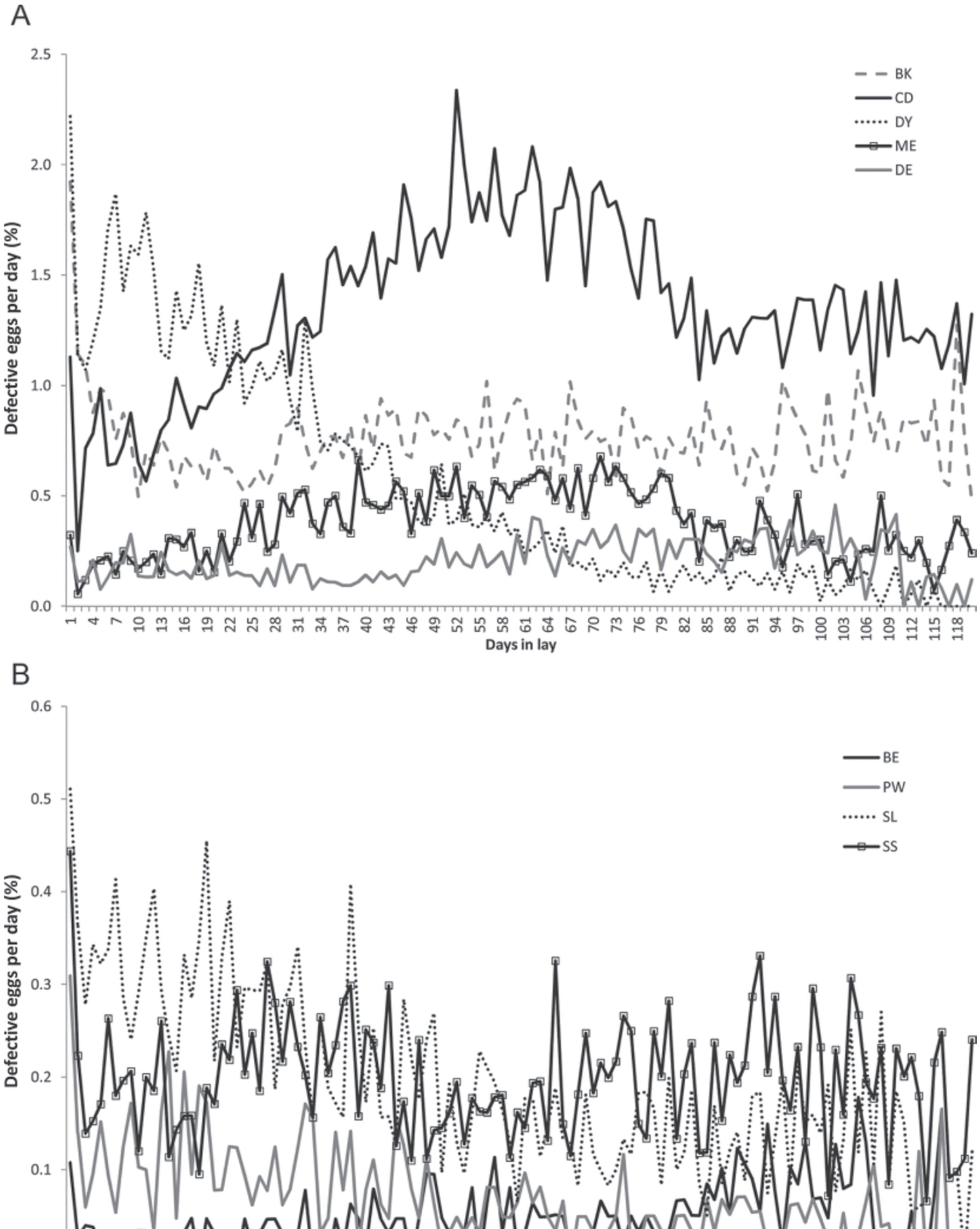

Figure 1. A) Proportion of defective eggs by day in lay (BK = broken egg, CD = calcium deposits, DY = double-yolk, ME = misshapen egg, DE = dirty egg). B) Proportion of defective eggs by day in lay (BE = bloody egg, PW = pee-wee, SL = shell less, SS = soft shell).

Table 3. Estimates of genetic parameters for liability to laying defective eggs, egg production, and egg quality traits[1]

Item[2]	BE	BK	CD	DE	DY	EN	ME	PW	SL	SS	AH	CO	PD	EW	PS	SM	YW	BW
V_g	0.26	0.65	1.21	0.28	1.29	0.73	0.76	0.56	0.95	0.85	0.57	47.15	45.99	18.1	475	24.36	0.61	0.03
V_{pe}	2.33	0.88	1.05	0.87	0.27	0.78	0.95	1.25	0.85	0.86								
V_e	3.29	3.29	3.29	3.29	3.29	3.29	3.29	3.29	3.29	3.29	0.46	18.56	70.78	6.36	1157	19.77	0.68	0.03
r	0.44	0.32	0.41	0.26	0.32	0.31	0.34	0.35	0.35	0.34								
c^2	0.40	0.18	0.19	0.20	0.06	0.16	0.19	0.25	0.17	0.17								
h^2	0.04	0.13	0.22	0.06	0.27	0.15	0.15	0.11	0.19	0.17	0.55	0.72	0.39	0.74	0.29	0.55	0.47	0.48
SE (h^2)	0.03	0.02	0.02	0.01	0.02	0.01	0.02	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.04

[1] See Table 1 for trait name abbreviations.

[2] V_g = additive genetic variance, V_{pe} = permanent environmental variance, V_e = residual variance, r = repeatability, h^2 = heritability, SE (h^2) = standard error of heritability.

(−0.25), puncture score (−0.62), and dynamic stiffness (−0.64; J. Arango, Hy-Line International, IA, personal communication). A threshold-linear model was used for analysis, with cracked as a categorical trait and the others as continuous linear traits.

In the current study, the estimate of heritability of misshaped eggs was 0.15, and the trait was positively genetically correlated with shell quality defects and negatively correlated with egg production (Tables 3 and 4). Previous studies (Dunn et al., 2005; Lwelamira et al., 2009) reported a moderate heritability of about 0.3 for an egg shape index, whereas others (Lubritz and Smith, 1996) reported even higher estimates ($h^2 = 0.55$) for egg shape score.

Internal Quality Traits

Our estimate of heritability for albumen height of 0.55 agrees with a previous estimate of 0.51 by Zhang et al. (2005). We also found positive genetic correlations of albumen height with egg weight (0.32) and sexual maturity (0.12). Yolk weight was highly heritable (estimate of 0.47), in agreement with results of Hartmann et al. (2003) in layers (0.43) and of Schuler et al. (1996) in quail (0.46).

Of the egg defect traits, the incidence of double-yolk eggs had the highest heritability estimate ($h^2 = 0.27$; Table 3). Studies from over half a century ago had indicated the presence of a strong genetic component for this trait in a layer line selected for egg number (Lowry, 1967). This was subsequently confirmed in a selection experiment for high numbers of multiple-yolked eggs (Abplanalp et al., 1987), where the number of double-yolked eggs until 40 wk of age increased from 2 to 30 over 11 generations of selection. The presence of double yolks was more frequent in hens that produced more eggs with shell defects. In our study (Table 4), double yolks were positively genetically correlated with egg weight (0.39), BW (0.34), albumen height (0.16), and yolk weight (0.19) and negatively correlated with egg number (−0.59) and percentage production (−0.26), indicating that, besides direct selection against this trait, intense selection for production may help keep incidence of double yolks under control. A similar estimate of a positive correlation between double yolks and BW was reported by Abplanalp et al. (1987). Weak positive or negligible correlation between egg production and frequency of double-yolk eggs was estimated by Lowry (1967) on the genetic and Machal et al. (2004) on the phenotypic level.

Table 4. Correlations between estimated breeding values for liability to laying defective eggs, egg production, and egg quality traits[1]

	BK	CD	DE	DY	EN	ME	PW	SL	SS	AH	CO	PD	EW	PS	SM	YW	BW
BE	0.22	0.37	0.04	0.09	−0.31	0.32	−0.22	0.10	0.28	0.08	−0.05	−0.25	0.17	0.12	0.00	−0.02	0.07
BK		0.53	0.20	0.38	−0.76	0.48	−0.12	0.48	0.73	0.17	0.12	−0.35	0.19	−0.26	−0.07	0.07	0.26
CD			0.08	0.13	−0.77	0.75	−0.05	0.24	0.62	0.11	−0.02	−0.48	0.13	0.00	−0.09	0.01	0.05
DE				0.19	−0.30	−0.01	0.04	0.10	0.22	0.04	0.02	−0.07	0.20	−0.03	0.05	0.11	0.24
DY					−0.59	0.18	0.03	0.43	0.37	0.16	0.00	−0.26	0.39	−0.04	−0.01	0.19	0.34
EN						−0.68	−0.05	−0.55	−0.78	−0.14	0.02	0.54	−0.27	0.09	0.06	−0.07	−0.25
ME							0.02	0.35	0.55	0.00	−0.02	−0.41	0.09	0.00	−0.09	−0.05	0.04
PW								0.09	−0.02	−0.04	−0.10	0.08	−0.32	−0.13	−0.12	−0.32	−0.13
SL									0.55	0.09	0.02	−0.29	0.17	−0.02	0.05	−0.07	0.18
SS										0.11	−0.03	−0.43	0.17	−0.10	−0.08	0.03	0.18
AH											0.04	−0.08	0.32	−0.18	0.12	−0.05	0.03
CO												−0.09	−0.01	−0.09	0.11	−0.02	0.09
PD													−0.33	−0.28	−0.09	−0.05	−0.14
EW														0.26	0.24	0.48	0.28
PS															0.03	0.13	−0.07
SM																0.02	0.02
YW																	0.37

[1] See Table 1 for trait name abbreviations. Weighted means of within-generation correlations of estimated breeding values of sires with at least 20 daughters and for dams with own performance and at least 10 daughters (altogether 676 EBV) were used to approximate genetic relationships between the traits.

Table 5. Expected response to selection using a selection index with or without egg defects in addition to egg production rate of salable eggs and egg quality traits[1]

Item	With defects	Without defects	% improvement
BE (%)	−0.087	−0.057	52.63
BK (%)	−0.289	−0.203	42.36
CD (%)	−0.512	−0.392	30.61
DE (%)	−0.008	0.027	129.63
DY (%)	−0.093	0.010	1,030.00
ME (%)	−0.428	−0.326	31.29
PW (%)	−0.333	−0.321	3.74
SL (%)	−0.333	−0.215	54.88
SS (%)	−0.447	−0.313	42.81
EW (g)	1.997	2.035	−1.87
PS (Newton)	4.993	4.967	0.52
AH (mm)	0.236	0.239	−1.26
CO (Lab)	1.158	1.180	−1.86
YW (g)	0.470	0.479	−1.88
PD (%)	3.952	4.044	−2.27
Traits not under direct selection			
EN (pcs)	0.435	0.315	38.10
SM (d)	0.232	0.236	−1.69
BW (kg)	0.017	0.017	0.00
Total economic units	68.031	66.613	2.13
Accuracy males	0.538	0.524	2.67
Accuracy females	0.661	0.642	2.96
% inbreeding	1.705	1.755	−2.85

[1] See Table 1 for trait name abbreviations.

Egg Weight

The heritability estimate was 0.11 for the presence of pee-wee eggs. This defect was most frequent at the beginning of lay and, as expected, was negatively correlated with age at first egg, egg weight, yolk weight, and puncture score. Egg weight itself was highly heritable ($h^2 = 0.74$), which confirms previous studies, for which estimates of heritability for egg weight ranged from 0.48 to 0.64 (Hartmann et al., 2003; Zhang et al., 2005; Kamali et al., 2007; Wolc et al., 2010). Egg weight was positively correlated with BW and with the egg components yolk weight and albumen height. The estimates of genetic correlations of double-yolk eggs, shell-less eggs, and dirty eggs with egg weight were positive, corresponding to a positive phenotypic association shown by Machal et al. (2004). It is therefore expected that controlling egg size (i.e., avoiding extreme large eggs), which is important for most markets, especially during the late laying phase, may have the desirable effect of keeping the level of egg defects down.

Opportunities for Selection

Two criteria for selection were compared: selection on egg production rate for salable eggs and egg quality traits versus selection on an index that also included egg defects. The predicted accuracies of the index without defects were 0.524 for males and 0.642 for females, which increased to 0.538 and 0.661 after including information on defects. The predicted response in economic units was driven by the traditional selection traits, which had higher economic weights per genetic standard deviation than the individual egg defects. However, because 9 traits related to egg defects were included, the cumulative selection pressure against defects was comparable to that on other traits. Expected responses differed considerably between defects for the economic and genetic parameters that were used. Further work is needed to define more precisely the economic values for individual traits, but that was beyond the scope of this study. The index with selection on egg production rate for salable eggs and egg quality led to an expected reduction in incidence for most of the egg defects. Although inclusion of egg defects in the index led to greater reduction, this was at some expense of gain in other traits (Table 5). By including information on egg defects, an additional response of 2.1% in the assumed breeding goal is expected under the population structure, selection intensities, economic weights, and genetic parameters used in this study.

Conclusions

Substantial genetic variation was found for the presence of shell defects and production of double-yolk eggs. Puncture score was confirmed as a good indicator of shell quality. High-producing hens had a lower genetic liability to lay defective eggs. High egg weight and BW were genetically associated with increased frequency of double yolks, and to a lesser extent, with shell quality defects. Each type of defect, except bloody eggs, which was lowly heritable, was genetically correlated ($|r_g| > 0.24$) with at least one production or quality trait. Selection against defective eggs was predicted to be more effective if egg defect traits were included in the selection criterion, in addition to egg production rate of salable eggs and egg quality traits.

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