Developmental Stability in Stocks of White Leghorn Chickens

A. YANG, E. A. DUNNINGTON, and P. B. SIEGEL1

Department of Animal and Poultry Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0306

ABSTRACT The degree of asymmetry in bilateral morphological characters may reflect genetic and environmental stressors. Shank length and diameter, weight and length of the first primary wing feather, and distance between the junction of upper and lower mandibles and auditory canal (face length) were used to classify bilateral types and measure relative asymmetry (RA) in six genetic stocks. The stocks were the S23 generation of White Leghorn lines selected for high or low antibody response to SRBC, sublines in which selection had been relaxed for eight generations, and reciprocal crosses of the selected lines. Differences were found among all stocks for the traits measured. Rankings among traits for RA in descending order were face length, shank diameter, feather weight, and shank and feather lengths. The RA of shank and feather lengths did not differ from each other. An overall RA composed of mean RA of the five traits showed that the two selected lines exhibited greater RA than the crosses between them. The RA of the two lines where selection had been relaxed was similar to that of selected lines. This research suggests that an overall RA created as a combination of RA of several bilateral traits can be a valid measure of genetic stress in chickens and provides a method of comparing developmental stability among populations.

(Key words: chicken, bilateral asymmetry, genetic stress, homeostasis)

1997 Poultry Science 76:1632–1636

INTRODUCTION

Both sides of a bilateral symmetrical trait of an animal are considered to be under genetic control (Leary and Allendorf, 1989; Parsons, 1990). Although sides may be expected to be identical because they are products of the same genome, this is not always the case, as seen in the functional ovary and heart atria and ventricles of chickens. The developmental axes of the embryo are defined in terms antero-posterior and dorso-ventral (Palmer, 1996), not left-right. Bilateral asymmetry, the deviation of part of an organism from perfect symmetry, can be categorized as anti-symmetry, directional asymmetry, or fluctuating asymmetry (van Valen, 1962). Each of these categories is characterized by a different combination of the mean and the distribution of left minus right. Palmer (1996) provided examples of frequency distributions for these three types of asymmetry.

Four genes have been reported to direct development of asymmetry of the internal organs during gastrulation and neurula stages in chick embryos (Yost, 1995). Therefore, asymmetry of bilateral traits may indicate perturbed development due to intra- (genetic) and extra- (environmental) stressors. Studied in a variety of organisms, asymmetries of bilateral traits appear to have promise as a tool in the study of evolution, conservation biology, and animal breeding (van Valen, 1962; Palmer and Strobeck, 1986; Jones, 1987; Parsons, 1990; Moller et al, 1995; Palmer, 1996).

Considerable research has been conducted on environmental stressors in poultry (e.g., Freeman, 1985; Siegel, 1995; Zulkifli and Siegel, 1995). In contrast, information on genetic stressors, such as major mutations, selection, inbreeding, and chromosomal imbalance, remains quite limited. For poultry breeding, selection for specific traits can disrupt homeostasis (Lerner, 1954), and heterosis is common for fitness traits (Fairfull, 1990). Of growing concern in commercial poultry is an increased incidence of leg disorders (Cahaner and Siegel, 1986), ascites (Julian, 1993), sudden death syndrome (Olkowski and Classen, 1995) in meat stocks, and osteomalacia and fatty liver syndrome (Schwartz, 1994) in layers. Although these conditions are associated with bilateral characteristics, the relationship of current health concerns in poultry and bilateral asymmetry are unclear in poultry breeding programs. Reported in this paper are comparisons of bilateral asymmetry in chickens from selected lines, sublines in which selection was relaxed, and F1 crosses of the selected lines.
MATERIALS AND METHODS

Genetic Stocks and Husbandry

The chickens used in this experiment were White Leghorn females from matings of lines selected for high (HAS) or low (LAS) antibody response to a single intravenous injection of 0.1 mL of a 0.25% suspension of SRBC (Siegel and Gross, 1980; Martin et al., 1990). The respective stocks were the S23 generation of Lines HAS and LAS, sublines of HAS and LAS in which selection had been relaxed (HAR and LAR, respectively) for eight generations, and reciprocal F1 crosses of the selected lines. All individuals were produced from age-contemporary parents. At hatch they were vaccinated against Mareks disease and reared as contemporaries in floor pens to 18 wk of age. They were then transferred to individual cages in an environmentally controlled room.

Traits Measured

At 28, 168, and 240 d of age, BW were obtained. Antibody titers to SRBC were measured during the 6th wk after hatch. On Day 150, data were obtained for the following bilateral characters: length (0.1 mm) of the metatarsus (shank), diameter (0.1 mm) of the shank perpendicular to the spur, and distance (0.1 mm) between the auditory canal and the posterior junction of upper and lower mandible (face length). The measurer and holder of the chickens were the same for all measurements. Also at this age, the left and right first primary wing feathers were removed and their length (millimeters) and weight (0.01 g) obtained. All first primary wing feathers were mature. Data were obtained for 29 HAR, 30 LAR, 51 LAS, 59 HAS × LAS, 60 HAS, and 60 LAS × HAS females.

There were three categories for left minus right (L − R) bilateral differences. Definitions were mean zero and normal distribution for fluctuating asymmetry (FA), mean not zero and normal distribution for directional asymmetry (DA), and mean zero with a distribution that was not normal for antisymmetry (AS). Relative asymmetry (RA) was defined as the ratio of the absolute value of asymmetry (L − R) divided by the value for the size of the bilateral trait:

$$RA = \left(\frac{|L - R|}{[(L + R)/2]}\right) \times 100.$$

Statistical Analyses

Analyses of variance (SAS Institute, 1985) were conducted for all measurements using the completely randomized model

$$Y_{ij} = \mu + g_i + e_{ij}$$

where \(i = 1, 2, \ldots, 6\) stocks (HAS, LAS, HAR, LAR, HAS × LAS, and LAS × HAS) or when \(i = 1, 2, \ldots, 5\) RA (shank length, shank diameter, face length, feather weight, and feather length) and \(j = 1, 2, \ldots, n\) individuals. When significant at \(P \leq 0.05\), multiple means were separated by Duncan’s multiple range test.

Prior to analysis, RA were transformed to arc sine square roots. Each signed (+ or −) bilateral asymmetry (L − R) was tested for normality with mean zero by Kolmogorov-Smirnov (sample size > 59) or the Shapiro-Wilk statistic W (sample size < 60) and by one-sample t tests (SAS Institute, 1985). The mean RA of each trait across stocks was calculated on an individual basis. Also, within each stock the RA of different characters were calculated on an individual basis for an overall measure of RA. Product-moment correlations between bilateral traits [(L + R)/2] and RA with BW and SRBC antibody titers were calculated within stocks. Correlations were also calculated between shank length and diameter and between feather weight and length.

RESULTS

Sizes of Bilateral Traits

Stocks differed for both length and diameter as well as the length × diameter of the left and right shanks (Table 1). There was a general consistency for both shanks in that they were longest for the F1 crosses, shortest for Line LAS, and intermediate for Lines HAS, HAR, and LAR. The single exception was for left shank of HAS females, which differed only from that of LAS females. For diameter of the shanks a different general pattern was noted among stocks with diameters being greater for Lines HAS and HAR, smaller for Lines LAR and LAS, with the crosses being intermediate but not different from lines HAR (left), LAR and LAS. When shank was expressed as the length by diameter, there was considerable overlapping of values across stocks. Face lengths were different among stocks with the order being LAS × HAS and HAR (left) > HAS × LAS > HAS, LAR, and LAS. Lines HAS and HAR had heavier first primary feathers than the other four stocks, which did not differ from each other. The ranking of stocks for feather length was HAR > HAS > F1 crosses > (LAS, LAR) with the exception that LAR (left) did not differ from the F1 crosses.

Bilateral Asymmetry

Except for cross LAS × HAS, which exhibited FA, stocks exhibited directional asymmetry for shank length, with the left shank being consistently longer than the right one (Table 2). For shank diameter, where left was generally less than right, there was anti-symmetry in Line HAS and both crosses, directional asymmetry for Lines HAR and LAS, and FA for Line LAR. For length by diameter of shank, the direction again was left generally less than right with FA for the crosses and Line LAR, directional asymmetry for Lines HAR and LAS, and anti-symmetry for Line HAS. For face length, there was FA for Stocks HAS, HAR, LAR and HAS × LAS whereas LAS and LAS × HAS exhibited anti-symmetry. Feather weight and feather
length exhibited anti-symmetry in all stocks. Neither logarithmic, square root, reciprocal, nor arc sine square root transformations resulted in normality for data that were anti-symmetric.

### Relative Asymmetry

The average RA for the five bilateral traits (Table 3) were highest for face length and least for shank and feather lengths (which did not differ). The average RA of 3.66 for shank diameter and 2.82 for feather weight differed from each other and the other traits.

Overall RA for the five bilateral traits are presented in Figure 1 by stock. There were no differences among the selected and relaxed lines. The RA of those four lines, however, were larger than those of the F1 crosses, which did not differ from each other. Although heterosis for each of the traits measured in this experiment was low (the highest was 10% for face length), the reduction in RA of the F1 crosses compared to their parental lines was considerable. Percentage reductions in RA were 38 for shank length, 64 for shank diameter, 31 for face length, 22 for feather weight, and 32 for feather length. For the overall RA, the reduction of the F1 crosses compared to the parental lines was 39%.

### Correlations

Neither bilateral traits nor their RA were correlated with BW at 28, 168, and 240 d of age or SRBC at 6 wk of age in any of the six stocks. Shank length and diameter were significantly correlated and ranged from 0.36 to 0.53 across stocks. The correlations of feather weights with lengths were significant and ranged from 0.74 to 0.96 across stocks.

### DISCUSSION

The selected lines used in this experiment had undergone long-term single trait selection for high or low antibody response to SRBC antigen. Correlated responses to this selection were heavier body weights for LAS than HAS chickens (Martin et al., 1990). Thus, it was not surprising that not only were there differences among the selected lines, relaxed lines, and crosses for growth allomorphic traits, but that there was evidence of heterosis.

Anti-symmetry occurs when asymmetry is normally present, but variable as to which side has greater development. It is distinguished by a platykurtic or bimodal distribution of L – R differences about a mean of zero. Directional asymmetry refers to greater development of a character on one side of the plane or planes of symmetry than the other side. Fluctuating asymmetry reflects small random deviations from symmetry in bilateral traits with a normal distribution of L ± R differences whose mean is zero. Any two or all three types of asymmetry may occur together for the same trait with fluctuating asymmetry thought to be ubiquitous (van Valen, 1962; Palmer and Strobeck, 1992).

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**TABLE 1. Mean ± SEM of traits at 150 d of age by genetic stock**

<table>
<thead>
<tr>
<th>Trait</th>
<th>HAS</th>
<th>HAR</th>
<th>LAR</th>
<th>LAS</th>
<th>HAS × LAS</th>
<th>LAS × HAS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shank, mm</td>
<td></td>
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<tr>
<td>Left</td>
<td>99.47 ± 0.38&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>98.04 ± 0.58&lt;sup&gt;b&lt;/sup&gt;</td>
<td>98.36 ± 0.48&lt;sup&gt;b&lt;/sup&gt;</td>
<td>96.25 ± 0.43&lt;sup&gt;a&lt;/sup&gt;</td>
<td>100.45 ± 0.34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>100.26 ± 0.34&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Right</td>
<td>98.62 ± 0.37&lt;sup&gt;b&lt;/sup&gt;</td>
<td>97.61 ± 0.57&lt;sup&gt;b&lt;/sup&gt;</td>
<td>98.86 ± 0.48&lt;sup&gt;b&lt;/sup&gt;</td>
<td>95.53 ± 0.44&lt;sup&gt;a&lt;/sup&gt;</td>
<td>100.13 ± 0.34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>100.23 ± 0.34&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diameter</td>
<td></td>
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<tr>
<td>Left</td>
<td>10.25 ± 0.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.10 ± 0.09&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>9.66 ± 0.14&lt;sup&gt;c&lt;/sup&gt;</td>
<td>9.72 ± 0.07&lt;sup&gt;c&lt;/sup&gt;</td>
<td>9.78 ± 0.07&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>9.90 ± 0.06&lt;sup&gt;bc&lt;/sup&gt;</td>
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<tr>
<td>Right</td>
<td>10.44 ± 0.11&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.46 ± 0.11&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.70 ± 0.14&lt;sup&gt;c&lt;/sup&gt;</td>
<td>10.03 ± 0.09&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>9.82 ± 0.06&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>9.84 ± 0.06&lt;sup&gt;bc&lt;/sup&gt;</td>
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<tr>
<td>Length × diameter</td>
<td></td>
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<tr>
<td>Left</td>
<td>1.021 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.991 ± 1.3&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.961 ± 1.6&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.936 ± 1.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.983 ± 0.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.993 ± 0.8&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td>Right</td>
<td>1.030 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.021 ± 1.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.956 ± 1.7&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.956 ± 1.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.983 ± 0.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.987 ± 0.8&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td>Face length, mm</td>
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<tr>
<td>Left</td>
<td>21.54 ± 0.26&lt;sup&gt;c&lt;/sup&gt;</td>
<td>23.57 ± 0.19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>20.87 ± 0.30&lt;sup&gt;c&lt;/sup&gt;</td>
<td>21.15 ± 0.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>22.81 ± 0.20&lt;sup&gt;b&lt;/sup&gt;</td>
<td>23.74 ± 0.17&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Right</td>
<td>21.87 ± 0.23&lt;sup&gt;c&lt;/sup&gt;</td>
<td>23.65 ± 0.20&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>20.26 ± 0.25&lt;sup&gt;d&lt;/sup&gt;</td>
<td>20.66 ± 0.22&lt;sup&gt;d&lt;/sup&gt;</td>
<td>23.11 ± 0.15&lt;sup&gt;b&lt;/sup&gt;</td>
<td>24.06 ± 0.14&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>First primary wing feather weight, g</td>
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<tr>
<td>Left</td>
<td>0.326 ± 0.006&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.325 ± 0.006&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.269 ± 0.003&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.266 ± 0.004&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.278 ± 0.005&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.278 ± 0.005&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td>Right</td>
<td>0.323 ± 0.006&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.325 ± 0.007&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.267 ± 0.003&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.267 ± 0.005&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.275 ± 0.005&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.276 ± 0.005&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td>Length, cm</td>
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<tr>
<td>Left</td>
<td>19.37 ± 0.11&lt;sup&gt;b&lt;/sup&gt;</td>
<td>19.77 ± 0.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>18.08 ± 0.08&lt;sup&gt;c&lt;/sup&gt;</td>
<td>17.85 ± 0.10&lt;sup&gt;d&lt;/sup&gt;</td>
<td>18.37 ± 0.09&lt;sup&gt;c&lt;/sup&gt;</td>
<td>18.36 ± 0.10&lt;sup&gt;c&lt;/sup&gt;</td>
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<tr>
<td>Right</td>
<td>19.30 ± 0.11&lt;sup&gt;b&lt;/sup&gt;</td>
<td>19.70 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>18.08 ± 0.08&lt;sup&gt;d&lt;/sup&gt;</td>
<td>17.87 ± 0.09&lt;sup&gt;d&lt;/sup&gt;</td>
<td>18.41 ± 0.09&lt;sup&gt;c&lt;/sup&gt;</td>
<td>18.40 ± 0.10&lt;sup&gt;c&lt;/sup&gt;</td>
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</tbody>
</table>

<sup>a,b</sup>Means in a row with no common superscript differ significantly (P ≤ 0.05).

<sup>1</sup>HAS = selected 23 generations for high antibody response to SRBC; LAS = selected 23 generations for low antibody response to SRBC; HAR and LAR = sublines of HAS and LAS, respectively, where selection was relaxed for 8 generations; HAS×LAS and LAS×HAS = F1 generation with sire line given first and dam line second.

<sup>2</sup>Distance between junction of upper and lower mandibles and auditory canal.
Results obtained in this experiment were consistent with those for data from several species showing that not all bilateral asymmetries are FA, i.e., normal distribution with mean zero (Summer and Huestis, 1921; Thoday, 1958; Lacy and Horner, 1996; Palmer, 1996). Also, our results showed that even for the same trait there were different distributions among genetic stocks.

It has been proposed that RA of morphological traits could provide a reliable indicator of genetic stress (Palmer and Strobeck, 1986; Leary and Allendorf, 1989). Our results are consistent with this thesis. The degree of RA varied among bilateral traits being greatest for face length, intermediate for shank diameter and weight of the first primary wing feather, and least for shank length and feather length. This variation in RA among traits suggests the value of an overall RA as a measure of developmental stability. Overall RAs of the five bilateral traits showed that the F1 crosses had better developmental stability than their parental lines and the lines in which selection was relaxed. That is, there was less developmental error, which may reflect superior buffering against genetic and environmental stressors. Genetic changes made by individual phenotypic selection for a specific trait are primarily due to additive gene effects. That the relaxed lines exhibited RA similar to those of the selected lines is consistent with their not regressing.

**FIGURE 1.** Mean of relative bilateral asymmetries for five traits measured at 150 d of age [length and diameter of shank, distance between junction of upper and lower mandibles and auditory canal (face length), and weight and length of first primary wing feather] by genetic stock. HAS = selected 23 generations for high antibody response to SRBC; LAS = selected 23 generations for low antibody response to SRBC; HAR and LAR = sublines of HAS and LAS, respectively, where selection was relaxed for 8 generations; HAS × LAS and LAS × HAS = F1 generation with sire line given first and dam line second. Columns with the same letter are not different ($P \leq 0.05$).
TABLE 3. Mean relative asymmetry of each bilateral trait at 150 d of age by genetic stock and when averaged across all stocks

<table>
<thead>
<tr>
<th>Trait</th>
<th>HAS</th>
<th>HAR</th>
<th>LAR</th>
<th>LAS</th>
<th>HAS × LAS</th>
<th>LAS × HAS</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shank, mm</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Length</td>
<td>1.13</td>
<td>0.76</td>
<td>1.16</td>
<td>1.17</td>
<td>0.80</td>
<td>0.63</td>
<td>0.93d</td>
</tr>
<tr>
<td>Diameter</td>
<td>3.71</td>
<td>4.93</td>
<td>3.04</td>
<td>4.94</td>
<td>2.79</td>
<td>0.30</td>
<td>3.66d</td>
</tr>
<tr>
<td>Face length, mm</td>
<td>7.31</td>
<td>4.75</td>
<td>9.06</td>
<td>7.47</td>
<td>5.41</td>
<td>4.81</td>
<td>6.35a</td>
</tr>
<tr>
<td>First primary wing feather</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight, g</td>
<td>3.51</td>
<td>4.61</td>
<td>1.80</td>
<td>2.56</td>
<td>2.54</td>
<td>2.22</td>
<td>2.82c</td>
</tr>
<tr>
<td>Length, cm</td>
<td>1.35</td>
<td>1.27</td>
<td>0.55</td>
<td>1.23</td>
<td>1.23</td>
<td>0.65</td>
<td>0.70</td>
</tr>
</tbody>
</table>

a-dMeans with no common superscript differ significantly ($P \leq 0.05$).

1$| (L - R)/[(L + R)/2] | \times 100.$

HAS = selected 23 generations for high antibody response to SRBC; LAS = selected 23 generations for low antibody response to SRBC; HAR and LAR = sublines of HAS and LAS, respectively, where selection was relaxed for 8 generations; HAS × LAS and LAS × HAS = F1 generation with sire line given first and dam line second.

3Distance (millimeters) between junction of upper and lower mandibles and auditory canal.

ACKNOWLEDGMENTS

The authors are thankful to S. Price for assistance in data collection and S. I. Jackson for help in preparation of the manuscript.

REFERENCES


