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Genetic parameters for egg quality traits in Pekin ducks

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ABSTRACT Pekin duck (*Anas platyrhynchos domesticus*) is the most widely consumed duck protein with nearly 35 million animals produced annually in the United States and exported worldwide. Pekin ducks are primarily utilized in meat production, so very little information is available about their heritability estimates and genetic correlations for traits related to egg quality. Genetically improving duck populations together with the implementation of more efficient nutritional and management strategies is paramount for the long-term sustainability of the US duck industry. There is a potential opportunity to increase meat duck productivity by improving hatching egg quality. The main objectives of this study were to estimate heritability and genetic correlations for various egg quality traits in a commercial population of Pekin ducks. Egg quality traits for 612 Pekin duck females were measured through 3 time points over 2 generations (**GEN**) [30, 32, and 35 wk of age (**WOA**)]. GEN 2 had an additional sampling occurring at 40 WOA. Genetic correlations and heritability estimates were calculated for all the traits using the BLUPF90 software, the Restricted Maximum Likelihood (**REML**) method, and a pedigree containing 9,418 individuals. All egg quality traits evaluated are moderately to highly heritable ranging from 0.20 for Haugh Unit (**HU**) and Vitelline Membrane Strength (**VMS**) to 0.71 for shell ratio (**SR**). Heritability estimates were calculated for each age of collection and in general heritability increased up to 35 WOA. Genetic correlations between egg quality traits showed a wide range of positive and negative relationships with correlation strengths ranging of −0.80 [yolk ratio (**YR**) and albumin ratio (**AR**)] to 0.99 [egg volume (**EV**) and egg weight (**EW**)]. The results of this study highlight the potential to improve hatching egg quality within Pekin ducks using a multi-trait selection scheme through direct genetic selection.

Key words: fertile egg, variance component, egg composition, pekin duck, selection

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INTRODUCTION

Egg quality traits are often associated with the table egg industry which provides eggs for human consumption. In China and Southeast Asia, duck eggs account for 10-30% of total egg consumption (Huang and Lin, 2011), and egg quality has been investigated in numerous species such as chickens, ducks, turkeys, guinea fowl, quail, pheasants and geese (Adamski, 2008; Zeng et al., 2018). Selection for specific egg quality parameters in meat type poultry may seem counter intuitive; however, egg quality has been found to influence hatchability and post hatch productivity (Cheng et al., 1995; Milisits et al., 2013; Alasahan and Copur, 2016; Abd El-Hack et al., 2019; Biesiada-Drzazga, 2020; Boğa Kuru et al., 2023). Little research has investigated the possibility of selecting for egg quality traits in meat type poultry such as broiler breeder chickens and Pekin breeding ducks. However, in broiler breeder chickens, yolk to albumen ratio in hatching eggs has been shown to have an impact on hatchability, liveweight post hatch, slaughter weight and body composition of broiler chickens (Milisits et al., 2010, 2013). Within a line of White Leghorns research found that yolk proportion can be increased in eggs after 1 generation of direct selection (Hartmann et al., 2000; Icken et al., 2014). Pekin ducks have an incubation period of 28 d and are ready for market as soon as 35 d post hatch. As a consequence, from the start of incubation, ducks grown for meat spend roughly 44% of their life in the egg. This highlights the potential for selection for an optimal environment to improve Pekin meat duck productivity.

Egg quality traits can be classified into 2 different categories, external traits or internal traits. External egg quality traits refer to any trait collected on the whole egg or shell, such as, egg weight, egg shape, eggshell thickness, eggshell strength, eggshell weight, and

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eggshell ratio. Internal egg quality traits are collected on internal egg components, such as albumen to total egg weight ratio, yolk weight, yolk to total egg weight ratio, yolk color, yolk index, albumen weight, Haugh Unit, and vitelline membrane strength. There are various reports of genetic parameter estimates for egg quality traits in laying hens, laying ducks, and quail (Cheng et al., 1995; Zhang et al., 2005; Begli et al., 2010; Narinc et al., 2015; Lin et al., 2016; Zeng et al., 2018; Wan et al., 2019). However, genetic parameters of egg quality traits in meat production breeds are not as well studied. Heritability estimates of 0.53, 0.38, and 0.38 have been reported in parent broiler chickens for specific gravity, egg weight loss, and Haugh unit, respectively (Wolc et al., 2010). These estimates in broiler chickens provide evidence that egg related traits are moderately heritable in a line of birds that has been under intense selection for meat production traits. However, the degree of these traits are heritable in Pekin duck populations is still in question. Recent interest in selecting for egg quality in meat-based poultry has highlighted the limited research on the relationship between hatching egg quality and offspring performance. Therefore, the primary objective of this study was to estimate variance components and genetic parameters for various egg quality traits in White Pekin ducks.

MATERIALS AND METHODS

Population and Data Collection

Procedures were approved by the Purdue University Institutional Animal Care and Use Committee (PACUC # 22110002205). This study took place over a year and followed a nucleus (breeding) line of White Pekin ducks for 2 generations. Generation (**GEN**) 1 was composed of 311 females and GEN 2 had 301 females both consisting of individuals selected from 3 separate hatches. Egg quality traits were measured at 30, 32, and 35 wk of age (**WOA**). GEN 2 had 1 additional egg quality collection occurring just before peak lay at 40 WOA. Collection of egg quality traits at WOA 30, 32, 35, and 40 correlate to 2, 4, 7, and 12 wk of egg production. A pedigree containing 9,418 individuals was used to create the relationship matrix used to calculate variance components and genetic parameters for the egg quality traits collected on 612 individuals in this study. The ducks in this study were raised and bred in modern commercial solid sidewall poultry housing with artificial lighting and fed a propriety multi-phase diet consisting of 3 phases which can be found in Table 1.

Table 1. Average Pekin duck multiphase diet composition.

Period (WOA)[1]	Calories (Kcal/kg)	Protein	Ca
0−5	3100	20%	1.2%
5−20	2600	16%	1.4%
20+	2500	18.5%	3.75%

[1]Period refers to the time frame in which the diet was fed. Defined by week of age (WOA).

Trait Measurements

Egg quality trait collections were measured according to Jones et al. (2002). Briefly, egg length, width, and volume (**EV**) were obtained using a volscan (VSP300 model; Texture Technologies) on the day of egg collection. Egg shape (**ESH**) was calculated by dividing the total egg length by egg width. The closer the ESH value is to 1 the closer the egg is in circular shape, while the lower the ESH value the egg is more oblong in shape (Jones et al., 2018). For all the remaining egg quality traits the eggs were kept in a cooler at 4°C overnight to allow egg temperatures to normalize. After equilibrating, the eggs were then weighed to collect the total egg weight (**EW**). A texture analyzer (TA-XTplus; Texture Technologies, Hamilton, MA) was used to measure eggshell strength (**ESS**) and vitelline membrane strength (**VMS**) (Jones et al., 2010). After the shell strength was collected, the egg was broken onto a breakout table and the albumen height was recorded. Albumen height was measured with a TSS QCD system (Technical Services and Supplies, Dunnington, York, UK). EW and albumen height were used to calculate Haugh unit (Eisen et al., 1962). Shells were rinsed with tap water to remove excess albumen, being cautious not to remove the shell membrane. Shells were left to dry at room temperature in open air for a minimum of 24 h before shell thickness (**EST**) and shell weight (**SW**) were measured. A micrometer (Model 25-5; Ames, Inc., Melrose, MA) was used to measure the shell thickness at 3 points along the shell's equator, and averaged to obtain EST. The albumen and yolk were separated by hand. The yolk was rolled on a paper towel to remove excess albumen prior to being weighed. Albumen weight was calculated by subtracting SW and yolk weight (**YW**) from the EW. Egg component ratios were calculated by dividing the weight of the egg component by EW resulting in albumen ratio (**AR**), shell ratio (**SR**), and yolk ratio (**YR**).

Statistical Analyses

All regressions were performed in R studio's lmtest (Zeileis and Horthorn, 2002). An ANOVA analysis was performed to test the influence of the main effects of GEN and WOA on all egg quality traits. A second ANOVA was conducted on every trait at each WOA subset which included GEN. In both analyses, pen was considered as a random effect and corelates to breeding pen. Significance was set at P-value < 0.05.

Genetic Analyses

Single-trait animal model analyses were used to estimate variance components and calculate heritability estimates for each age of collection considered as a different trait. Repeatability estimates were also obtained for traits with repeated records. Bivariate Multi-trait analyses were used to calculate (co)variance components and genetic and genetic correlations among all trait pairs (Falconer and Mackey, 1996). Genetic analyses were performed using the BLUPF90+ family of software (Aguilar et al., 2018) and the Restricted Maximum Likelihood (**REML**) method. The significant (P < 0.05) fixed effects were included based on linear model tests. Fixed effects used for each trait of the repeatability models, Single-trait models, and correlations were defined by significance found during the ANOVA tests. Heritability for single-trait repeated records and for nonrepeated records can be found in Equation 1 and 3 respectively. The models used for the analyses are presented in Equations 2 and 4 for single traits with repeated records and nonrepeated records, respectively. A pedigree of 9,418 individuals was used to create the relationship matrices. The phenotypic value of an individual is represented by y in Equations 2, 4, 5, and 6. X is a design matrix of fixed effects with b as a vector of these fixed effects; Z is a design matrix of random effects with a as the vector of these random effects in Equations 2, 4, 5, and 6. Repeated record models in Equations 2 and 5 W represents the design matrix of permanent environmental effects with pe as the corresponding vector. e is the vector of the residuals. For the relationship matrix, p_i represents the frequency of the second allele at locus i based on a biallelic model for the entire genotype.

Equation 1: Heritability for the repeated record analyses

$$h^2 = \frac{\sigma_a}{\sigma_a + \sigma_{pe} + \sigma_e} \quad (1)$$

Equation 2: Matrix model for single trait repeated record

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wpe} + \mathrm{e} \begin{bmatrix} a \\ pe \\ \mathrm{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}\sigma_{\mathrm{a}}^2 & 0 & 0 \\ 0 & \mathbf{I}\sigma_{\mathrm{pe}}^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_{\mathrm{e}}^2 \end{bmatrix} \quad (2)$$

Equation 3: Heritability for the single nonrepeated record traits:

$$h^2 = \frac{\sigma_a}{\sigma_a + \sigma_e} \quad (3)$$

Equation 4: Model for single trait nonrepeated records:

$$\mathrm{y} = \mathbf{X}\mathrm{b} + \mathbf{Z}\mathrm{a} + \mathrm{e} \begin{bmatrix} a \\ \mathrm{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}\sigma_{\mathrm{a}}^2 & 0 \\ 0 & \mathbf{I}\sigma_{\mathrm{e}}^2 \end{bmatrix} \quad (4)$$

Equation 5: Bivariate model for traits with repeated records:

$$\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{x}_1 & 0 \\ 0 & \mathrm{x}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{z}_1 & 0 \\ 0 & \mathrm{z}_2 \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{w}_1 & 0 \\ 0 & \mathrm{w}_2 \end{bmatrix} \begin{bmatrix} pe_1 \\ pe_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix} \quad (5)$$

Equation 6: Bivariate model for traits with single records:

$$\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{x}_1 & 0 \\ 0 & \mathrm{x}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{z}_1 & 0 \\ 0 & \mathrm{z}_2 \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix} \quad (6)$$

RESULTS AND DISCUSSION

Summary Statistics

The mean, SEM, minimum (**min**), maximum (**max**) and coefficient of variation (**CV%**) for each egg quality trait are found in Tables 2 and 3 for GEN 1 and GEN 2, respectively. Mean and SEM for AR ranged from 0.59 ± 0.00 to 0.61 ± 0.00, YR ranged from 0.29 ± 0.00 to 0.31 ± 0.00, and SR ranged from 0.09 ± 0.00 to 0.10 ± 0.00 for both GEN. All CV% fell below 12% except for ESS and VMS. Why the CV% was high for strength of the shell and vitelline membrane is unclear, but most likely the result of natural variation.

The phenotypic values observed for EV, ESH, EW, SW, EST, ESS, VMS, and HU are within ranges reported in previous Pekin duck egg quality studies (OnbaŞilar et al., 2011; Biesiada-Drzazga et al. 2014; Ipek et al., 2017; Galic et al., 2019; Oluwagbenga et al., 2022). When compared to other duck breeds, the Pekin appears to have higher EW and thinner EST. Shaoxing ducks had a reported EW and EST of 72.30 ± 5.13 g and 0.48 ± 0.05 mm, while Jinyun ducks had EW and EST of 73.12 ± 5.76 g and 0.52 ± 0.06 mm (Zeng et al., 2018). In Sha Ma ducks EW, EST was reported as 67.30 ± 5.23 g, 0.31 ± 0.03 (Lin et al., 2016). The difference in egg quality between the Jinyun, Shaoxing, and Sha Ma common egg laying duck breeds and the Pekin duck most likely is the result of divergent selection and the different environment experienced by the Pekin duck in this study. Zeng et.al (2018) found that egg weight at WOA 30 and WOA 40 had positive genetic correlations with body weight at 300 d of age of 0.66 ± 0.19 and 0.78 ± 0.09, respectively. The relationship between body weight and egg weight may explain why Pekin duck eggs are much heavier than that of their egg laying counterparts. These observations suggest that comparing duck breeds is not ideal when determining "normality" or expected values; thus, highlighting the need for further research into Pekin duck egg quality.

The results of the ANOVA analyses on the main effects of GEN and WOA have on egg quality traits can be found in Table 4. GEN influences all egg quality traits except VMS, ST, and ESS ($P < 0.05$).

The effects of GEN on egg quality traits in each WOA subset can be found in Table 5. GEN affects WOA 30, 32, and 35 in YR, YW, EST and HU ($P < 0.05$). AR, EW, EV and ESH, were only influenced by GEN up to WOA 32, and SW was significantly influenced by GEN only at WOA 35 ($P < 0.05$). SR is influenced by GEN at WOA 30 and 35. The linear regression highlights that the egg quality trait values are significantly different between each GEN. While it is likely that seasonal environmental effects are responsible for these results, further research needs to be conducted to investigate the possibility of genetic trends.

Heritability Estimates

Heritability estimates ranged from 0.20 for VMS and HU to 0.71 for SR (Table 6). Results found within

Table 2. Summary statistics for generation 1 Pekin duck breeder hen egg quality traits.

Trait[1]	WOA[2]	Egg Count (n)	Min	Mean ± SEM	Max	CV%
AR	30	221	0.51	0.61 ± 0.00	0.75	4.43
	32	249	0.56	0.61 ± 0.00	0.70	3.24
	35	267	0.56	0.60 ± 0.00	0.65	2.95
YR	30	225	0.19	0.30 ± 0.00	0.38	7.99
	32	257	0.25	0.30 ± 0.00	0.35	6.10
	35	268	0.26	0.31 ± 0.00	0.35	5.49
SR	30	221	0.07	0.09 ± 0.00	0.12	9.52
	32	249	0.05	0.09 ± 0.00	0.11	6.94
	35	267	0.08	0.09 ± 0.00	0.11	6.14
EW (g)	30	223	60.30	80.20 ± 0.51	119.0	9.52
	32	257	62.30	81.90 ± 0.38	98.1	7.46
	35	267	64.80	83.60 ± 0.36	99.1	6.94
EV (ml)	30	225	73.10	73.10 ± 0.47	109.0	9.58
	32	257	74.60	74.60 ± 0.35	89.4	7.53
	35	268	76.10	76.10 ± 0.33	91.0	7.02
YW (g)	30	225	18.00	23.70 ± 0.17	31.8	10.10
	32	257	16.20	24.30 ± 0.15	30.9	9.60
	35	268	18.90	25.50 ± 0.14	31.8	8.53
SW (g)	30	221	5.47	7.38 ± 0.06	9.9	11.3
	32	249	4.41	7.46 ± 0.05	9.51	9.48
	35	267	6.20	7.60 ± 0.04	9.61	8.18
ESH	30	225	0.65	0.73 ± 0.01	1.02	9.21
	32	257	0.63	0.72 ± 0.00	0.93	5.85
	35	268	0.66	0.72 ± 0.00	0.94	6.60
EST (mm)	30	225	0.33	0.41 ± 0.00	0.50	7.25
	32	257	0.28	0.41 ± 0.00	0.47	6.21
	35	268	0.36	0.42 ± 0.00	0.50	5.82
ESS (N)	30	221	1182.00	4587 ± 45.80	6399	14.83
	32	251	1750.00	4804 ± 46.70	6742	15.39
	35	264	3228.00	4944 ± 44.40	7190	14.60
VMS (N)	30	205	31.70	173.85 ± 5.12	434.0	42.15
	32	239	19.30	175.31 ± 4.73	459.0	41.70
	35	247	22.70	169.45 ± 4.11	359.0	38.15
HU	30	210	72.20	95.08 ± 0.48	110.0	7.32
	32	234	75.70	95.48 ± 0.46	110.0	7.44
	35	255	66.40	92.10 ± 0.43	103.0	7.39

[1]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.

[2]WOA: week of age.

Table 6 contain pooled data from 2 generations containing WOA 30, 32 and 35 and WOA 40 in GEN 2. All traits are moderate to highly heritable and estimates calculated were close to those for other avian species. The heritability estimates calculated in this project show that through selection progress can be made on hatching egg quality in Pekin ducks.

In the current project, a heritability estimates of 0.46 ± 0.03 for EW was obtained, falling in the range of previously reported EW heritability estimates. EW heritability estimates of 0.32 ± 0.05, 0.45 ± 0.09, and 0.65 ± 0.10 have been reported in for Rhode Island White layers, Iranian native chickens, and Shan Ma laying ducks, respectively (Begli et al., 2010; Lin et al., 2016; Wan et al., 2019). ESS had heritability estimates of 0.09 and 0.20 for Brown Tsaiya and Shan Ma laying ducks (Cheng et al., 1995; Lin et al., 2016), respectively which are lower than that of 0.38 ± 0.03 estimated in this population. YW had a heritability estimate of 0.46 ± 0.03 in the current study which is higher than the previously reported YW heritability estimates of 0.19 and 0.09 in Brown Tsaiya and Gallang ducks respectively (Cheng et al., 1995; Purwantitni et al., 2022). The heritability estimate of 0.53 ± 0.03 for EST calculated in this study was also higher than the heritability of 0.28 calculated in Brown Tsaiya ducks and 0.21 ± 0.11 in Gallang ducks (Cheng et al., 1995; Purwantitni et al., 2022). Shan Ma laying duck had a higher heritability for ESH (0.34 ± 0.15) Lin et al. (2016) than the 0.23 ± 0.03 calculated in this project. EV and VMS did not have previously calculated heritability estimate. The heritability of SR, YR, and AR were calculated as 0.71 ± 0.00, 0.43 ± 0.03 and 0.41 ± 0.03. Although little research has been conducted on the ratio of component weight to total egg weight in ducks, a heritability estimates of 0.33 was calculated for Brown Tsaiya for YR (Cheng et al., 1995). There have been a few studies which investigated the traits heritability in other avian species. A heritability estimates of 0.61 ± 0.22 was reported for Rhode Island Whites, and 0.44 ± 0.04 for White Leghorns YR (Rath et al., 2015; Wan et al., 2019). When investigating albumen percentage, Wan et al. (2019) reported heritability for thin and thick albumen percentages separately. They found that the percentage of the EW consisting of the thick albumen had a heritability of 0.39 ± 0.05 and the thin albumen was 0.31 ± 0.14 (Wan et al., 2019). These heritability estimates are comparable to 0.41 ± 0.03 that was calculated for our project. In quail, a heritability of 0.55 ± 0.05 was reported for shell percentage (Narinc et al., 2015), which is lower than the 0.71 found in our study.

Table 3. Summary statistics for generation 2 Pekin duck breeder hen egg quality traits.

Trait[1]	WOA[2]	Egg Count (n)	Min	Mean ± SEM	Max	CV%
AR	30	253	0.56	0.62 ± 0.00	0.71	3.34
	32	252	0.55	0.62 ± 0.00	0.69	3.08
	35	199	0.54	0.61 ± 0.00	0.65	3.20
	40	238	0.54	0.59 ± 0.00	0.64	3.31
YR	30	253	0.19	0.29 ± 0.00	0.34	7.08
	32	253	0.23	0.29 ± 0.00	0.37	6.53
	35	264	0.25	0.30 ± 0.00	0.35	5.91
	40	239	0.27	0.31 ± 0.00	0.36	5.54
SR	30	257	0.07	0.09 ± 0.00	0.12	6.85
	32	260	0.08	0.09 ± 0.00	0.119	6.43
	35	208	0.08	0.10 ± 0.00	0.137	9.44
	40	251	0.05	0.09 ± 0.00	0.134	11.20
EW (g)	30	257	63.70	77.3 ± 0.36	99.2	7.36
	32	261	61.30	80.5 ± 0.34	97.5	6.87
	35	274	68.70	83.0 ± 0.35	97.2	6.94
	40	252	70.60	84.0 ± 0.34	97.6	6.40
EV (ml)	30	260	58.00	70.9 ± 0.38	105.0	8.61
	32	261	55.00	73.2 ± 0.36	89.1	7.87
	35	274	62.40	75.8 ± 0.32	88.7	6.95
	40	253	41.40	76.7 ± 0.35	92.5	7.19
YW (g)	30	253	12.70	22.4 ± 0.14	28.7	10.2
	32	253	14.20	23.3 ± 0.13	29.9	9.16
	35	264	19.10	24.8 ± 0.13	30.1	8.54
	40	239	20.50	26.3 ± 0.14	32.0	7.94
SW (g)	30	257	5.51	7.28 ± 0.04	9.25	9.28
	32	260	5.57	7.45 ± 0.04	9.53	9.29
	35	208	6.24	7.99 ± 0.06	10.1	10.00
	40	251	4.42	7.78 ± 0.06	10.0	11.40
ESH	30	260	0.62	0.71 ± 0.00	0.93	6.16
	32	261	0.65	0.71 ± 0.00	0.94	5.04
	35	274	0.64	0.71 ± 0.00	0.91	5.26
	40	253	0.63	0.72 ± 0.00	0.93	7.07
EST (mm)	30	257	0.29	0.39 ± 0.00	0.51	11.6
	32	260	0.36	0.43 ± 0.00	0.52	6.70
	35	208	0.36	0.43 ± 0.00	0.56	6.93
	40	251	0.34	0.41 ± 0.00	0.49	6.25
ESS (N)	30	257	1637.00	4668 ± 45.50	6645	15.64
	32	252	2788.00	4752 ± 49.20	7559	16.44
	35	264	2993.00	4925 ± 42.10	6904	13.88
	40	245	1846.00	4763 ± 48.60	6984	15.97
VMS (N)	30	245	27.30	171.22 ± 4.16	392.0	38.03
	32	241	39.70	176.22 ± 4.37	439.0	38.53
	35	250	38.40	167.26 ± 4.18	449.0	39.54
	40	227	38.40	159.18 ± 4.08	426.0	38.59
HU	30	234	73.50	96.82 ± 0.43	112.0	6.74
	32	240	71.30	92.47 ± 0.45	107.0	7.50
	35	245	73.30	89.85 ± 0.45	108.0	7.52
	40	233	63.30	87.05 ± 0.54	104.0	9.39

[1]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.

[2]WOA: week of age.

Differences in heritability estimates reported for a given trait may result from methodological differences in trait definition, measurement methods, sample size, model choice, and the accuracy and completeness of the pedigree. In addition, differences in environments, including flock nutrition, housing and management, can contribute to differences in the amount of environmental variation, with more uniform environmental conditions allowing for fuller gene expression and consequently higher levels of heritability. Most significantly, heritability estimates for egg quality traits in the Pekin duck population in this study may differ from previously reported estimates in other duck populations as a result of genetic causes such as founder sampling effects, genetic drift, and divergent genetic selection histories. The magnitude of heritability of a given trait is directly proportional to the amount of additive genetic variation for that trait in a population. In closed breeding flocks of poultry, the magnitude of additive genetic variation, and consequently the heritability, of a trait is decreased as a result of both direct and indirect genetic selection for that trait. The Pekin breed has historically been selected for meat production, and that is especially true for the population in this study. In contrast, the Sha Ma and Brown Tsaiya breeds have historically been selected with a focus on egg related traits, such as egg number, size, and integrity. As a result, the amount of genetic variation in most egg quality traits of the Pekin duck population in this study would be expected to be greater, resulting in higher heritability values.

Table 4. Main effects of WOA, and GEN on egg quality traits in Pekin duck breeders.[1,2]

TRAIT[3]	AR	YR	SR	EW (g)	EV (ml)	YW (g)	SW (g)	ESH	EST (mm)	ESS (N)	VMS (N)	HU
WOA												
30	0.613 ± 0.001^{C}	0.294 ± 0.001^{C}	0.093 ± 0.000^{C}	78.70 ± 0.27^{C}	72.00 ± 0.26^{C}	23.10 ± 0.10^{D}	7.33 ± 0.03^{B}	0.72 ± 0.002^{A}	0.399 ± 0.001^{C}	4630 ± 33.4^{C}	$172.00 \pm 3.18^{A,B}$	96.00 ± 0.34^{A}
32	0.614 ± 0.001^{C}	0.294 ± 0.001^{C}	0.092 ± 0.000^{B}	81.20 ± 0.26^{B}	73.90 ± 0.26^{B}	23.80 ± 0.10^{C}	7.46 ± 0.03^{B}	0.72 ± 0.002^{A}	0.422 ± 0.001^{A}	4778 ± 32.5^{B}	176.00 ± 3.07^{B}	94.00 ± 0.33^{B}
35	0.604 ± 0.001^{B}	0.302 ± 0.001^{B}	0.094 ± 0.000^{C}	83.30 ± 0.26^{A}	75.90 ± 0.25^{A}	25.10 ± 0.10^{B}	7.78 ± 0.03^{A}	0.72 ± 0.002^{A}	0.423 ± 0.001^{A}	4934 ± 31.7^{A}	$168.00 \pm 3.02^{A,B}$	90.00 ± 0.32^{C}
40	0.592 ± 0.001^{A}	0.317 ± 0.001^{A}	0.091 ± 0.001^{A}	84.80 ± 0.41^{A}	77.40 ± 0.39^{A}	26.80 ± 0.15^{A}	7.74 ± 0.05^{A}	0.73 ± 0.003^{A}	0.411 ± 0.002^{B}	$4762 \pm 50.2^{C,B}$	160.00 ± 4.81^{A}	87.70 ± 0.51^{D}
GEN												
1	0.604 ± 0.001	0.305 ± 0.001	0.091 ± 0.000	82.81 ± 0.25	75.45 ± 0.24	25.20 ± 0.09	7.53 ± 0.03	0.73 ± 0.002	0.412 ± 0.001	4775 ± 30.1	170.00 ± 2.87	92.79 ± 0.30
2	0.608 ± 0.001	0.298 ± 0.001	0.094 ± 0.000	81.22 ± 0.19	74.15 ± 0.18	24.20 ± 0.07	7.62 ± 0.02	0.71 ± 0.001	0.417 ± 0.001	4777 ± 22.9	168.00 ± 2.17	91.54 ± 0.23
P-Value	***	***	***	***	***	***	*	***	*NS*	*NS*	*NS*	***

[1]Data is presented as LSM and SE; GEN effect excluded in WOA 40 as it only appeared in GEN 2.
[2]Significance Levels: NS - no significance; · < 0.1; * < 0.05; ** <0.01; ***<0.001.
[3]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.
[A-D]WOA means within a column with differing letters are different according to a Tukey-Kramer pairwise comparison (*P*-value < 0.05).

Table 5. Main effects of GEN on egg quality traits in Pekin duck breeder females WOA subsets.

Main effect of GEN on each WOA subsets for egg quality traits in Pekin duck breeders[1,2]

Trait[3]	WOA	GEN 1	GEN 2	P-value
AR	30	0.611 ± 0.002	0.615 ± 0.001	*
	32	0.611 ± 0.001	0.617 ± 0.001	***
	35	0.603 ± 0.001	0.605 ± 0.001	NS
	40	-	-	-
YR	30	0.297 ± 0.002	0.290 ± 0.001	*
	32	0.298 ± 0.001	0.290 ± 0.001	***
	35	0.305 ± 0.001	0.298 ± 0.001	***
	40	-	-	-
SR	30	0.092 ± 0.0005	0.094 ± 0.0004	*
	32	0.091 ± 0.0004	0.093 ± 0.0004	NS
	35	0.091 ± 0.0005	0.097 ± 0.0005	***
	40	-	-	-
EW (g)	30	80.20 ± 0.44	77.30 ± 0.42	***
	32	82.90 ± 0.36	80.50 ± 0.36	*
	35	83.60 ± 0.35	83.00 ± 0.35	NS
	40	-	-	-
EV (ml)	30	73.10 ± 0.44	70.90 ± 0.41	**
	32	74.60 ± 0.36	73.20 ± 0.35	*
	35	76.10 ± 0.32	75.80 ± 0.32	NS
	40	-	-	-
YW (g)	30	23.70 ± 0.16	22.40 ± 0.15	***
	32	24.30 ± 0.14	23.30 ± 0.14	***
	35	25.50 ± 0.13	24.80 ± 0.13	***
	40	-	-	-
SW (g)	30	7.38 ± 0.05	7.28 ± 0.05	NS
	32	7.46 ± 0.04	7.45 ± 0.04	NS
	35	7.60 ± 0.04	7.99 ± 0.05	***
	40	-	-	-
ESH	30	0.73 ± 0.00	0.71 ± 0.00	***
	32	0.72 ± 0.00	0.71 ± 0.00	*
	35	0.72 ± 0.00	0.71 ± 0.00	.
	40	-	-	-
EST (mm)	30	0.41 ± 0.00	$0.39 + 0.00$	***
	32	0.41 ± 0.00	0.43 ± 0.00	***
	35	0.42 ± 0.00	0.43 ± 0.00	***
	40	-	-	-
ESS (N)	30	4586 ± 47.6	4668 ± 44.1	NS
	32	4803 ± 48.0	4752 ± 47.9	NS
	35	4944 ± 43.3	4925 ± 43.3	NS
	40	-	-	-
VMS (N)	30	174 ± 4.82	171 ± 4.40	NS
	32	175 ± 4.56	176 ± 4.54	NS
	35	169 ± 4.16	167 ± 4.14	NS
	40	-	-	-
HU	30	95.10 ± 0.47	96.80 ± 0.44	.
	32	95.50 ± 0.46	92.50 ± 0.45	***
	35	92.10 ± 0.43	89.80 ± 0.44	***
	40	-	-	-

[1]Data is presented as LSM and SE.
[2]Significance Levels: NS - no significance; · < 0.1; * < 0.05; ** <0.01; ***<0.001.
[3]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.

Selecting for increased meat production could influence allele representation in the Pekin duck line used in our study and as a result affect heritability estimate. A biproduct of intensive selection for meat production traits could have resulted in the loss of alleles needed to improve egg quality traits resulting in low heritability estimates for egg quality traits. However, heritability estimates for the Pekin duck appeared to be higher than that for egg specific breeds. Genes related to egg quality could be in high linkage disequilibrium with genes needed for meat production or directly participate in

Table 6. Pekin duck breeder egg quality traits mean heritability estimates and standard errors.[1]

Trait[2]	α_A[3]	α_P[4]	h[2]
AR	0.18E-03 ± 0.19E-04	0.25E-03 ± 0.11E-04	0.41 ± 0.03
YR	0.16E-03 ± 0.17E-04	0.22E-03 ± 0.90E-05	0.43 ± 0.03
SR	0.81E-04 ± 0.11E-0.5	0.33E-04 ± 0.125E-05	0.71 ± 0.00
EW	16.90 ± 1.67	20.12 ± 0.81	0.46 ± 0.03
EV	12.72 ± 1.41	21.58 ± 0.86	0.37 ± 0.03
YW	0.41E-03 ± 0.41E-0.4	0.48E-03 ± 0.20E-0.4	0.46 ± 0.03
SW	5.02 ± 0.79	16.639 ± 0.66	0.23 ± 0.03
ESH	0.49 E-03 ± 0.78E-04	0.16E-03 ± 0.66E-04	0.23± 0.03
EST	0.43E-03 ± 0.39E-04	0.37E-03 ± 0.16E-04	0.53 ± 0.03
ESS	0.21E+06 ± 22838	0.33E+06 ± 13511	0.38 ± 0.03
VMS	904.24 ± 153.94	3583.4 ± 147.10	0.20 ± 0.03
HU	9.98 ± 1.70	41.02 ± 1.67	0.20 ± 0.03

[1]Estimates were calculated using pooled data from 2 generations at WOA 30,32,35, and 40.
[2]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.
[3]α_A: additive genetic variance.
[4]α_P: phenotypic variance.

meat production. This situation could preserve genes needed to improve egg quality in the population and result in a high heritability estimate. These concepts of genetic diversity loss and indirect selection highlight the importance of further investigating egg quality traits in meat type species.

Age plays a substantial role in the composition of the egg. As the female ages yolk deposition increases and albumen deposition decreases (Applegate et al., 1998; Johnston et al., 2007). Table 7 provides the heritability estimates and SE for WOA 30, 32, 35, and 40. Heritability estimates did not converge for SW, ESS, and VMS at WOA 40 most likely as a result of the reduced sample size. There is little research investigating the change in heritability across time for egg quality traits in duck production. However, heritability estimates for egg weight for Sha Ma laying ducks have been calculated for 30 and 40 WOA, 0.47 ± 0.13 and 0.51 ± 0.13 respectively (Lin et al., 2016). These heritability estimates fall in the same range as the EW calculations in our project. The highest heritability for SW and VMS was calculated at WOA32. EW, EV SR and HU had the highest heritability at WOA 40. For ESS the highest heritability was calculated as 0.43 ± 0.14 at both WOA 32 and 35. WOA 35 had the highest heritability estimates for the remaining egg quality traits. The results for weekly heritability estimates show that selection for egg quality traits can be made as early as 30 wk of age as the individuals come into lay. Further investigation is needed to understand how selection for egg quality traits at the beginning of lay will affect egg quality at later ages.

Table 7. Pekin duck breeder heritability estimates and standard error of egg quality traits for WOA[1] 30, 32, 35, and 40.

Trait[2]	WOA 30	WOA 32	WOA 35	WOA 40[3,4]
AR	0.11 ± 0.00	0.36 ± 0.00	0.45 ± 0.12	0.22 ± 0.02
YR	0.08 ± 0.14	0.26 ± 0.09	0.52 ± 0.11	0.11 ± 0.01
SR	0.12 ± 0.00	0.37 ± 0.10	0.37 ± 0.15	0.49 ± 0.39
EW	0.40 ± 0.11	0.52 ± 0.10	0.52 ± 0.13	0.54 ± 0.33
EV	0.27 ± 0.10	0.51 ± 0.11	0.54 ± 0.13	0.77 ± 0.33
YW	0.35 ± 0.10	0.17 ± 0.09	0.50 ± 0.11	0.36 ± 0.40
SW	0.37 ± 0.11	0.65 ± 0.14	0.34 ± 0.01	DNC
ESH	0.05 ± 0.07	0.24 ± 0.09	0.36 ± 0.10	0.09 ± 0.02
EST	0.06 ± 0.07	0.47 ± 0.10	0.52 ± 0.10	0.33 ± 0.31
ESS	0.32 ± 0.14	0.43 ± 0.14	0.43 ± 0.14	DNC
VMS	0.10 ± 0.13	0.34 ± 0.15	0.30 ± 0.13	DNC
HU	0.26 ± 0.09	0.25 ± 0.09	0.15 ± 0.08	0.58 ± 0.37

[1]WOA: week of age.
[2]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.
[3]DNC: did not converge
[4]WOA 40 collection only occurred in GEN 2 and has half the number of records than WOA 30, 32, and 35.

Genetic Correlations

The strength of the genetic correlations found in Table 8 ranged from −0.80 (YR and AR) to 0.99 (EV and EW) and highlighted the relationship between each of the traits. Many pairs of traits had no genetic relationship. For example, ESH had no correlation with shell-based traits such as SR, EST, and ESS. This highlights that improvement can be made to egg shape too without sacrificing the value of other egg quality traits. In quail, ESH was found to significantly influence hatchability, slaughter weight, and left leg weight (Alasahan and Copur, 2016). A large negative correlation exists between YR and AR showing the antagonistic relationship between the 2 when occupying the volume shell, while SR appears to be lowly negatively influenced by YR and AR. With respect to EW and EV the researchers in this project found that AR was moderately positively correlated, and SR and YR were moderately negatively correlated. This relationship is seen in Rhode Island White chickens where genetic correlations of −0.54 for EW and YR and 0.12 and 0.25 correlation EW and thick and thin albumen were calculated, respectively (Wan et al., 2019). In White Leghorns YR and EW had a genetic correlation of −0.75 ± 0.05 (Rath et al., 2015). The trend is the same; however, values vary which could be the result of species and population differences. Genetic correlations notoriously differ markedly in different populations as they are strongly influenced by gene frequencies (Falconer and MacKay, 1996).

These results highlight the potential to select for egg component ratio without having a substantial negative effect on other egg quality traits. Previous research sought to select White Leghorns for yolk proportion to egg weight only and as a result saw a decrease in overall egg weight (Hartmann et al., 2000). This result of decreased egg size in the individuals selected for a larger yolk proportion is consistent with the results found in this research. YR and EW had a correlation of −0.27 ± 0.07, highlighting the need for a selection criterion with more than just 1 egg quality trait. A selection criterion that balances YR, EV, and EW would be more likely to result in a line of individuals that produce a larger egg and yolk than selecting for YR alone. Egg volume was based on the external size of the egg and did not consider

Table 8. Genetic correlations and standard errors for Pekin duck breeder egg quality traits.[1]

	YR	SR	EW	EV	YW	SW	ESH	EST	ESS	VMS	HU
AR	−0.80 (0.00)	−0.12 (0.00)	0.33 (0.07)	0.37 (0.07)	-0.42 (0.06)	0.01 (0.08)	−0.08 (0.09)	−0.15 (0.07)	-0.01 (0.01)	−0.22 (0.10)	0.30 (0.09)
YR		−0.08 (0.00)	−0.27 (0.07)	−0.30 (0.07)	0.52 (0.06)	−0.22 (0.08)	0.08 (0.09)	−0.15 (0.07)	0.04 (0.08)	−0.22 (0.10)	-0.33 (0.09)
SR			−0.26 (0.08)	−0.31 (0.08)	−0.22 (0.08)	0.55 (0.08)	0.03 (0.00)	0.60 (0.01)	0.88 (0.07)	0.03 (0.10)	−0.02 (0.12)
EW				0.99 (0.00)	0.68 (0.04)	0.64 (0.05)	−0.02 (0.09)	0.16 (0.07)	0.05 (0.08)	−0.03 (0.10)	−0.00 (0.10)
EV					0.66 (0.05)	0.58 (0.06)	−0.00 (0.10)	0.15 (0.07)	0.06 (0.08)	−0.02 (0.10)	0.04 (0.10)
YW						0.41 (0.07)	0.04 (0.10)	0.03 (0.07)	0.11 (0.08)	0.16 (0.10)	−0.24 (0.10)
SW							0.02 (0.10)	0.83 (0.03)	0.74 (0.05)	0.00 (0.10)	−0.03 (0.11)
ESH								0.02 (0.09)	0.20 (0.07)	−0.15 (0.12)	−0.05 (0.12)
EST									0.81 (0.04)	−0.08 (0.10)	−0.06 (0.10)
ESS										−0.03 (0.10)	−0.03 (0.10)
VMS											0.12 (0.12)

[1]AR: albumen ratio; ESH: egg shape; ESS: eggshell strength; EST: eggshell thickness; EV: egg volume; EW: egg weight; HU: haugh unit; SR: shell ratio; SW: shell weight; VMS: vitelline membrane strength; YR: yolk ratio; YW: yolk weight.

the air cell. The air cell volume in relationship to total egg volume and egg components is crucial as the air cell plays a crucial role in gas exchange for the embryo and correlates to egg freshness (i.e. moisture loss and CO_2 build up) (Sauter et al., 1953; Seymour et al., 1988; Brand et al., 2013).

Before implementing egg quality traits into a Pekin duck breeding program more research is needed. For example, very little information is available on what an ideal egg quality would be for a hatching egg. There is research that investigates yolk to albumen ratio (Milisits et al., 2013). Overall egg volume could play a role in offspring production potential, but results have been inconclusive and not repeated in ducks. The inability to collect egg quality traits on the same eggs that are used for hatching continues to be a challenge when investigating the effects of egg quality and offspring performance. Additional information is needed to investigate the genetic correlations between egg quality and production traits to ensure selection for egg quality traits will not have detrimental effects on economically important juvenile traits in our Pekin ducks.

CONCLUSIONS

Our current research highlights the potential to begin selection for egg quality traits in meat ducks, specifically Pekin ducks. All traits evaluated have moderate to high heritability estimates. The significant influence of GEN on many egg quality traits may be indicating that selection for increased production performance could already be altering the hatching egg quality. However, the generation difference is most likely the result of environment/seasonal difference. Whether this underlying selection has a positive or negative effect on hatchability and duckling performance should be further investigated. Common egg quality measurements require the destruction of the egg, making the determination of the effects of egg quality traits on the commercial meat duck performance challenging. Selection for egg quality traits appears to be heritable in Pekin ducks and selection towards an optimal hatching egg quality could provide a method to further improve Pekin duck productivity.

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DISCLOSURES

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: William Lee reports financial support and administrative support were provided

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