

A DOUBLE SELECTION EXPERIMENT FOR BODY WEIGHT AND BREAST ANGLE AT EIGHT WEEKS OF AGE IN CHICKENS¹

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Received April 25, 1962

A CORRELATED response denotes the associated change of an unselected trait when artificial selection is made for a particular characteristic. The theory of correlated response has been discussed by LERNER (1950) and more recently by FALCONER (1960). These authors along with HAZEL (1943) and HAZEL, BAKER and REINMILLER (1943) have shown how the genetic correlation coefficient measures the genetic association between two traits, and the application of it as a predictor in selection indexes. In addition, these authors have provided outlines of the computational procedures necessary for obtaining estimates of the genetic correlation coefficient. ROBERTSON (1959) and VAN VLECK and HENDERSON (1961) have shown that the estimates obtained by these procedures usually have large sampling variances.

REEVE and ROBERTSON (1953) and CLAYTON, KNIGHT, MORRIS and ROBERTSON (1957) have utilized *Drosophila* populations in experiments to determine whether correlated responses occur in that species. Only FALCONER (1954), however, who worked with body size and tail length in mice, has published data on the reliability of the genetic correlation coefficient as a measure of correlated responses in higher organisms.

When two traits are genetically correlated, a change in the mean genotypic value of one is accompanied by changes in the other. The change in the average value of the genotype for the selected trait (G) should result in an average change in the genotype for the unselected trait (G'). The change in G' should be proportional to the genetic correlation between the traits and the ratio of the square roots of the genetic variance of the selected and unselected traits. Thus provided the two traits were equally variable and equally heritable symmetrical responses, in terms of a common measurement, to selection could be expected in the trait not under direct selection if selection was for trait A in one population and trait W in the other. Reported here are results of a double selection experiment which provided a comparison of the genetic correlations obtained between body weight and breast angle at eight weeks of age in White Plymouth Rock chickens.

¹ This investigation was conducted as a portion of the cooperative research under the Southern Regional Poultry Breeding Project S-41.

MATERIALS AND METHODS

The foundation stock for the selected lines utilized in the experiment was composed of a heterogeneous gene pool obtained by crossing seven inbred lines of White Plymouth Rocks which had been developed at the Virginia Agricultural Experiment Station. At hatching, chicks from the foundation population were assigned to two subpopulations, angle (A) and weight (W). To make the subpopulations as similar as possible, initially a full sib of each chick in the A group was assigned to the W group. Thereafter the two subpopulations were maintained separately.

Within the A subpopulation, two-way selection was practiced for broad and narrow breast angles at eight weeks of age while in the W subpopulation the two-way selection was for body weights at eight weeks of age. Details of the selection procedures within in each pair of lines, the response to each generation of selection, and general management procedures have been reported elsewhere (SIEGEL 1962a, b).

At eight weeks of age both breast angles and body weights were determined for all chickens. Hence, in the A subpopulation the selected trait was either broad or narrow breast angles with body weight being the unselected characteristic while in the W subpopulation the selected trait was either high or low body weight and the unselected characteristic was breast angle. Within a generation chicks from all lines were hatched on the same dates and reared in pens within the same building.

Analyses were conducted within subpopulations for each sex separately, thus allowing one sex to serve as a replicate for the other. For one sex to serve as an adequate replicate for the other the assumption was made that sex-line interactions were unimportant. To test this assumption analyses of variances were computed within each subpopulation in the F_4 generation. The summary of these analyses which are presented in Table 1 show that the sex-line interaction was not significant in three analyses and barely significant in the fourth. Thus, the assumption appeared to be valid.

The response of the selected and unselected traits was measured by the divergence between the upward and downward pair of lines. The realized heritability of the selected characteristic was determined by the cumulative effect of selection as outlined by DICKERSON and GRIMES (1947).

TABLE 1
Summary of analyses of variance to test for sex-line interactions

Source of variation	W subpopulation			A subpopulation		
	df	Weight	Angle	df	Weight	Angle
Between sexes	1	6,428,990**	1,444**	1	5,245,211**	810**
Between lines	1	23,164,242**	6,192**	1	1,676,428**	6,942**
Sex-line	1	30,394	2	1	40,826*	34
Error	718	11,179	14	638	9,234	10

** $P \leq .01$.

* $P \leq .05$.

Genetic, phenotypic and environmental correlations between the selected and unselected traits were computed according to the procedures outlined by FALCONER (1954). Three formulas were used:

$$(1) \text{ Genetic correlation } (r_{GG'}) = \frac{\Delta G' h \sigma p}{\Delta G h' \sigma p'}$$

where ΔG and $\Delta G'$ represent the genetic change in the selected and unselected traits, respectively; h and h' the square roots of the heritabilities of the selected and unselected traits, respectively; and σp and $\sigma p'$, the phenotypic standard deviations of the selected and unselected traits, respectively.

(2) Phenotypic correlation ($r_{PP'}$) = $hh'r_{GG'} + ee'r_{EE'}$, where, $e = \sqrt{1-h^2}$ and $e' = \sqrt{1-h'^2}$.

$$(3) \text{ Environmental correlation } (r_{EE'}) = \frac{r_{PP'} - hh'r_{GG'}}{ee'}$$

The analysis of data within each subpopulation according to these formulas provided independent estimates of the genetic, phenotypic and environmental correlations between the two characteristics.

The relative efficiency of indirect selection through direct selection for a correlated trait was measured by the ratio $\Delta G'/\Delta G$. Since a double selection experiment was conducted, pooled estimates of the genetic correlation between body weight and breast angle were also obtained from the square root of the product of the two estimates of relative efficiency of indirect selection.

RESULTS AND DISCUSSION

The responses of the selected and unselected characteristics, by sexes, within each pair of lines are presented in Figures 1 and 2. Males and females responded consistently within each pair of lines, whereas between pairs of lines the response was not symmetrical. Selection for body weight apparently resulted in greater changes in breast angle than selection for breast angle did for body weight. The differences in breast angle between lines declined within each subpopulation in the F_4 generation. This was probably caused by an environmental effect as it occurred both in the lines where breast angle was the selected trait and in those where it was the correlated characteristic.

Parameters in the F_4 generation for each pair of divergently selected lines are presented in Table 2. Parameters for the prior generations may be found in two other publications (SIEGEL 1962a, b). The relative efficiency of indirect selection for one trait through primary selection for an associated trait was calculated from the response data in Table 2. The relative efficiency for changing breast angles through selection for body weight as compared to direct selection for breast angle was 71 percent in males where $\Delta G' = 5.04$ and $\Delta G = 7.06$. For females it was 94 percent. Contrariwise, the percentage efficiency for changing body weight through selection for breast angle as compared to direct selection for breast angle was 33 for males and 29 for females. The asymmetrical response could be due to unequal heritabilities, unequal variances or a combination of the two. This should not influence the prediction of the expected change in the un-

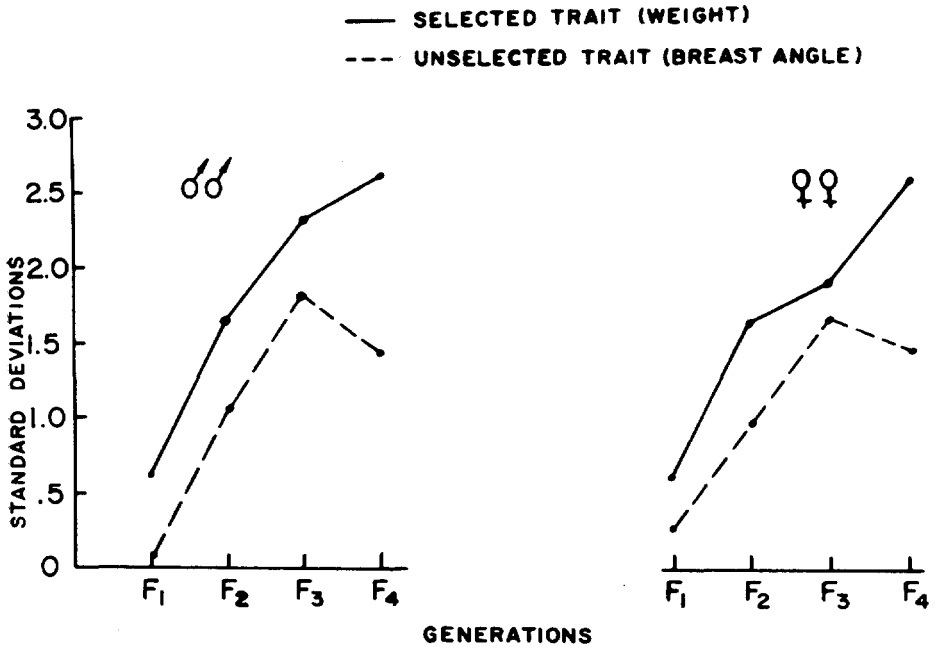


FIGURE 1.—Differences in standard deviations between lines selected for body weight at eight weeks of age.

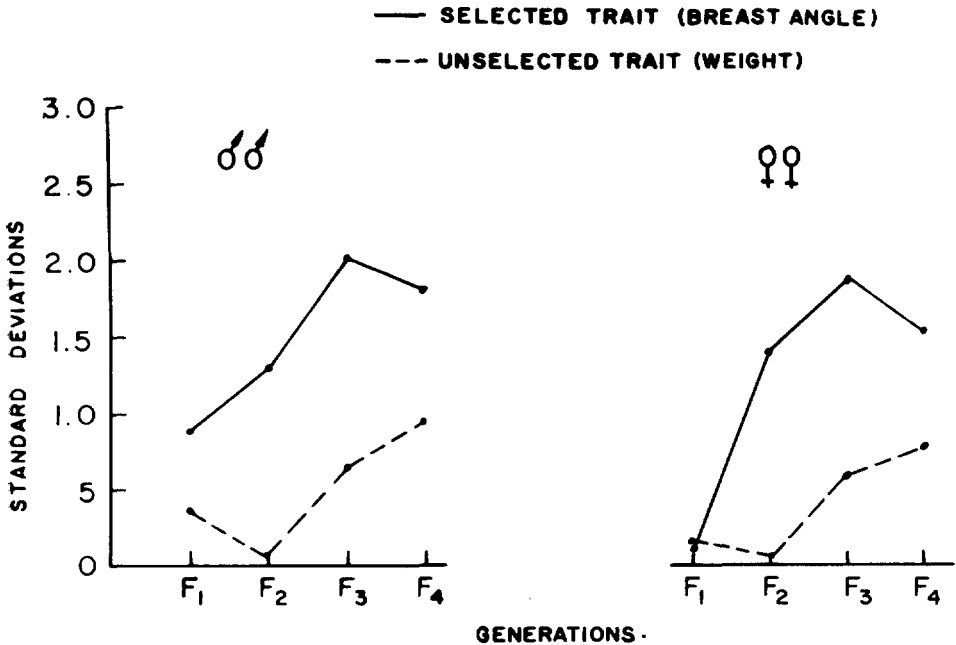


FIGURE 2.—Differences in standard deviation between lines selected for breast angle at eight weeks of age.

TABLE 2

Observed and calculated parameters, by sexes, from the divergence in the two pairs of selected lines*

Parameter	Lines selected for			
	Body weight (W)		Breast angle (A)	
	M	F	M	F
Response (ΔG_W)	320.32±10.64	294.00±11.68	118.93±10.48	85.52±11.06
Response (ΔG_A)	5.04± 0.35	5.81± 0.47	7.06± 0.33	6.13± 0.38
Selection diff. (W)	1040.77	1036.10
Selection diff. (A)	29.17	28.95
h^2_W	0.31	0.28
h^2_A	0.24	0.21
$\sigma_p(W)$	103.26± 5.28	106.18± 5.73	94.39± 5.22	97.84± 5.51
$\sigma_p(A)$	3.36± 0.17	4.24± 0.23	2.95± 0.16	3.38± 0.19
$r_{PP'}\dagger$	0.70± 0.05 ^a	0.75± 0.05 ^a	0.58± 0.05 ^b	0.60± 0.05 ^b
$r_{GG'}$	0.54	0.57	0.48	0.42
$r_{EE'}$	0.76	0.80	0.62	0.66

* Measurements were obtained in grams for body weight and in degrees for breast angle. Standard errors are given where known.

† Phenotypic correlations with different superscripts were heterogeneous.

selected trait when genetic variances and covariances are known. The expected change in the unselected trait ($\Delta G'$), assuming additive gene action and a constant genetic correlation, may be obtained from the formula:

$$(1a) \Delta G' = \Delta G \frac{h' \sigma_p'}{h \sigma_p} r_{GG'}$$

The realized heritability of each trait given in Table 2, was computed only in the subpopulation where that particular trait was under selection. The realized heritability of eight-week body weight for the weight pair of lines was .31 for males and .28 for females. The respective values for breast angle in the angle pair of lines were .24 and .21. Thus, the heritability of body weight was somewhat greater than that of breast angle.

Phenotypic standard deviations of both characteristics in each subpopulation indicate that these values were similar for each trait in both sexes within a pair of lines. Variances for body weight were homogeneous across lines and sexes. For breast angle, however, they were heterogeneous indicating that some unknown difference did exist for this parameter. This was somewhat surprising because an effort was made to have the two subpopulations as similar as possible initially and to utilize concurrent experimental procedures whenever possible.

Phenotypic correlations between selected and unselected traits were homogeneous for males and females within each pair of lines (Table 2). Between pairs of lines, however, phenotypic correlations were heterogeneous indicating again that differences existed between the two subpopulations. Since phenotypic correlations are influenced by the magnitude and signs of the genetic and environmental correlations it was of interest to compare these values with each other and to make comparisons of each within and between subpopulations.

Genetic correlations between eight-week body weight and breast angle were consistently lower than the environmental correlations. LERNER, ASMUNDSON and CRUDEN (1947) and SIEGEL and ESSARY (1959) also found that the genetic correlation between these traits was lower than the environmental correlation. The positive environmental correlation indicated that environmental influences on either trait had a similar effect on the other. Pooled estimates of the genetic correlation across subpopulations were .51 for males and .53 for females. This indicated that the genetic influences on one characteristic had a positive effect on the other. These values while denoting the gross genetic relationship between the traits masked the genetic association within each pair of lines.

As shown in Table 2 genetic correlations were similar for males and females within each subpopulation. Values for the weight subpopulation, however were greater than those for the angle subpopulation. This demonstrated further that the change in breast angle was greater when selection was for body weight than the change in body weight when selection was for breast angle.

It might appear from these data that the genetic correlation between two traits would not be a good predictor of the response of an unselected trait to direct selection for a correlated trait. This is not so, particularly when the relative magnitude of the realized heritabilities of the two characteristics are considered. In this experiment the realized heritability of body weight was approximately one third larger than the respective value for breast angle. This difference may be considered real since the standard errors of the realized heritabilities calculated each generation were .02 for body weight and .03 for breast angle. The difference in heritabilities of these two traits indicated that the number of additive genes which influence body weight were considerably less than those which influence breast angle. If the same number of pleiotropic genes influenced both traits equally, then selection for body weight should cause relatively a greater correlated change in breast angle than selection for breast angle would in body weight. Thus, breeders in the application of genetic correlations as predictors of changes due to selection should give adequate consideration to the magnitude of the heritabilities of each characteristic.

SUMMARY

An experiment was conducted which provided a comparison of the genetic correlation between body weight and breast angle at eight weeks of age. Selection in divergent directions was made for eight-week body weight in one pair of lines and eight-week breast angle in another pair of lines. Both pairs of lines were derived from the same gene pool and the response of each trait was measured in all lines. The response of the unselected characteristics were not similar in the two pairs of lines. These differences were probably due to differences in the heritability of the two traits under investigation. Evidence is presented which demonstrates the reliability of the theory on which the formulas for the estimation of genetic correlations are based.

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