ABSTRACT
Albumen height, albumen weight (AW), eggshell color (ESC), eggshell index, eggshell strength, eggshell thickness, eggshell weight (ESW), egg weight (EW), Haugh units, and yolk weight (YW) were measured in 2,272 eggs collected 3 d sequentially from 920 brown-egg dwarf layers caged individually. The restricted maximum likelihood procedure was applied to estimate heritabilities and genotypic and phenotypic correlations for these egg quality traits. Heritabilities of albumen height, AW, ESC, eggshell index, eggshell strength, eggshell thickness, ESW, EW, Haugh units, and YW were 0.51, 0.59, 0.46, 0.40, 0.24, 0.34, 0.64, 0.63, 0.41, and 0.45, respectively. The genetic correlations between EW and AW, YW, and ESW were high ranging from 0.67 to 0.97, whereas those for ESC with external and internal egg quality traits were low ranging from −0.23 to 0.13. Thus although heritabilities for these traits were moderate to high, genetic correlations with ESC were low, suggesting a minor relationship between shell color and physical attributes of the shell as well as internal egg quality in brown-egg dwarf layers.

(Key words: dwarf layer, egg quality, genetic correlation, heritability, restricted maximum likelihood)

INTRODUCTION
Feed consumption is an important cost in the production of eggs. The sex-linked dwarf gene (dw) reduces body weight and egg weight of chickens (Cole, 2000; Missouhou et al., 2003). In general, the dw gene depresses growth in layer-type stocks by approximately 30% (Hutt, 1959) and reduces egg size primarily due to the reduction in body size (Benoff and Renden, 1980). Dwarf layers, in spite of their reproductive performance, were more efficient than nondwarf layers; this advantage in efficiency has been attributed to reduced maintenance requirements (Bernier and Arscott, 1972). When comparisons were made between nondwarf hens and dwarf hens, enhanced feed efficiency was obtained due to the dw gene (Sadjadi et al., 1983). Facing a global lack of animal and poultry feedstuffs, the potential in using the dw gene to reduce feed intake may once again gain importance in certain areas of the world. Therefore it is important to revisit the role of dw gene on egg production and egg quality of current laying chickens. Recently, a line of brown-egg dwarf layers was developed at the China Agricultural University (CAU) by 4 repeated backcrosses of the meat type dwarf ISA-Vedette to the female CAU brown egg layer (Yang et al., 1996). Body weight of this brown-egg dwarf commercial layer at 20 wk age was about 1,200 g. Total egg number to 72 wk was approximately 285 with an average egg weight of 56 g.

Although there is considerable literature on genetic parameters of egg characteristics, most are from several decades ago, and associations with egg color are lacking. Moreover, eggs have to be broken to measure their internal egg quality, and information on genetic parameters of interior and exterior egg quality traits may allow for selection via sib relationships. This possibility may be so with the development of the restricted maximum likelihood (REML) method (Boldman et al., 1995), which allows for more accurate estimates of genetic parameters and estimates of breeding values. Studies related to the egg quality traits of nondwarf chicken have been reported (e.g., Marks and Kinney, 1964; Kumar and Kapri, 1966; Curtis et al., 1985; Bell et al., 2001; Buitenhuis et al., 2004). There is, however, a dearth of information on genetic parameters for interior and exterior egg quality of dwarf layers using REML.

Abbreviation Key: AH = albumen height; AW = albumen weight; CAU = China Agricultural University; ELL = long length of egg; ESC = egg shell color; ESI = egg shell index; ESR = eggshell ratio; ESS = egg shell strength; EST = egg shell thickness; ESW = egg shell weight; EW = egg weight; HU = Haugh unit; REML = restricted maximum likelihood; VLI = Veterinary and Livestock Instruments; YC = yolk color; YW = yolk weight.
MATERIALS AND METHODS

Stock, Husbandry, and Traits Measured

A pure line of brown-egg layers developed at CAU was used for the current study. Forty-four sires were selected, and each was mated to 9 to 10 dams. Eggs obtained from these families with full pedigree were incubated at the same time. Chicks were hatched on September 1 and were vent sexed, pedigreed, wing-banded, and vaccinated against Marek’s disease. In the open-sided house, the period of light was gradually decreased from 24 h to 22 h during the first 2 wk, then birds were continued on natural light until transferred to single-hen cages at 16 wk of age when the daily length of natural light was approximately 8 h. Then the photoperiod was increased by 1 h/wk until 17 h of light was achieved. All pullets were kept in the same laying house to minimize environmental effects. The laying mash consisted of 19% CP and 2,750 kcal of ME/kg.

Eggs (n = 2,272) were obtained from 920 hens on 3 d consecutively when hens were 40 wk of age. Data were obtained daily for the eggs laid on that day with the average for the 3 d used as the value for each hen. Cracked, soft-shell, and double-yolked eggs were not used. External and internal egg quality traits including egg weight (EW), eggshell index (ESI), eggshell strength (ESS), eggshell thickness (EST), eggshell color (ESC), albumen height (AH), albumen weight (AW), Haugh units (HU), yolk weight (YW), and yolk color (YC) were measured. The procedure followed was to weigh the egg to the nearest 0.01 g. Then shell color was measured on the blunt region, equatorial region, and sharp region, respectively using a EQReflectometer2 and its length and width at midpoint were measured in millimeters using Veterinary and Livestock Instruments2 (VLI) for ESI. Eggs were broken using VLI for ESS with strength of shell measured in kg/cm². The shell of the egg was then weighed (0.01 g), and AH was measured (mm) using VLI for AH and the EST was measured (mm) using VLI for EST on the blunt region, equatorial region, and sharp region, respectively, and the average of the 3 was considered the value for the egg. Yolk and albumen were then separated and weighed (0.01 g), and YC was measured using Roche Yolk Color Fan.3 Haugh units were obtained daily for the eggs laid on that day with the average for the 3 d used as the value for each hen. Yolk and albumen were used for the current study. Forty-four sires were selected, and each was mated to 9 to 10 dams. Eggs obtained from these families with full pedigree were incubated at the same time. Chicks were hatched on September 1 and were vent sexed, pedigreed, wing-banded, and vaccinated against Marek’s disease. In the open-sided house, the period of light was gradually decreased from 24 h to 22 h during the first 2 wk, then birds were continued on natural light until transferred to single-hen cages at 16 wk of age when the daily length of natural light was approximately 8 h. Then the photoperiod was increased by 1 h/wk until 17 h of light was achieved. All pullets were kept in the same laying house to minimize environmental effects. The laying mash consisted of 19% CP and 2,750 kcal of ME/kg.

Internal egg quality

<table>
<thead>
<tr>
<th>Trait</th>
<th>Mean ± SE</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AH (mm)</td>
<td>7.25 ± 0.03</td>
<td>18.11</td>
</tr>
<tr>
<td>AW (g)</td>
<td>32.02 ± 0.07</td>
<td>10.45</td>
</tr>
<tr>
<td>AR (%)</td>
<td>59.39 ± 0.05</td>
<td>4.00</td>
</tr>
<tr>
<td>HU</td>
<td>86.20 ± 0.15</td>
<td>9.37</td>
</tr>
<tr>
<td>YC</td>
<td>6.77 ± 0.01</td>
<td>7.49</td>
</tr>
<tr>
<td>YW (g)</td>
<td>14.77 ± 0.03</td>
<td>9.60</td>
</tr>
<tr>
<td>YR (%)</td>
<td>27.45 ± 0.04</td>
<td>7.02</td>
</tr>
</tbody>
</table>

1 ^n = 2,272.
2 ^EW = egg weight; ESL = short length of egg; ELL = long length of egg; ESI = eggshell index; EST = eggshell thickness; ESS = eggshell strength; ESC = eggshell color; ESW = eggshell weight; ESR = eggshell ratio; AH = albumen height; AW = albumen weight; AR = albumen ratio; HU = Haugh unit; YC = yolk color; YW = yolk weight; YR = yolk ratio; ESI = ESL/ELL; ESS (%) = ESW/EW×100; AR (%) = AW/EW×100; YR (%) = YW/EW×100.

Statistical Analysis

The units for analysis were the average of the values for eggs from each hen over the 3 d. The means of egg quality traits were calculated with the MEANS procedure of the SAS software package (SAS Institute, 2001). An animal model was constructed as follows:

\[ Y_{ij} = \mu + a_i + e_{ij} \]

where \( Y_{ij} \) is the \( i \)th average phenotypic record of the egg quality trait, \( \mu \) is the common mean, \( a_i \) is the \( i \)th individual breeding value, and \( e_{ij} \) is the error. The REML procedure was applied to estimate heritabilities and phenotypic and genotypic correlations using the MTDFREML software package (Boldman et al., 1995). The procedures were run following the manual for MTDFREML, while referring to applications to the software package by Riley et al. (2002). Pedigree information for one generation of ancestors was included in the relationship matrix. Heritabilities were estimated using single-trait analysis. Initial values of genetic and environmental variances were the value of variance for corresponding trait and random values, respectively. The procedures were started with a low \((10^{-9})\) level of convergence then to higher level of convergence. The values converging at \(10^{-9}\) were taken as final estimates of heritabilities. Genetic and phenotypic correlations between pairs of traits were estimated using a 2-trait analysis. The genetic and environmental variance estimates from the results of single-trait analyses and random covariance values were set as initial values. Then the 2-trait analyses were run to a higher level of convergence criterion \((10^{-8})\). Cold starts were again run to the same level of convergence with initial values from the former 2-trait analyses results until a −2log likelihood did not change in the first 3 decimal positions. Convergence to a global maximum instead of a local maximum was examined.
TABLE 2. Heritabilities of, and genetic and phenotypic correlations among, external egg quality traits1,2

<table>
<thead>
<tr>
<th>External egg quality traits3</th>
<th>EW</th>
<th>ESI</th>
<th>ESS</th>
<th>EST</th>
<th>ESC</th>
<th>ESW</th>
</tr>
</thead>
<tbody>
<tr>
<td>EW</td>
<td>0.63 (0.11)</td>
<td>−0.09 (0.17)</td>
<td>−0.19 (0.20)</td>
<td>0.32 (0.16)</td>
<td>−0.12 (0.16)</td>
<td>0.67 (0.10)</td>
</tr>
<tr>
<td>ESI</td>
<td>−0.07</td>
<td>0.40 (0.10)</td>
<td>0.19 (0.22)</td>
<td>−0.04 (0.20)</td>
<td>0.08 (0.18)</td>
<td>0.15 (0.18)</td>
</tr>
<tr>
<td>ESS</td>
<td>−0.05</td>
<td>0.18</td>
<td>0.24 (0.08)</td>
<td>0.77 (0.10)</td>
<td>−0.13 (0.20)</td>
<td>0.27 (0.19)</td>
</tr>
<tr>
<td>EST</td>
<td>0.13</td>
<td>0.08</td>
<td>0.69</td>
<td>0.34 (0.09)</td>
<td>−0.23 (0.18)</td>
<td>0.59 (0.12)</td>
</tr>
<tr>
<td>ESC</td>
<td>−0.08</td>
<td>0.01</td>
<td>−0.20</td>
<td>−0.25</td>
<td>0.46 (0.09)</td>
<td>−0.19 (0.16)</td>
</tr>
<tr>
<td>ESW</td>
<td>0.50</td>
<td>0.06</td>
<td>0.28</td>
<td>0.45</td>
<td>−0.15</td>
<td>0.64 (0.12)</td>
</tr>
</tbody>
</table>

1Heritabilities are given on diagonal, genetic correlations above diagonal, and phenotypic correlations below diagonal.

2Standard errors of the estimates are in parentheses.

3EW = egg weight; ESI = eggshell index; ESS = eggshell strength; EST = eggshell thickness; ESC = eggshell color; ESW = eggshell weight.

TABLE 3. Heritabilities of, and genetic and phenotypic correlations among, internal egg quality traits1,2

<table>
<thead>
<tr>
<th>Internal egg quality traits3</th>
<th>AH</th>
<th>AW</th>
<th>HU</th>
<th>YW</th>
</tr>
</thead>
<tbody>
<tr>
<td>AH</td>
<td>0.51 (0.11)</td>
<td>0.34 (0.15)</td>
<td>0.98 (0.01)</td>
<td>0.07 (0.17)</td>
</tr>
<tr>
<td>AW</td>
<td>0.25</td>
<td>0.59 (0.11)</td>
<td>0.13 (0.17)</td>
<td>0.63 (0.11)</td>
</tr>
<tr>
<td>HU</td>
<td>0.97</td>
<td>0.07</td>
<td>0.41 (0.10)</td>
<td>−0.11 (0.18)</td>
</tr>
<tr>
<td>YW</td>
<td>−0.03</td>
<td>0.45</td>
<td>−0.16</td>
<td>0.45 (0.10)</td>
</tr>
</tbody>
</table>

1Heritabilities are given on diagonal, genetic correlations above diagonal, and phenotypic correlations below diagonal.

2Standard errors of the estimates are in parentheses.

3AH = albumen height; AW = albumen weight; HU = Haugh units; YW = yolk weight.

Using 2 to 3 cold restarts from converged estimates holding the same converged F-value.

RESULTS

Descriptive Statistics of Egg Quality Traits

Means, SE, and CV of the traits measured in the current experiment are presented in Table 1. Means for EW, ESI, EST, ESS, ESC, and ESW were 53.85 g, 0.740, 0.343 mm, 3.25 kg/cm², 41.79, and 7.07 g, respectively. Means for AH, AW, HU, YC, and YW were 7.25 mm, 32.02 g, 86.20, 6.77, and 14.77 g, respectively. The CV for most traits were generally less than 10%. Those with greater CV were ESS, ESC, and AH.

Heritabilities and Genetic and Phenotypic Correlations

Heritabilities ranged from 0.24 for ESS to 0.64 for ESW (Tables 2 and 3), and few values were low. The genetic and phenotypic correlations among external and internal egg quality traits are summarized in Tables 2 and 3, respectively. The genetic and phenotypic correlations between external egg quality traits followed a similar pattern. The highest genetic and phenotypic correlations were between ESS and EST (0.77 and 0.69, respectively). The genetic correlations between AH and AW (0.34), AH and HU (0.98), and AW and YW (0.63) were positive. Respective values for phenotypic correlations were 0.25, 0.97, and 0.45. When genotypic and phenotypic correlations were estimated between internal and external traits (Tables 4 and 5), the pattern showed high part-whole relationship for EW with AW and YW and a low relationship with variable signs among the others.

DISCUSSION

Heritabilities of EW from recent reports ranged from 0.52 (Wei and van der Werf, 1995) to 0.71 (Besbes and Gibson, 1998). The value of the current estimation was 0.63. The estimations of heritability for YW and AW were similar to previous reports (Rodda et al., 1977; Hartmann et al., 2003). The heritability for ESC estimated by Francesch et al. (1997) was similar to the present study. The heritability of ESS obtained here was similar to that reported by Buitenhuis et al. (2004). Heritabilities for HU and AH were twice those reported by Ledur et al. (2002). Reported heritabilities for EST, ESI, and ESW are generally lacking; however, those obtained here suggest that they are moderate to high.

The genetic correlations of EW with ESW and AW with YW for dwarf layers were similar to those for nondwarf layers (Silversides and Scott, 2001). Both the phenotypic correlation and the genetic correlation between EW and ESC were low, which in turn inferred that larger eggs were not weaker than smaller eggs. Although the phenotypic correlation between EW and EST was low, the genetic correlation was moderate, implying heavier eggs tended to have thicker shells.

Through his research, Carter (1975) found that the industry’s interpretation, namely that brown shells are
stronger than white ones and that brown shells are thicker than white ones was not valid. Briggs and Teulings (1974) showed that the correlation between eggshell color and breaking strength was essentially zero (0.08), which was consistent with the research presented here for the correlations between ESC and ESS and between ESC and EST. The results indicated that the association between ESC and ESS and EST were not inevitable. The large genetic correlation between EST and ESS and between ESC and EST explained that EST was a major factor affecting ESS. Finally, the results obtained here demonstrated that eggshell color had little, if any, relationship to exterior or interior egg quality.

ACKNOWLEDGMENTS

The authors gratefully acknowledge Paul B. Siegel (Virginia Tech, Blacksburg, VA) for his assistance in the manuscript preparation and Shumei Yu and Bing Liu for their technical assistance. This work was supported by grants from the National Outstanding Youth Science Foundation of China (number 30225032) and the 10th Five Years Key Program for Science and Technology Development of China (number 2002BA514-5).

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