CORRELATED RESPONSES AND SEXUAL DIMORPHISM IN BIDIRECTIONAL SELECTION EXPERIMENTS

by

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Thesis submitted to the Graduate Faculty of the
Virginia Polytechnic Institute
in partial fulfillment for the degree of

DOCTOR OF PHILOSOPHY

in

Genetics

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February, 1968

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GLOSSARY OF SYMBOLS

$\sigma^2_{G_1}$ - Genetic variance of males.

$\sigma^2_{G_2}$ - Genetic variance of females.

$\sigma_{G_{12}}$ - Genetic covariance of males and females.

$\sigma^2_{P_1}$ - Phenotypic variance of males.

$\sigma^2_{P_2}$ - Phenotypic variance of females.

$\sigma_{P_{12}}$ - Phenotypic covariances of males and females.

σ_{P_x} - Phenotypic standard deviation of selected trait.

σ_{P_y} - Phenotypic standard deviation of unselected trait.

σ^2_B - Variance between lines.

σ^2_S - Variance between sires.

σ^2_W - Variance within lines or sires.

$b_{P_{yx}}$ - Phenotypic regression of unselected on selected trait.

$b_{G_{yx}}$ - Genotypic regression of unselected on selected trait.

$b_{E_{yx}}$ - Environmental regression of unselected on selected trait.

$r_{P_{yx}}$ - Phenotypic correlation of unselected and selected trait.

$r_{G_{yx}}$ - Genetic correlation of unselected and selected trait.

$r_{E_{yx}}$ - Environmental correlation of unselected and selected trait.

h^2_x - Heritability of selected trait.

h^2_y - Heritability of unselected trait.

h_x - Square root of h^2_x.

h_y - Square root of h^2_y.

x - Selected trait.

y - Unselected trait.

ΔG_1 - Genetic change in trait 1.

$\hat{P}$ - Mean of selected parents.

$\bar{P}$ - Population mean.

ix - Selection differential of selected trait.

iY_x - Expected secondary selection differential of unselected trait.

ΔY_x - Change in unselected trait y when selecting for trait x.

e_x - Square root of $1 - h^2_x$.

e_y - Square root of $1 - h^2_y$.

HW - High weight line.

LW - Low weight line.

BA - Broad breast angle line.

NA - Narrow breast angle line.

k - Average number of full sib families per sire.

MCP - Mean cross product.

n - Number of individuals per line.

$\bar{x}_{BA}$ - Mean of BA line.

$\bar{x}_{NA}$ - Mean of NA line.

$\bar{x}_{HW}$ - Mean of HW line.

$\bar{x}_{LW}$ - Mean of LW line.

MS_B - Mean square between lines.

MS_W - Mean square within lines.

MS_{LS} - Mean square of line-sex interaction.

MS_S - Mean square between sires.

ACKNOWLEDGEMENTS

The author expresses his sincere gratitude and thanks to Dr. Paul B. Siegel, Poultry Geneticist and major advisor for his guidance, suggestions, and consideration during the course of this dissertation project.

Appreciation is extended to Dr. C. E. Howes, Head, Department of Poultry Science, for his advice and making available finiancial and material facilities fot this study. Gratitude is also expressed to those students who preceded me and were involved in the early generations of these selection experiments. Special thanks are also extended to Dr. J. A. Gaines, Department of Animal Science; Dr. K. H. Hinkelmann, Department of Statistics; and Dr. D. A. West, Department of Biology for their aid and assistance in reviewing this dissertation.

Special thanks are also extended to my wife, Patti, for her never tiring moral support and encouragement throughout the course of this study.

INTRODUCTION

The change in population means produced by selection is of considerable interest to students of quantitative genetics. These changes or responses are dependent on the selection differential and the heritability of the trait. Each gene probably influences more than one trait. Hence changes in unselected traits are also of considerable interest.

Numerous single trait selection experiments have been conducted to measure changes in populations over time. The designs of such experiments with higher organisms have frequently failed to have either adequate controls or replication, both of which are costly but necessary for valid estimation of parameters. The fowl is unique because of the low individual cost and the fact that it is an economic species. These facts have allowed modern breeding procedures to be used in the development of the commercial poultry industry.

The difference in nutritional requirements of males and females suggests the desirability of rearing the sexes separately. Sexual dimorphism of body weight in chickens also changes with selection and causes a greater response in males. Selection for traits in commercial broilers has resulted in changes in other traits. Frequently these changes have been greater than expected. Specific experiments are necessary to investigate these changes.

This dissertation is concerned with two studies,

(1) correlated responses and (2) sexual dimorphism. The desire was to provide basic information in these areas which could explain the phenomena suggested by field observations. The results involved should be of value to other investigators in the field of quantitative genetics and also provide practical application to those in commercial breeding organizations.

REVIEW OF LITERATURE

Heritability

Numerous procedures are available for the calculation of the heritability (h^2) of a quantitative trait. One of the most basic and reliable procedures is the division of the difference between the means of divergently selected lines by the cumulative selection differential. This method was developed by Student (1934) for the calculation of the heritability of the oil content in Winter's corn experiment.

Heritability may be defined in the broad sense as the ratio of total genetic variance to the total phenotypic variance and in the narrow sense as the ratio of additive genetic variance to the total phenotypic variance. Procedures for estimation and the genetic effects included in the estimates have been presented in several texts (eg. Lerner, 1950 and 1958; Lush, 1948; and Falconer, 1960).

Computational Procedures:

Methods commonly used in experiments with poultry will be discussed briefly. Perhaps the most popular, but least reliable, are those based on full and half sib intraclass correlations. The nested statistical model for such an analysis is:

$$Y_{ijk} = u + s_i + d_{ij} + e_{ijk}$$

where, Y_{ijk} is the measurement of the kth progeny of the jth dam mated to the ith sire. Heritability estimates are obtained from the variance components by the following formulas:

$$h^2 = 2(S + D)/(S + D + E),$$

$$h^2 = 4S/(S + D + E),$$

$$h^2 = 4D/(S + D + E)$$

where, S is the among sire variance component, D the among dam within sire component, and E the variance within full sib families. The coefficients 2, 4, and 4 are used in the numerator because the sire (S) and dam (D) components each contain one-fourth of the additive genetic variance.

Falconer (1953) has discussed perhaps the most reliable method for measuring additive genetic effects. It consists of the regression of response on the cumulative selection differential in single trait selection experiments and is essentially the regression of breeding value on phenotypic value (Falconer 1960). Several other methods such as the regression of offspring on mid-parent and the intra sire regression of offspring on dam are adequate in certain situations.

Body Weight:

Body weight is a complex trait influenced by many physiological systems. Asmundson and Lerner (1933) showed that the body weight of chickens was influenced by multiple genetic factors. Siegel (1962a) obtained a mean of .41 from a summary of 176 published heritability estimates for juvenile body weight. Realized heritabilities of body weight at eight weeks of age after four generations of selection were .31 and .28 for males and females, respectively (Siegel, 1962a). Realized heritabilities after ten generations of selection for juvenile weight were .34 in the upward direction, .07 in the downward direction, and .22 for the divergence of the lines (Maloney *et al.*, 1963). After 15 generations of selection the heritabilities for the divergence between the high and low weight lines were .35 and .27 for males and females, respectively (Maloney *et al.*, 1967). Heritability estimates of juvenile body weight summarized by Kinney and Shoffner (1965) were .54, .53, .46, and .54 from the 4S/(S + D + E), 4D/(S + D + E), 2(S + D)/(S + D + E), and intra sire regression of offspring on dam methods, respectively.

The above demonstrates the large number of published heritabilities of juvenile body weight of chickens. From this literature it may be inferred that juvenile body weight has a moderate to high heritability and that the heritability is somewhat greater for males than for females.

Breast Angle:

Heritability estimates of breast angle at 12 weeks of age were obtained in New Hampshires by Lerner *et al.* (1947).

Estimates from paternal, maternal, and full sib correlations .13, .29, and .21, respectively. An estimate of .46 for breast angle at ten weeks of age was reported by Brunson _et al._ (1956) while Godfrey and Goodman (1956) obtained values for nine-week breast angle of .4 in Silver Oklabars and .5 in New Hampshires. A mean heritability estimate of .4 for breast angle in eight-week old White Rocks was computed by Siegel and Essary (1959). Siegel (1962b) obtained heritability estimates for this trait from several computational methods. Estimates were .31, .23, .37, .26, and .32 for realized, intra-sire regression of offspring on dam, maternal half sib correlation, paternal half sib correlations, and full sib correlations, respectively. It appears from this review that juvenile breast angle is moderately heritable with values somewhat less than those for body weight.

Selection Differentials:

A review of selection differentials is pertinent because they are the limiting aspect in obtaining realized heritabilities of unselected traits in single trait selection experiments. Harvey and Bearden (1962) presented procedures for the calculation of expected changes in the unselected trait when direct selection was practiced for another trait. Flower _et al._ (1964) indicated that to predict genetic changes for any trait required simultaneous consideration of all traits under either direct or indirect selection. If genotype-sex interactions are important, then consideration must be given to them in addition to those conditions cited by Flower et al. (1964).

Magee (1965) showed that the expected genetic change of a trait (when more than one trait was under selection) was not equal to the heritability times the selection differential. He stated that when selection was practiced for two traits (1 and 2) the genetic change in trait 1 was equal to:

$$\Delta G_1 = (b_1 \; \sigma^2_{G_1} + b_2 \; \sigma_{G_1G_2})(\hat{P} - \bar{P})/(b_1 \; \sigma^2_{P_1} + b_2 \; \sigma_{P_1P_2} \qquad (1)$$

where,

ΔG_1 = genetic change in trait 1,

$\sigma^2_{G_1}$ = genetic variance of trait 1,

$\sigma_{G_1G_2}$ = genetic covariance between trait 1 and 2,

$\sigma^2_{P_1}$ = phenotypic variance of trait 1,

$\sigma_{P_1P_2}$ = phenotypic covariance between trait 1 and 2,

$\hat{P}$ = mean of selected parents, and

$\bar{P}$ = mean of population in which parents were born.

The b_i values were obtained from the selection index,

$$I = b_1P_1 + b_2P_2 \; .$$

Ideta and Siegel (1966) termed the selection differential of unselected trait as the expected secondary selection differential. They showed that the term was equal to the selection differential of the selected trait times the phenotypic regression of the unselected trait on the selected trait. The formula was represented symbolically as:

$$iY_x = ix \; b_{P_{yx}} \qquad (2)$$

where,

iY_x = expected secondary selection differential of the unselected trait

ix = selection differential of selected trait, and

$b_{P_{yx}}$ = phenotypic regression of unselected on selected trait

Ideta and Siegel (1966) used this procedure to calculate realized heritabilities of the following unselected traits: body weight at 24 and 38 weeks of age, egg weight, age at first egg, and hen-day percentage egg production. They did not, however, have data to fully ascertain the reliability of their procedure. Since this dissertation is partially concerned with a double bidirectional selection experiment it may enable further evaluation of the reliability of obtaining realized heritabilities of unselected traits.

Correlations

The correlation between two traits can result from a conbination of genetic causes, environmental influences, and an interaction of the two. The genetic causes may be due to the transient effects of linkage and the permanent effects of pleiotrophy. The theory of genetic correlations and methods of calculation have been discussed by Hazel (1943), Lerner (1950), and Falconer (1960). The aspects covered in those publications will not be reviewed here.

Several underlying mechanisms that could cause genetic correlations were discussed by Rendel (1963). He suggested that common resources could develop two correlated characters and that a portion of the resource would be contributed to each character. He also demonstrated how the sign of the genetic correlation changed in a selection experiment for scutellar and abdominal bristle in _D. melanogaster_. Robertson (1959) and VanVleck and Henderson (1961) discussed problems involved in sampling when basing genetic correlations on full and half sib variances and covariances. Robertson (1959) developed a procedure based on an analysis of variance and making use of the genotype-sex interaction for estimation of the genetic correlation between males and females for a given trait.

Body Weight and Breast Angle:

Lerner _et al._ (1947) studied the relationship between breast width and body weight at twelve weeks of age from full-sib variances and covariances. Genetic, environmental, and phenotypic correlations were .10, .16, and .13, respectively. Collins et al. (1950) found that breast width tended to increase with body weight and Siegel (1962c) obtained realized genetic correlations of .51 for males and .53 for females between body weight and breast angle at eight weeks of age.

Selection and Correlated Responses

Most selection experiments are conducted to change the mean values of a population for specific quantitative traits. As the mean value of a population is changed it is often difficult to separate the genetic gain from environmental influences. Recently the need for control populations to help detect the amount of environmental influence has been realized and steps have been taken to utilize them in selection experiments.

Randombred controls have been recommended for use in poultry by King et al. (1959) and Gowe et al. (1959). Bray et al. (1962) studied 15 methods of maintaining control populations in Tribolium for eight generations and considered the effects of genotype-environment interactions. They concluded that the selected stock should originate from the control populations so that they would respond similary when exposed to environmental variations.

The most efficient method for obtaining estimates of additive genetic variance free of environmental bias was given by Student (1934). His biometrical procedure showed that differences between the means of bidirectionally selected lines divided by the cumulative selection differential was equal to the heritability of a trait. This allowed one line to serve as a control of the other. Although this does provide a good method for obtaining the amount of additive genetic variance, it does not allow an estimate of response in one direction independent of the other. Since asymmetry may introduce a bias in two-way selection experiments, it is necessary to use a reliable control in conjunction with bidirectional selection experiments.

Falconer (1953) discussed possible causes of asymmetry in selection experiments. When asymmetry exists predicted responses could be overestimated in one direction and underestimated in the other direction. Falconer suggested that the primary causes of asymmetry were unequal initial gene frequencies and directional dominance. Other causes could be scale effects and inbreeding.

Consideration may be given to correlated responses of unselected traits in selection experiments. Reeve and Robertson (1953) and Falconer (1954) utilized an approach that gave valid estimates of genetic correlations from double two-way selection experiments between selected and correlated traits. Drosophila and mice were used in these studies. Their procedure requires that trait 1 be selected in both a positive and negative direction in one pair of lines and that trait 2 be selected in a similar manner in a second pair of lines. The response of both traits must be measured in each pair of lines. The formula for measuring the genetic correlation is:

$$r_{G_{xy}} = \Delta Y_x \; h_x \; \sigma_{P_x} / \Delta x \; h_y \; \sigma_{P_y} \tag{3}$$

where

$r_{G_{xy}}$ = genetic correlation between selected and correlated trait,

Δx = genetic change in selected trait,

ΔY_x = genetic change in correlated trait,

σ_{P_x} = phenotypic standard deviation of selected trait,

σ_{P_y} = phenotypic standard deviation of correlated trait,

h_x = square root of selected trait heritability, and

h_y = square root of correlated trait heritability.

The formula may be rewritten to predict the response of correlated traits, when the genetic correlation between the selected and correlated trait is known. That formula is:

$$\Delta Y_x = r_G \; \Delta x \; h_y \; \sigma_{P_y} / h_x \; \sigma_{P_x} \tag{4}$$

Although double two-way selection experiments are highly desirable for measuring certain genetic parameters few have been conducted because they are costly and time consuming. Siegel (1962b) conducted such an experiment with selection for body weight and breast angle at eight weeks of age. Realized genetic correlations between the two traits suggested a directionality of the correlation. Reasons for such asymmetry have been given by Siegel (1962b) and Bohren et al. (1966). Nordskog and Festing (1962) conducted a two-way bidirectional selected experiment for body weight and egg weight in Fayoumi and Leghorn fowl. They observed a discrepency in the ratio of correlated response to the direct response of the traits and also suspected directionality of the genetic correlation.

Sexual Dimorphism

Males are usually larger than females in most species of birds. There are, however, exceptions where the sexes are of comparable size and where females are larger than males (Darwin, 1895; Amadon, 1959; Mayr, 1963). Asmundson (1948) showed that sexual dimorphism accounted for 60 percent of the variation in body weight of turkeys. Shaklee et al. (1952) reported that in turkeys, males showed a greater response to selection for body weight than females.

A significant strain-sex interaction for body weight in meat type chickens was reported by Horton and McBride (1964). Heritability estimates of body weight at four and eight weeks of age and gain (4-8 weeks) were higher in males than in females. They suggested that in artificial selection of meat type chickens for body weight, where selection is more intense in males, sexual dimorphism would tend to increase. Becker et al. (1964) reported genetic correlations between sexes of .80 for eight-week body weight in Leghorns, .91 for 24-week body weight of Broad Breasted turkeys, and 1.00 for 4-week body weight of Coturnix. Eisen and Legates (1966) estimated the heritability of sex dimorphism of body weight in mice at 3, 6, and 8 weeks of age. Estimates were .01, .08, and .14, respectively. Yoshida and Collins (1967) reported a genetic correlation coefficient of .90 between male and female body weight at four weeks of age in Coturnix. They also obtained a heritability estimate of .09 for sexual dimorphism of weight at this age from the method of Eisen and Legates (1966).

Korkman (1957) reported on the only apparent artificial selection for sexual dimorphism in mammals. Selection was for a smaller and larger sex difference for body weight in two lines of mice at 90 days of age. In one line in which the males were selected upward and the females selected downward the ratio of males to female body weight changed from 1.18 to 1.23. In a second line in which the sexes were selected in the reverse directions the ratios changed from 1.22 to 1.17 in ten generations.

The above suggests that there is variability in sex dimorphism for body weight and in some species this relationship can be changed through artificial selection. Additional evidence, however, is necessary and hypotheses are needed on the mechanisms involved in the inheritance of sexual dimorphism for body weight.

EXPERIMENT I: CORRELATED RESPONSES

Materials and Methods

Stocks:

The data for this experiment were obtained from four generations of a double bidirectional selection experiment for body weight and breast angle at eight weeks of age. Selection within each pair of lines was in a high and low direction with the selected trait being body weight in one pair of lines and breast angle in the other. The selected lines were derived from a common gene pool that resulted from crosses of seven inbred lines of White Plymouth Rocks which were developed at the Virginia Agricultural Experiment Station.

At hatching, chicks from the base population were assigned to two subpopulations, angle and weight. To make each subpopulation as similar as possible a full sib of each chick in the weight subpopulation was assigned to the angle subpopulation. Thereafter the two subpopulations were maintained separately.

Within the weight subpopulation two-way mass selection was practiced for high and low body weight at eight weeks of age while in the angle subpopulation two-way mass selection was for breast angle. The parents for subsequent generations were chosen on a within line basis for high and low body weight and broad and narrow breast angle. Pullets were assigned at random to individual cockerels with no matings of half sib or closer allowed.

Management and Measurements:

Progeny for each generation were obtained from two hatches which were on the first and third Tuesdays of March. All chicks were removed from the hatcher on the 22nd day of incubation, pedigreed, and placed in floor pens where temperature, humidity, and lighting were controlled. This provided a similar environment for all pens over all generations. The same formulation of the ration was used each generation. A starter ration was fed to eight weeks, a grower ration from eight to 24 weeks, and a breeder ration thereafter.

Starting with the first filial generation chicks from the Athens-Canadian randombred population (Hess, 1962) were hatched each year and reared as contemporaries of the selected birds. These birds served as controls so that directional response could be measured in a single line.

Measurements of body weights in g and breast angles in degrees (Bywaters and Siegel, 1958) were obtained for each bird at eight weeks of age. The breast angle measurements were taken approximately one-half inch from the anterior end of the keel. Breast angle was considered as a correlated trait in the weight subpopulation while body weight was considered as a correlated trait in the breast angle subpopulation.

Heritability estimates based on full and half sib correlations, were obtained on a within sex basis, each generation for both traits in both subpopulations. Unequal subclass numbers existed, hence the procedures of King and Henderson (1954) were employed to estimate the variance components. The statistical model was:

$$Y_{ijkl} = u + l_i + s_{ij} + d_{ijk} + e_{ijkl}$$

where,

Y_{ijkl} = the observed phenotypic value of the _lth_ individual of the _kth_ dam mated to the _jth_ sire of the _ith_ line,

u = the population mean,

l_i = common effect of all individuals of the _ith_ line,

s_{ij} = common effect of all individuals mated to the _jth_ sire in the _ith_ line,

d_{ijk} = common effect of all individuals of the _kth_ dam mated to the _jth_ sire in the _ith_ line, and

e_{ijkl} = residual error of the _lth_ individual of the _kth_ dam mated to the _jth_ sire in the _ith_ line.

Realized heritabilities of selected traits were calculated within sexes for successive generations by dividing the difference between the means of the two selected lines by the cumulative selection differential (Student, 1934). A second realized heritability of divergence was conducted by the regression of response on the selection differential (Falconer, 1954). Realized heritabilities within lines were obtained from the regression of the control-adjusted response from the F_1 through the F_4 generation on the cumulative selection differential.

The realized heritabilities of the unselected traits were calculated by dividing the difference between the means of the two lines by the cumulative expected secondary selection differential iY_x and the regression of the correlated response on the iY_x (Ideta and Siegel, 1966). The iY_x was obtained each generation by multiplication of the phenotypic regression coefficient of the unselected on the selected trait times the selection differential of the selected trait. Since data were from two selection experiments, in which body weight and breast angle served as both the selected and correlated traits, the realized heritabilities of the correlated traits were comparable with the actual heritability of the trait in the selected lines. This comparison enabled an evaluation of the validity of the procedure whereby iY_x was an estimator of the selection differential of the correlated trait.

The genetic correlation between body weight and breast angle was calculated in both selected subpopulations. This was because the experiment was designed for double bidirectional selection. Equation 3 was used to calculate the genetic correlation in each filial generation. The phenotypic ($r_{P_{xy}}$) and environmental ($r_{E_{xy}}$) correlations were also calculated. The phenotypic correlation between the two traits was calculated directly as a simple product momment correlation and was partitioned to estimate the environmental correlation coefficient. Since,

$$r_{P_{xy}} = h_x h_y r_{G_{xy}} + e_x e_y r_{E_{xy}} \tag{5}$$

then,

$$r_{E_{xy}} = (r_{P_{xy}} - h_x h_y r_{G_{xy}}) \div e_x e_y \tag{6}$$

where,

e_x = square root of $1 - h^2{}_x$,

e_y = square root of $1 - h^2{}_y$,

h_x = square root of $h^2{}_x$, and

h_y = square root of $h^2{}_y$.

Phenotypic, environmental, and genetic correlations enabled an evaluation of the variation and covariation influencing the traits. Such information facilitates a more meaningful evaluation of the realized heritability of the unselected trait because the expected secondary selection differential includes the genetic and environmental correlations. This may be demonstrated symbolically as:

$$ix\ b_{P_{yx}} = ix\ \sigma_{P_y}(r_{G_{xy}} h_x h_y + r_{E_{xy}} e_x e_y)/\sigma_{P_x} .$$

Results and Discussion

Response to Selection

A double two-way selection experiment enabled a biological evaluation of the reliability of the procedures used by Ideta and Siegel (1966) to measure the realized heritability of unselected traits. This was because the design allowed a comparison of the heritability obtained by their method with that from direct selection for the trait.

The results presented and discussed were obtained from the following four lines: (1) the HW line where selection was for high weight, (2) the LW line where selection was for low weight, (3) the BA line where selection was for broad breast angle, and (4) the NA line where selection was for narrow breast angle. Body weights and breast angles of males and females were measured in all lines at eight weeks of age. Body weight was the correlated trait in the angle lines and breast angle the correlated trait in the weight lines.

Body weight as the selected trait:

Mean body weights by lines, generations, and sexes are presented in Table 1. Divergent selection for body weight at eight weeks of age resulted in a significant difference between the HW and LW lines in the F_1 and all subsequent generations. The difference between lines in the F_4 generation was 321 g for males and 294 g for females. The response of

Table 1. Means ($\overline{x}$), standard deviations (s), and coefficients of variation (cv) %, for body weight at eight weeks of age.

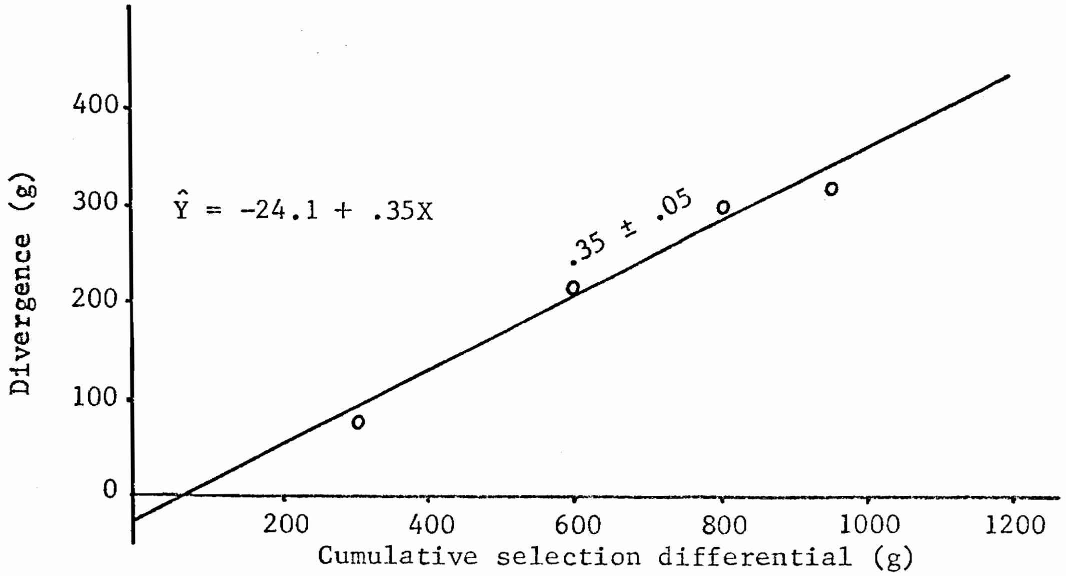
		Line							
		HW[1]		LW[1]		BA[1]		NA[1]	
Sex	Gen.	$\overline{x} \pm s$	cv	$\overline{x} \pm s$	cv	$\overline{x} \pm s$	cv	$\overline{x} \pm s$	cv
♂♂	P_1	879 ± 123	14	879 ± 123	14	879 ± 123	14	879 ± 123	14
	F_1	944 ± 120	13	868 ± 113	13	882 ± 110	12	837 ± 113	13
	F_2	946 ± 158	17	746 ± 152	20	836 ± 142	17	833 ± 138	17
	F_3	1037 ± 105	10	755 ± 104	14	918 ± 134	14	838 ± 107	13
	F_4	1156 ± 114	10	835 ± 98	12	1025 ± 94	9	906 ± 94	10
♀♀	P_1	715 ± 117	16	715 ± 117	16	715 ± 117	16	715 ± 117	16
	F_1	776 ± 100	13	705 ± 94	13	727 ± 91	12	708 ± 94	13
	F_2	774 ± 141	18	588 ± 132	33	693 ± 131	19	692 ± 104	15
	F_3	833 ± 87	10	615 ± 104	17	766 ± 107	14	702 ± 98	14
	F_4	951 ± 98	10	657 ± 112	17	829 ± 100	12	743 ± 95	13

[1] HW - selection for high body weight.
LW - selection for low body weight.
BA - selection for broad breast angle.
NA - selection for narrow breast angle.

body weight to mass selection is illustrated for males in Figure 1 and females in Figure 2. Although the response was significant in both directions the regression was greater in the LW line than in the HW line. The differences between regressions however, were not significant through the F_4 generation. The rapid response of juvenile body weight to mass selection obtained here agreed with the results of Schnetzler (1936), Maloney *et al*. (1963), and Arboleda *et al*. (1966). All of these investigations showed that a few generations of selection for body weight moves the mean from that of the base population.

Heritabilities of body weight based on the divergence between lines and full and half sib correlations are presented in Table 2. Realized heritabilities were more consistent than those based on full and half sib correlations. This was expected because the method of calculation for realized heritabilities (cumulative response ÷ cumulative selection differential) included data from the previous generations while those based on sib correlations were for a single generation *per se*. Further, the variance components used in estimating heritabilities from full and half sib correlations have large sampling errors (Robertson, 1959 and VanVleck and Henderson, 1961).

The realized heritabilities (cumulative response ÷ cumulative selection differential) were .31 for males and .28 for females. The regression of divergent response on the



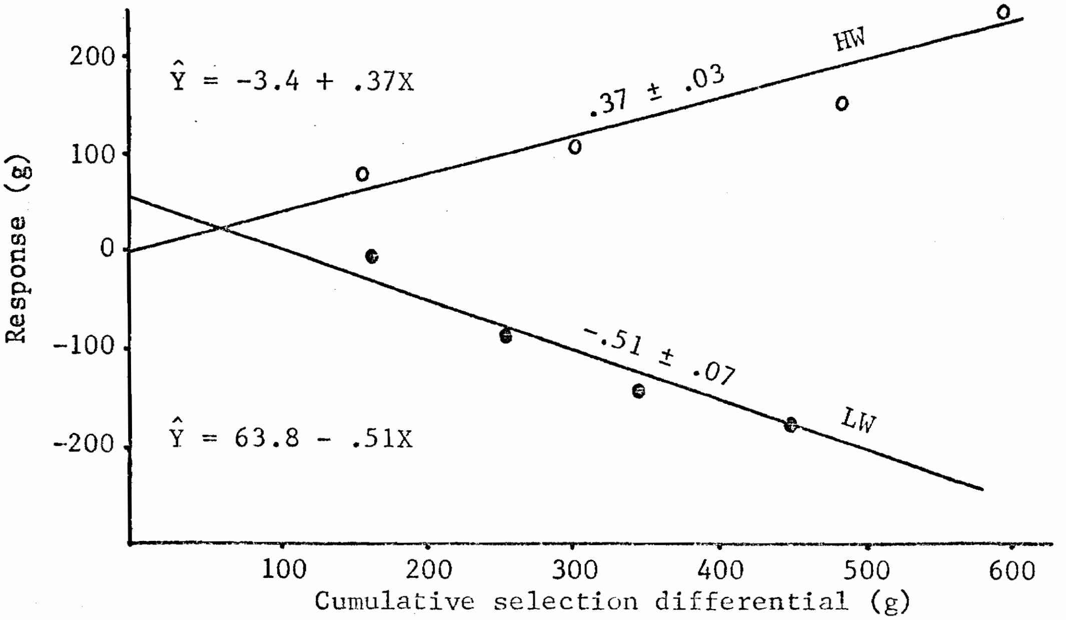
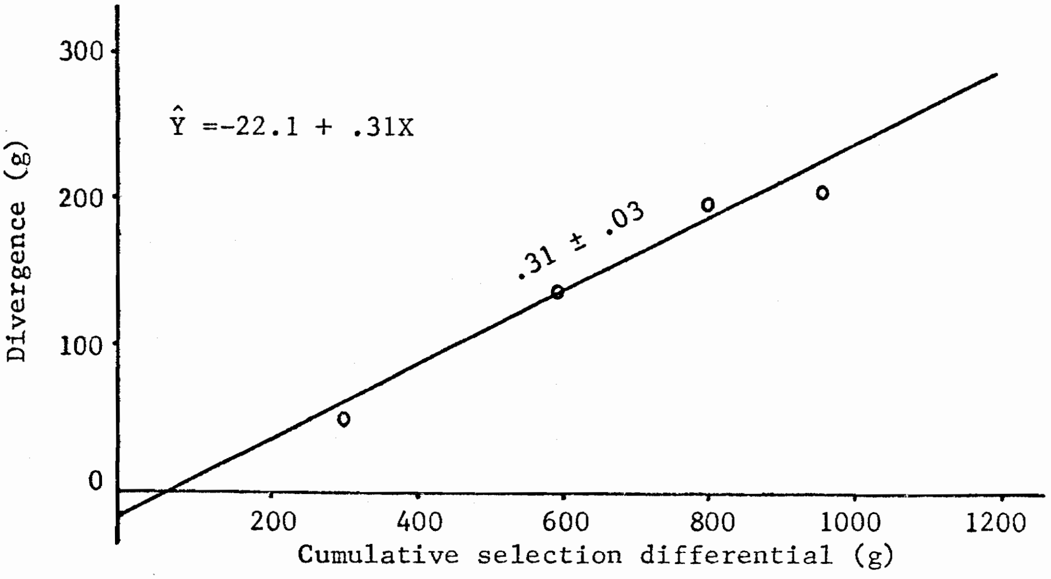


Figure 1. Direct response of body weight to selection in the weight lines (males).



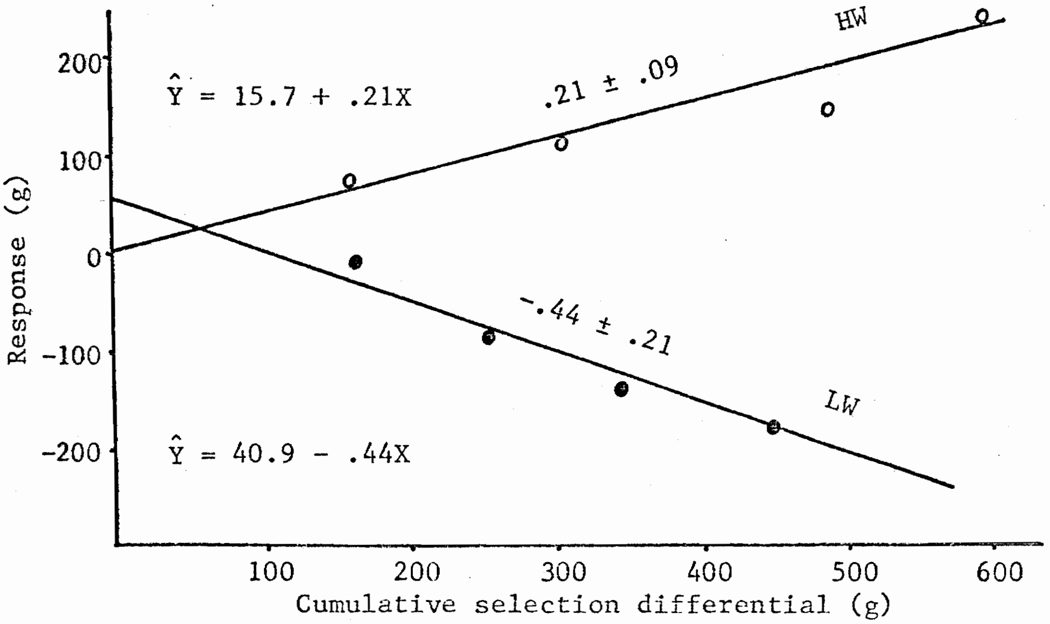


Figure 2 Direct response of body weight to selection in the weight lines (females).

Table 2. Heritability estimates of body weight at eight weeks of age in the weight lines.

		Heritability			
Sex	Gen.	Realized[1]	4S/(S+D+E)	4D/(S+D+E)	2(S+D)/(S+D+E)
♂♂	P_1	--	.90	.52	.71
	F_1	.23	.26	.48	.37
	F_2	.33	.21	.48	.34
	F_3	.35	.24	.78	.51
	F_4	.31	.45	.65	.55
	$\bar{x}$	--	.41	.58	.50
♀♀	P_1	--	-1.01	.04	.52
	F_1	.21	.13	.65	.39
	F_2	.32	.07	.05	.06
	F_3	.27	.02	.76	.39
	F_4	.28	.21	.84	.56
	$\bar{x}$	--	-.12	.47	.38

Realized[2]
♂ .35 ± .05
♀ .31 ± .03

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[1] $(\bar{x}_{HW} - \bar{x}_{LW}) \div \Sigma ix$

[2] $b(\bar{x}_{HW} - \bar{x}_{LW}) \cdot \Sigma ix$

cumulative selection differential estimates were .35 ± .05 and .31 ± .03 for males and females, respectively. These heritabilities were comparable to those obtained by Maloney _et_ _al_. (1967) and slightly lower than those of Kinney and Shoffner (1965). Therefore, it may be concluded that juvenile body weight is a moderate to highly heritable trait when heritability is considered in the narrow sense.

Body weight as the correlated trait:

Mean body weights at eight weeks of age in the angle lines are given in Table 1. Selection for breast angle resulted in concommitant changes in body weight with the difference between lines being significant in the F_1, F_3, and F_4 generations. The divergence and response of body weight in the BA and NA lines are illustrated in Figure 3 for males and Figure 4 for females. The regression of divergence on iY_x approached significance. Examination of Figure 3 shows that the divergence in body weight between the BA and NA line males was primarily due to the response in the BA line. The response in the NA line was negative in that the regression of low weight response on iY_x was positive (.10). The response for females (Figure 4) appeared different with a larger regression in the NA than the BA line. The regression coefficients of the response were not different between lines within sexes and the difference may not be real. Conclusions concerning the asymmetry of response are not warranted at

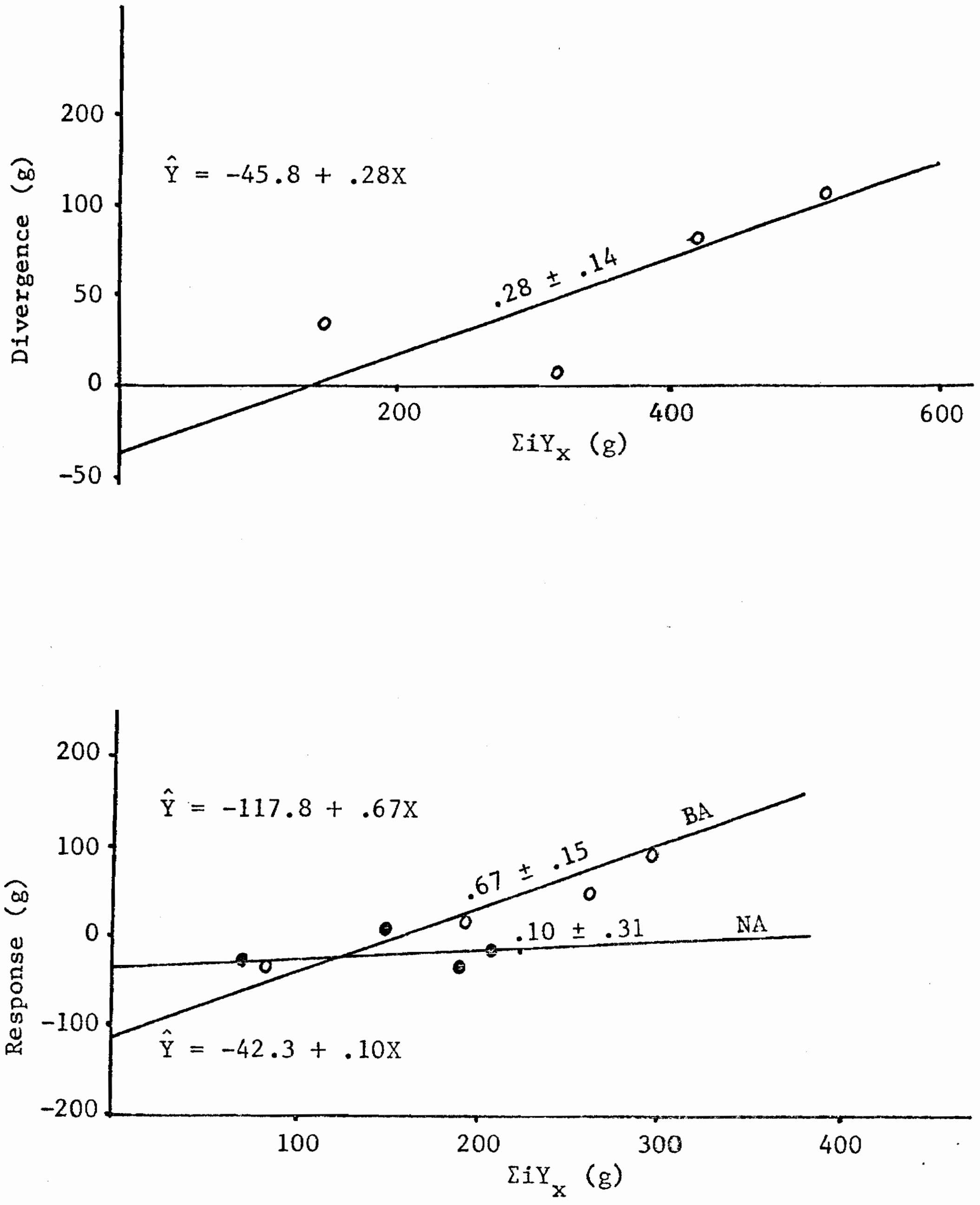


Figure 3. Correlated response of body weight to selection in the angle lines (males).

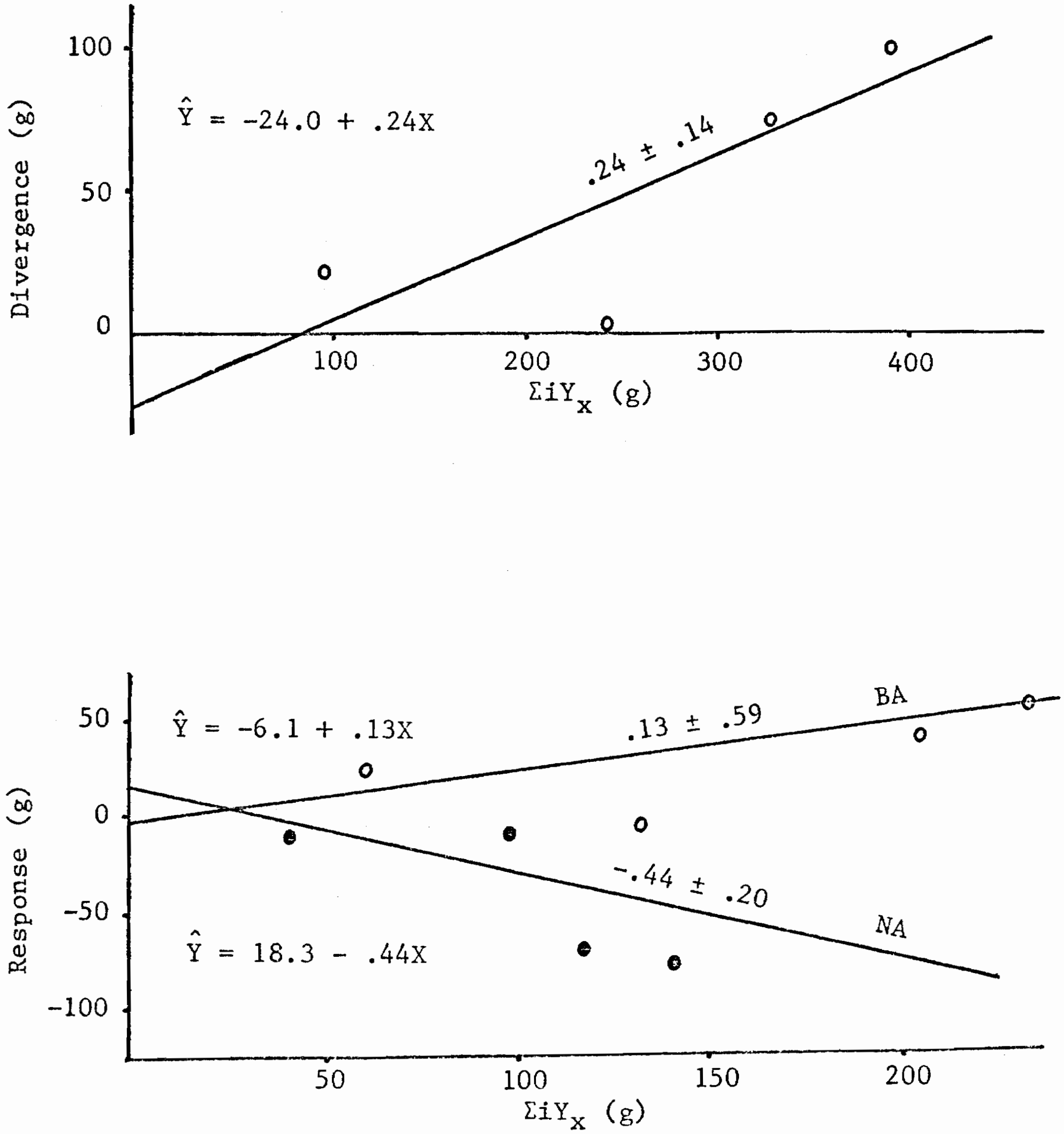


Figure 4. Correlated response of body weight to selection in the angle lines (females).

this time.

The heritabilities obtained for body weight in the angle lines are given in Table 3. Although estimates based on full and half sib correlations fluctuated among generations, the mean values were consistent with the estimates obtained for body weight in the HW and LW lines. The realized heritabilities of body weight calculated as $(\bar{x}_{BA} - \bar{x}_{NA}) \div \Sigma\, iY_x$ was .25 for males and .21 for females through the F_4 generation. Heritabilities based on the regression of the divergence of body weight on iY_x in the BA and NA lines were .28 ± .15 for males and .24 ± .13 for females. Although, there was close agreement between the two methods, the important comparison is between the weight and angle lines for the realized heritability of body weight. This is because such a comparison allows a biological evaluation of the method of Ideta and Siegel (1966).

Realized heritabilities of body weight were higher for males than females in both pairs of lines. This was expected since Siegel (1962a) and Beilharz (1960) have suggested some additive sex-linked gene action for body weight. The realized heritabilities of body weight were slightly lower for both sexes in the angle than in the weight lines (Table 4). Method 2 allowed the calculation of standard errors for the realized heritabilities. Standard errors were considerably larger in the angle than in the weight lines. Much of this variation was due to the lack of a correlated response of

Table 3. Heritability estimates of body weight at eight weeks of age in the angle lines.

		Heritability			
Sex	Gen.	Realized[1]	4S/(S+D+E)	4D/(S+D+E)	2(S+D)/(S+D+E)
♂♂	P_1	---	.90	.52	.71
	F_1	.11	.48	.48	.48
	F_2	.01	.16	.60	.38
	F_3	.18	.10	.68	.39
	F_4	.25	.17	.17	.17
	$\bar{x}$	---	.36	.49	.43
♀♀	P_1	---	-1.01	.04	.52
	F_1	.17	.18	1.01	.59
	F_2	.002	.21	.55	.38
	F_3	.20	.42	.14	.28
	F_4	.21	-.06	1.14	.54
	$\bar{x}$	---	-.05	.58	.46

Realized[2]
♂ .28 ± .15
♀ .24 ± .13

---

[1] $(\bar{x}_{BA} - \bar{x}_{NA}) \div \Sigma iY_x$

[2] $b(\bar{x}_{BA} - \bar{x}_{NA}) \cdot \Sigma iY_x$

Table 4. Comparisons of heritability of body weight at eight weeks of age in the body weight and breast angle lines.

		Line	
Sex	Method[1,2]	Body weight	Breast Angle
♂♂	1	.31	.25
	2	.35 ± .05	.28 ± .15
♀♀	1	.28	.21
	2	.31 ± .03	.24 ± .13

---

[1] $(\bar{x}_{HW} - \bar{x}_{LW}) / \Sigma ix$ in the weight lines and $(\bar{x}_{BA} - \bar{x}_{NA}) / \Sigma iY_x$ in the angle lines.

[2] $b(\bar{x}_{HW} - \bar{x}_{LW}) \cdot \Sigma ix$ in the weight lines and $b(\bar{x}_{BA} - \bar{x}_{NA}) \cdot \Sigma iY_x$ in the angle lines.

body weight in the F_2 generation for the angle lines. Further discussion of the reliability of the procedure given by Ideta and Siegel (1966) will be given subsequently in the dissertation.

Breast angle as the selected trait:

Mean breast angles by lines, generations, and sexes are presented in Table 5. Mass selection for breast angle resulted in a significant difference between lines in the F_1 and each succeeding generation. The cumulative divergence in the F_4 generation between the BA and NA lines for the selected trait was 7.0 degrees for males and 6.2 degrees for females.

The divergence between lines and response of each line is shown in Figure 5 for males and Figure 6 for females. Most of the divergence between lines was due to the response of the NA line. Although as shown in Figure 5, there was a positive regression of response on the selection differential, the means in the F_1, F_2, and F_3 generations were less than the means of the P_1 generation. The Y intercept was -6.1 degrees. Thus the positive regression of response on ix is misleading and the response of the BA line males to selection was essentially zero. The regression in the NA line was negative and not significant, but, the Y intercept was -6.3 degrees, suggesting a negative response. The closeness of the Y intercept for the NA and BA lines suggests a large environ-

Table 5. Means ($\bar{x}$), standard deviations (s), and coefficients of variation (cv) %, for breast angle at eight weeks of age.

		Line							
		BA[1]		NA[1]		HW[1]		LW[1]	
Sex	Gen.	$\bar{x} \pm s$	cv	$\bar{x} \pm s$	cv	$\bar{x} \pm s$	cv	$\bar{x} \pm s$	cv
♂♂	P_1	57.1 ± 3.9	7	57.1 ± 3.9	7	57.1 ± 3.9	7	57.1 ± 3.9	7
	F_1	55.0 ± 3.0	5	51.6 ± 4.0	8	54.4 ± 3.4	6	53.8 ± 3.7	7
	F_2	52.1 ± 3.6	7	47.1 ± 3.9	8	51.4 ± 3.7	7	47.8 ± 4.1	8
	F_3	55.9 ± 2.7	5	48.1 ± 3.2	7	54.9 ± 2.8	5	48.5 ± 3.8	8
	F_4	59.6 ± 2.3	4	52.6 ± 3.0	6	57.3 ± 3.3	6	52.2 ± 3.4	6
♀♀	P_1	55.2 ± 4.0	7	55.2 ± 4.0	7	55.2 ± 4.0	7	55.2 ± 4.0	7
	F_1	53.0 ± 3.2	7	49.7 ± 1.7	3	52.7 ± 3.5	7	51.6 ± 3.7	7
	F_2	50.2 ± 3.9	8	44.6 ± 4.2	7	48.5 ± 3.4	7	44.6 ± 4.6	10
	F_3	54.0 ± 2.7	5	46.4 ± 3.9	8	52.4 ± 3.0	6	45.8 ± 4.2	9
	F_4	57.0 ± 3.3	6	50.8 ± 3.5	7	55.3 ± 3.3	6	49.5 ± 4.8	7

[1] BA - Broad breast angle line.
NA - Narrow breast angle line.
HW - High body weight line.
LW - Low body weight line.

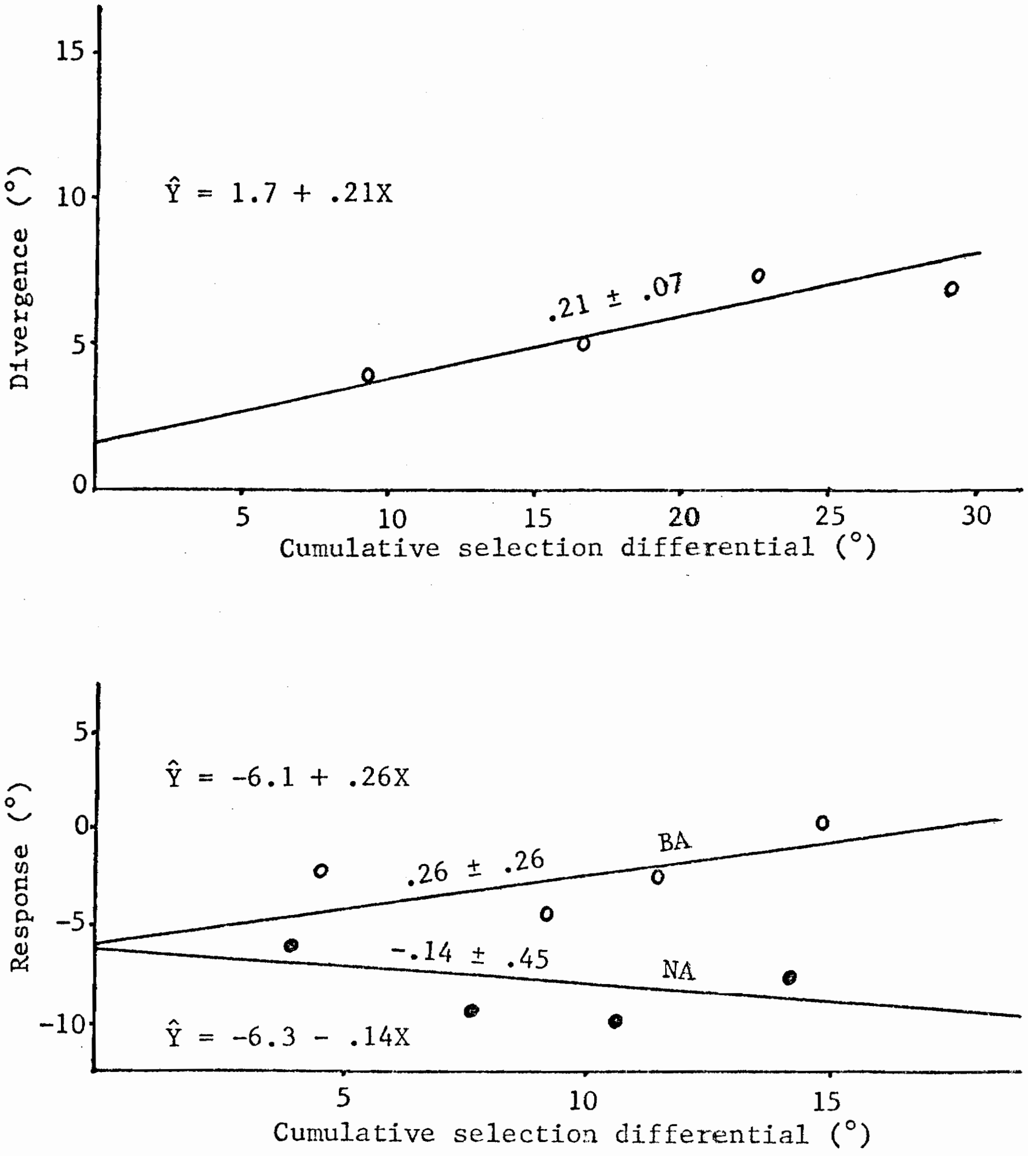


Figure 5. Direct response of breast angle to selection in the angle lines (males).

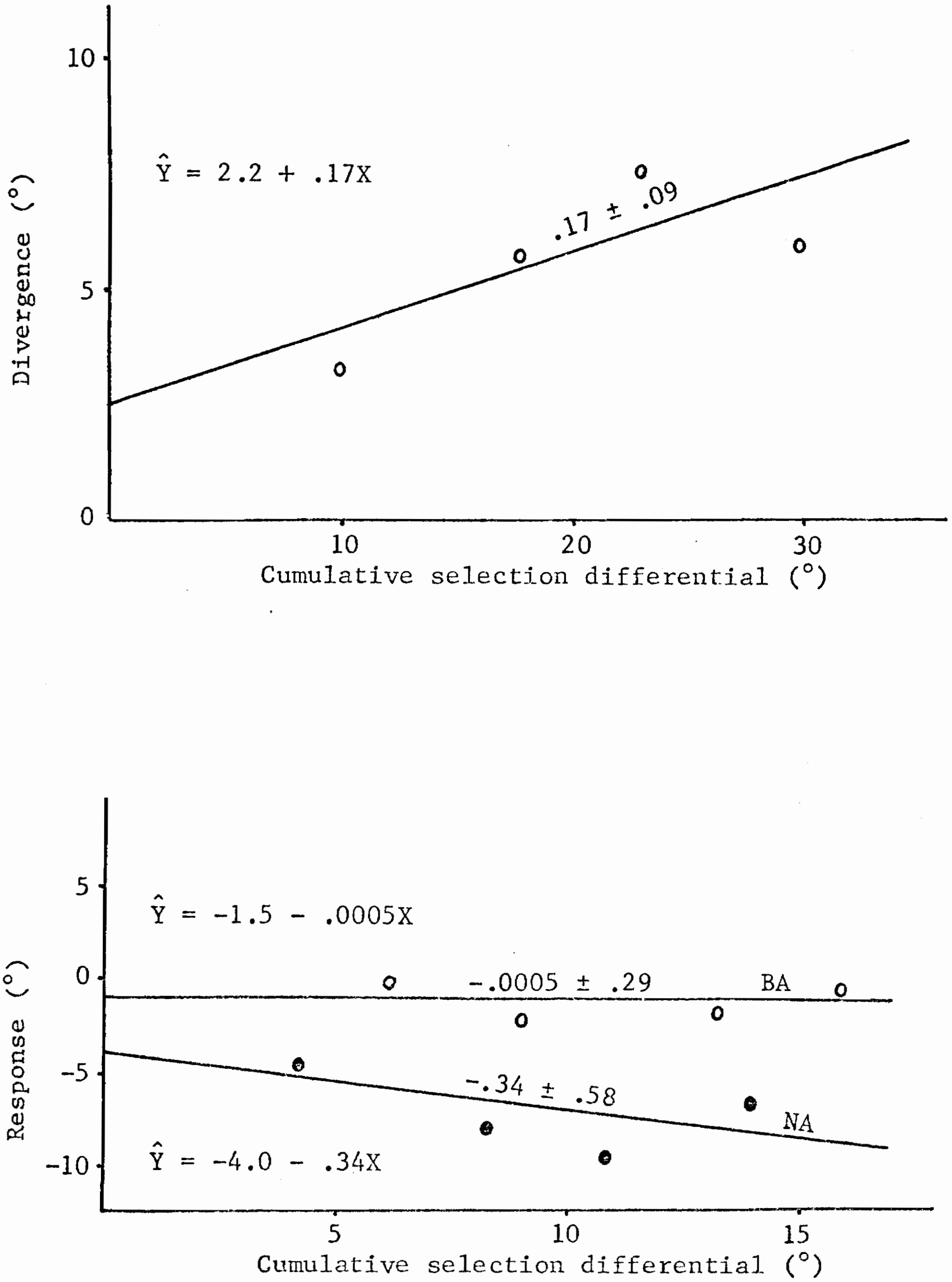


Figure 6. Direct response of breast angle to selection in the angle lines (females).

mental change from the P_1 to F_1 generations in this experiment. The reason for this is not known.

For females the divergence between the lines was primarily due to response in the NA line (Figure 6). As with males the standard errors were large and the conclusion can only be considered tentative.

Heritability estimates of breast angle in the angle lines are presented in Table 6. The realized values to the F_4 generation $(\bar{x}_{BA} - \bar{x}_{NA}) \div \Sigma\, ix$ was .24 for males and .21 for females, and those based on the regression of divergence on the cumulative selection differential were .21 ± .07 for males and .17 ± .09 for females. Estimates based on full and half sib correlations fluctuated among generations but, when averaged over generations, were of a magnitude comparable to the realized heritabilities. The realized breast angle heritabilities obtained in this experiment were consistent with the mean of those obtained by Lerner _et_ _al_. (1947), Brunson _et_ _al_. (1956), Godfrey and Goodman (1956), Siegel and Essary (1959), and Masic (1967). The divergence of lines in response to selection for breast angle was expected in light of the reported genetic variation in breast angle present in other populations.

Breast angle as the correlated trait:

Means, standard deviations, and coefficients of variation for breast angle in the lines selected for body weight

Table 6. Heritability estimates of eight-week breast angle in the angle lines.

		Heritability			
Sex	Gen.	Realized[1]	4S/(S+D+E)	4D/(S+D+E)	2(S+D)/(S+D+E)
♂♂	P_1	---	.76	.20	.48
	F_1	.37	.23	.52	.37
	F_2	.30	.27	.39	.33
	F_3	.34	.24	.39	.32
	F_4	.24	-.02	.46	.22
	$\bar{x}$	---	.30	.39	.34
♀♀	P_1	---	.54	.42	.48
	F_1	.32	-.02	1.03	.51
	F_2	.31	.42	.12	.27
	F_3	.34	.19	.15	.17
	F_4	.21	.14	.03	.08
	$\bar{x}$	---	.25	.35	.30

Realized[2]
♂ .21 ± .07
♀ .17 ± .09

---

[1] $(\bar{x}_{BA} - \bar{x}_{NA}) / \Sigma ix$

[2] $b(\bar{x}_{BA} - \bar{x}_{NA}) . \Sigma ix$

are shown in Table 5 by sex and generation. Differences between the HW and LW lines for the correlated trait, breast angle, were significant in the F_2, F_3, and F_4 generations and the cumulative correlated divergence was 5.1 degrees for males and 5.8 degrees for females.

The divergence between the HW and LW lines and the response of each line for breast angle are presented in Figure 7 for males and Figure 8 for females. The divergence of breast angle in the weight lines was primarily due to the response of the LW line. Again, as in the selected lines, the males (Figure 7) showed a positive regression coefficient for response on iY_x which was due to a decrease in the negative response. Actually, there was no positive correlated response of BA in any generation. Although for females there was a negative regression in both the HW and LW lines (Figure 8), the regression coefficients were not significantly different between the HW and LW lines. This was expected because the data from the selected lines showed that little, if any, additive genetic variation for broad breast angle was present in the base population.

Heritabilities of breast angle calculated in the weight lines are presented in Table 7. Realized heritabilities were comparable to those based on maternal half sib correlations and higher than those based on full and paternal half sib correlations. The realized heritabilities of breast angle in the weight lines were higher than those obtained when

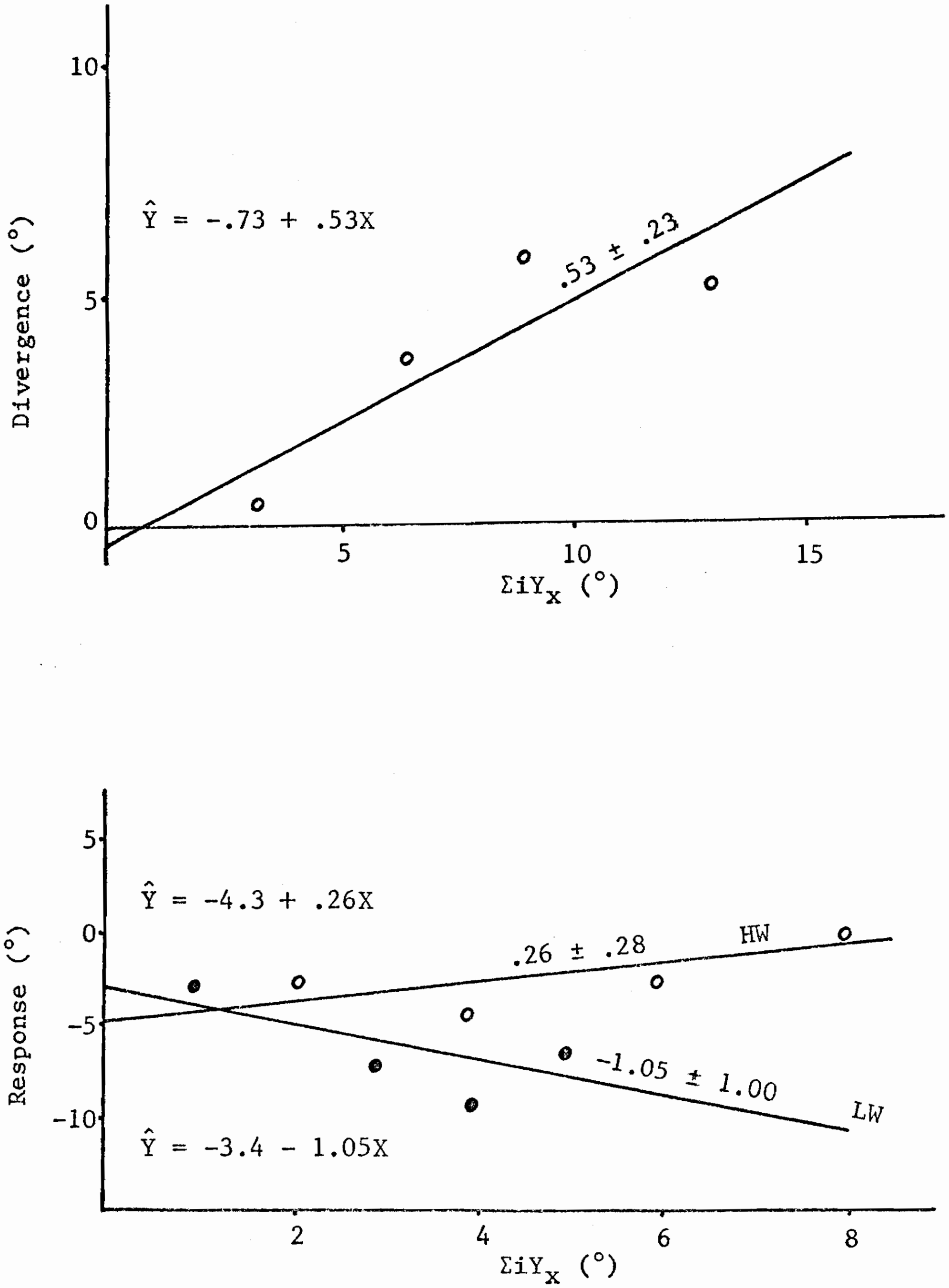
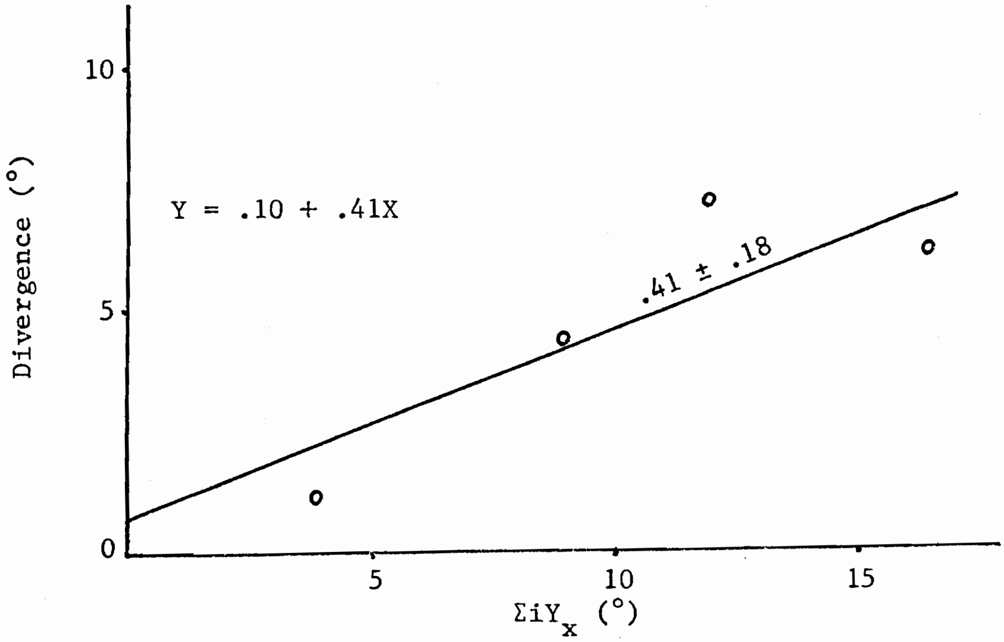


Figure 7. Correlated response of breast angle to selection in the weight lines (males).



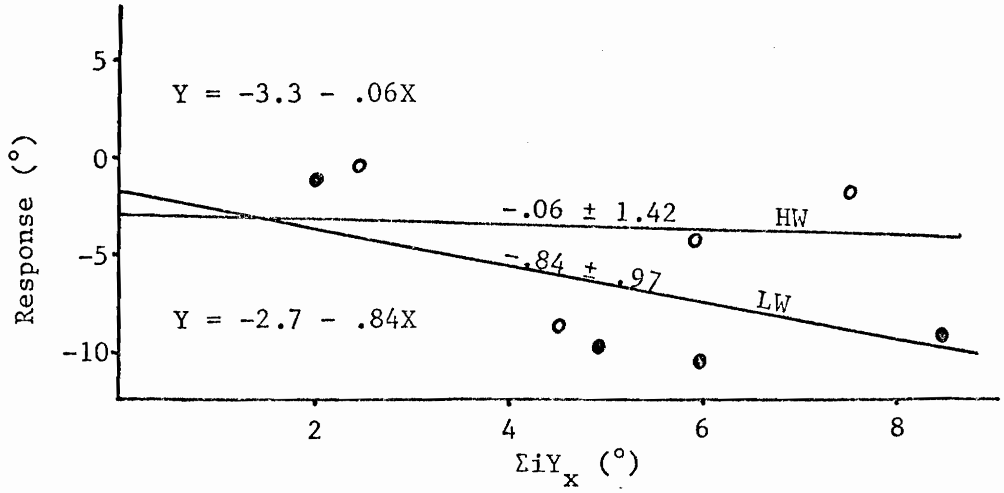


Figure 8. Correlated response of breast angle to selection in the weight lines (females).

Table 7. Heritability of eight-week breast angle in the weight lines.

		Heritability			
Sex	Gen.	Realized[1]	4S/(S+D+E)	4D/(S+D+E)	2(S+D)/(S+D+E)
♂♂	P_1	---	.76	.20	.48
	F_1	.01	.21	.16	.18
	F_2	.51	.16	.46	.31
	F_3	.67	.01	.41	.21
	F_4	.40	.13	.60	.37
	$\bar{x}$	---	.25	.37	.31
♀♀	P_1	---	.53	.42	.48
	F_1	.24	.04	.55	.30
	F_2	.43	.03	.50	.23
	F_3	.56	.01	.36	.19
	F_4	.35	.16	.16	.16
	$\bar{x}$	---	.15	.40	.27

Realized[2]
♂ .53 ± .23
♀ .41 ± .18

---

[1] $(\bar{x}_{HW} - \bar{x}_{LW}) / \Sigma iY_x$

[2] $b(\bar{x}_{HW} - \bar{x}_{LW}) \cdot \Sigma iY_x$

there was direct selection for breast angle i.e., the angle lines (Table 8). The regression in the weight lines of divergent response of breast angle on iY_x was higher than the regression of divergent response of breast angle in the angle lines on the ix. These regressions were .53 ± .23 for males and .41 ± .18 for females in the weight lines as compared to .21 ± .07 for males and .17 ± .09 for females in the angle lines. This result was not consistent with that found for the heritability of body weight. The realized heritabilities for body weight were higher in the weight lines than in the angle lines. Considerably more variation existed between generations for the breast angle estimates in the weight lines as shown by the higher standard errors of the regression of divergent response of iY_x in those lines.

General

The realized heritabilities obtained for body weight were comparable for the weight and angle selected lines. Realized heritabilities for breast angle, however, were higher in the lines selected for weight than in those selected for breast angle. This suggests that the correlated response of body weight in the angle lines was not as great as the correlated response of breast angle in the weight lines and/or there was a difference in the expected secondary selection

Table 8. Comparison of heritability of breast angle at eight weeks of age in the breast angle and body weight lines.

		Line	
Sex	Method[1,2]	Breast angle	Body weight
♂♂	1	.24	.40
	2	.21 ± .07	.53 ± .23
♀♀	1	.21	.35
	2	.17 ± .09	.41 ± .18

[1] $(\bar{x}_{BA} - \bar{x}_{NA}) / \Sigma ix$ in breast angle lines and $(\bar{x}_{HW} - \bar{x}_{LW}) / \Sigma iY_x$ in body weight lines.

[2] $b(\bar{x}_{BA} - \bar{x}_{NA}) \cdot \Sigma ix$ in breast angle lines and $b(\bar{x}_{HW} - \bar{x}_{LW}) \cdot \Sigma iY_x$ in body weight lines.

differential of the two unselected traits. The first possibility was demonstrated from the changes in population means.

The second possibility may be evaluated by a comparison of the ratio of the selection differentials to the expected secondary selection differentials within each pair of lines. If these ratios are unequal and the responses are equal the result would be heritabilities of different magnitudes. To investigate this the phenotypic regression of unselected on selected traits were calculated (Table 9). These regressions were part of the expected secondary selection differential of body weight and breast angle when each was considered as the correlated trait. All regressions were highly significant, demonstrating that selection for one trait resulted in a corresponding selection for the other trait. The ratio of the ix and iY_X for body weight and breast angle are given in Table 10. Examination of these ratios reveals that the relationship of iY_X to ix was fairly comparable in both pairs of lines. They show that the asymmetry was due to differences in the correlated responses rather than selection differentials.

The asymmetry of genetic response demonstrates the chance of error when genetic parameters between two traits are estimated in one biological environment, i.e., one pair of selected lines. Also the calculation of genetic correlations from regression and component analyses could be biased unless the two traits had equal phenotypic and genetic

Table 9. Phenotypic regressions (b) and their standard errors (se) of unselected on the selected traits.

Regression of breast angle on body weight

Sex	Gen.	HW[1]	LW[1]
		b ± se[2]	b ± se[2]
♂♂	F_1	13 ± 1.4	6 ± 2.0
	F_2	13 ± 1.4	19 ± 1.4
	F_3	10 ± 1.7	15 ± 2.2
	F_4	17 ± 1.7	12 ± 2.2
♀♀	F_1	16 ± 2.2	11 ± 2.0
	F_2	12 ± 1.4	25 ± 2.0
	F_3	11 ± 2.4	20 ± 2.4
	F_4	13 ± 2.6	30 ± 2.2

Regression of body weight on breast angle

Sex	Gen.	BA[1]	NA[1]
		b ± se[2]	b ± se[2]
♂♂	F_1	16.8 ± 1.9	15.6 ± 1.5
	F_2	27.7 ± 2.1	22.2 ± 2.2
	F_3	23.8 ± 2.9	9.8 ± 2.8
	F_4	10.7 ± 2.4	9.5 ± 2.5
♀♀	F_1	12.1 ± 1.6	9.1 ± 1.5
	F_2	24.0 ± 1.8	13.6 ± 1.8
	F_3	13.4 ± 2.7	10.2 ± 2.2
	F_4	19.5 ± 1.8	8.7 ± 2.2

[1] HW - High weight line.
LW - Low weight line.
BA - Broad angle line.
NA - Narrow angle line.

[2] 10^{-3}, all regressions were highly significant ($P \leq .01$)

Table 10. Ratio of selection differentials (ix) and expected secondary selection differentials (iY_x) of body weight and breast angle by lines, sexes and generations.

		Trait					
		W[1]			A[2]		
Sex	Gen.	ix	iYx	iYx/ix(%)	ix	iYx	iYx/ix(%)
♂♂	F_1	334	150	44.9	9.2	3.0	32.6
	F_2	597	340	57.0	16.8	7.1	42.3
	F_3	814	440	54.0	22.8	9.6	42.1
	F_4	1041	504	48.4	29.2	12.8	43.8
♀♀	F_1	337	109	32.3	10.2	4.5	44.1
	F_2	600	257	42.8	18.0	9.1	50.6
	F_3	804	324	40.3	23.6	11.8	50.0
	F_4	1036	414	40.0	30.0	16.7	55.7

[1] W - Weight selected lines.

[2] A - Angle selected lines.

covariances. Since these assumptions are rarely met in biological material the common situation would be for $b_{G_{xy}} \neq b_{G_{yx}}$. Biases can be shown symbolically to result in either a component genetic correlation estimate or a one-way realized estimate of a genetic correlation in the following manner:

Since,

$$r_{G_{xy}} = \sqrt{b_{G_{xy}} \cdot b_{G_{yx}}}$$

$$= \sqrt{\sigma^2 G_{xy} \div \sigma^2 G_x \; \sigma^2 G_y}$$

$$= \sigma G_{xy} \div \sigma G_x \; \sigma G_y \qquad (7)$$

then, the $r_{G_{xy}}$ is dependent on both the regression of x on y and y on x.

Therefore,

$$b_{G_{yx}} = \Delta Y_x \div \Delta x$$

$$b_{G_{xy}} = \Delta X_y \div \Delta y$$

and by transposing,

$$\Delta Y_x = \Delta x \; b_{G_{yx}}$$

$$\Delta X_y = \Delta y \; b_{G_{xy}}$$

When $r_{G_{xy}} = c$ from either variance-covariance analyses or one-way selection experiments and there is a directionality of response, $b_{G_{xy}} \neq b_{G_{yx}}$, and $r_{G_{xy}}$ would not be valid for maximum efficiency in the prediction of the correlated responses.

Heritability in the narrow sense is the ratio of additive genetic variance to the total phenotypic variance. This is not the case, however, for the realized heritability of a correlated trait from the method of Ideta and Siegel (1966). They showed that:

$$h^2 = \text{Response} \div iY_x$$

Since the response of the correlated trait (y) when selection is for trait (x) is equal to:

$$\Delta Y_x = \Delta x \; b_{G_{yx}} = ix \; h^2_x \; b_{G_{yx}}$$

then the expected secondary selection differential is equal to

$$iY_x = ix \; b_{P_{yx}}$$

Therefore,

$$h^2_y = ix \; h^2_x \; b_{G_{yx}} \div ix \; b_{P_{yx}}$$

The selection differentials cancel and since

$$h^2_x = \sigma^2_{G_x} \div \sigma^2_{P_x} \text{ and}$$

$$b_{G_{yx}} = \sigma_{G_{yx}} \div \sigma^2_{G_x}$$

the numerator becomes

$$\sigma^2_{G_x}/\sigma^2_{P_x} \cdot \sigma_{G_{yx}}/\sigma^2_{G_x} ,$$

and the denominator becomes

$$b_{P_{yx}} = \sigma_{P_{yx}} \div \sigma^2_{P_x} ,$$

thus,

$$h^2_y = (\sigma^2_{G_x} \div \sigma^2_{P_x})(\sigma_{G_{yx}} \div \sigma^2_{G_x}) \div (\sigma_{P_{yx}} \div \sigma^2_{P_x})$$

$$= \sigma_{G_{yx}} \div \sigma_{P_{yx}} \qquad (8)$$

So the method of estimation of realized heritabilities of correlated traits is actually the ratio of the genetic to the phenotypic covariances of the selected and correlated traits. The term realized correlated heritability would probably be a better word than realized heritability which was used by Ideta and Siegel (1966). This is because the heritability of correlated traits contains genetic covariances and its value may fluctuate more among generations than the realized heritabilities of the primary trait. Variation could in addition to genetic deviations be due to environmental deviations and genotype-environment interactions. The phenotypic regression of one trait on another contains both genetic and environmental influences in the following manner

$$b_{P_{yx}} = b_{G_{yx}}\, h^2_x + b_{E_{yx}}\, (1-h^2_x) \qquad (9)$$

Table 11 shows the phenotypic, genetic, and environmental correlations between body weight and breast angle in both pair of lines.

Table 11. Phenotypic (^{r}p), realized genetic (^{r}G), and environmental (^{r}E) correlations between eight-week body weight and breast angle calculated in weight^1 selected lines and breast angle^2 selected lines.

		r_P		r_G		r_E	
Sex	Gen.	W^1	A^2	W^1	A^2	W^1	A^2
♂♂	F_1	.32	.51	.07	.24	.43	.63
	F_2	.64	.65	.76	.01	.58	.94
	F_3	.40	.40	.71	.24	.24	.48
	F_4	.46	.32	.55	.46	.53	.27
♀♀	F_1	.42	.42	.33	.14	.46	.53
	F_2	.64	.64	.74	0.002	.59	.94
	F_3	.42	.36	1.07	0.28	.46	.40
	F_4	.54	.48	.57	.41	.53	.50

[1] W - Weight selected lines.

[2] A - Angle selected lines.

Bohren et al. (1966) simulated conditions between loci contributing to a correlation between two traits and suggested that different loci might contribute positively to the covariance in one generation, negatively in the next generation, and even interact differently among generations. They suggested that the least variation would be with a gene frequency of .5 and a large number of genes affecting the two characters in a pleiotropic manner. Rendel (1963) also showed that genetic covariances between correlated traits could change signs during the course of selection.

Based on the evidence for the variability of genetic covariances, it seems that the proposed method of Ideta and Siegel (1966) for the estimation of realized heritabilities of correlated traits could be biased among generations. The directionality of the bias appears unpredictable for any single generation unless the genetic covariances between traits are known before hand. This information is not available, therefore, when the method is employed the correlated response should be regressed on iY_X over a period of several generations. This would provide an average realized correlated heritability that could be used to predict the average response of the correlated trait.

EXPERIMENT II: SEXUAL DIMORPHISM

Materials and Methods

This experiment involved data from ten generations of a bidirectional selection experiment for body weight at eight weeks of age. Data for the first four generations were part of that used in Experiment 1 for the eight-week weight in the HW and LW lines. Selection and management procedures are described in the Materials and Methods section of Experiment 1.

Birds were individually weighed. However, in the sex dimorphism phase of this experiment differences were taken between male and female full sib family weights. Differences between full sib families were used because it was felt that they would yield more reliable estimates of genetic variability for sex dimorphism than differences between half sib families. Those families that did not have at least one male and female full sib were eliminated from the analyses. The amount of data lost by using this procedure was small.

Heritability estimates for sex dimorphism were estimated, in the broad sense, from a one-way analysis of variance between the HW and LW lines. The statistical model was:

$$Y_{ij} = u + l_i + e_{ij}$$

where, Y_{ij} was the j<u>th</u> measurement of the sex difference of an individual full sib family of the i<u>th</u> line. Falconer

(1960) described the relationship as:

$$h^2 = (MS_B - MS_W)/[MS_B + (n - 1)\ MS_W]$$

where,

MS_B = mean square between lines,

MS_W = mean square within lines, and

n = mean number of full sib families per line.

Heritability estimates in the narrow sense were estimated from a nested design using the model:

$$Y_{ijk} = u + l_i + s_{(i)j} + e_{(ij)k}$$

where, Y_{ijk} was the measurement of the k<u>th</u> male and female full sib family difference of the j<u>th</u> sire of the i<u>th</u> line. The heritability in this sense is:

$$h^2 = 4(MS_S - MS_W)/[MS_S + (k - 1)\ MS_W]$$

where,

MS_S = mean square between sires,

MS_W = mean square within sires, and

k = mean number of full sib families per sire.

Realized heritabilities (Student, 1934 and Falconer, 1954) and estimates based on full and half sib correlations (King and Henderson, 1954) of body weight at eight weeks of age were calculated on a within sex basis. Since analyses were on a within sex basis the requirement of male and female sibships was not necessary.

Two methods were used to estimate genetic correlations between males and females for body weight at eight weeks of age. The first was a covariance analysis (Eisen and Legates, 1966) which provided the expected genetic covariance component of the males and females ($\sigma_{G_{12}}$). The formula used was:

$$E(MCP) = (n\sigma_{G_{12}}) \tag{10}$$

where,

MCP = mean cross product of sexes between lines, and

$n\sigma_{G_{12}}$ = expected mean cross product.

Transposing yields,

$$\sigma_{G_{12}} = MCP/n$$

where,

n = number of individual measurements.

The genetic variances, $\sigma^2_{G_1}$ for males and $\sigma^2_{G_2}$ for females were obtained from a between line analysis. This enabled estimation of the genetic correlation from formula (7).

The second method for estimation of the genetic correlation between sexes was from a two-way analysis of variance that utilized the line-sex interaction (Robertson, 1959). This procedure considers males and females as two environments and the statistical model was:

$$Y_{ijk} = u + l_i + s_j + ls_{ij} + e_{ijk}$$

where,

u = mean,

l_i = effect common to the lines,

s_j = effect common to the sexes,

sl_{ij} = effect due to the interaction of lines and sexes, and

e_{ijk} = error due to individual measurements.

The genetic correlation between males and females was expressed by Robertson (1959) as:

$$r_G = \frac{MS_L - MS_{LS}}{MS_L + MS_{LS} - 2(MS_W)} \tag{11}$$

where,

MS_L = mean square between lines,

MS_{LS} = mean square of line-sex interaction,

MS_W = mean square within sexes and lines,

r_G = genetic correlation of sexes between lines, and

n = number of individuals per line.

Utilization of both a variance and covariance analysis to estimate the genetic correlation between males and females enabled a comparison of the efficiency of the two procedures.

Although the line-sex interaction component can be used to estimate the heritability of sexual dimorphism of a character (Eisen and Legates, 1966) it was not used in this experiment because of the more direct method which considers a difference between male and female full sib family means as a single trait. To provide a measure of the magnitude of the line-sex interaction, however, a least squares analysis was made for lines and sexes over ten generations. This was necessary to interpret the genetic variability for sex dimorphism. Least squares procedures were necessary because of disproportionate subclass numbers and the requirement of male and female full sib was relaxed for this analysis. The statistical model was:

$$Y_{ijkl} = u + l_i + s_j + g_k + ls_{ij} + lg_{ik} + sg_{jk} + lsg_{ijk} + e_{ijkl}$$

where,

u = means,

l_i = effect due to lines,

s_j = effect due to sexes,

g_k = effect due to generations,

ls_{ij} = effect due to interaction of lines and sexes,

lg_{ik} = effect due to interaction of lines and generations,

sg_{jk} = effect due to interaction of sexes and generations,

lsg_{ijk} = effect due to interaction of lines, sexes, generations, and

e_{ijkl} = error due to individual measurements.

The second order interaction was not obtained because the amount of data contained in this experiment was too large for the I.B.M. 7040 computer and the variation for this interaction was included in the error term. Prior to pooling a check was made on data from the first four generations to determine whether the second order interaction was significant. Since the interaction was not significant there was validity in pooling it with the error term.

The predicted response of sexual dimorphism for body weight was made by multiplying the selection differential by the heritability in the narrow sense. Selection differentials for sex dimorphism were estimated as the difference between mean male and female selection differentials for body weight each generation.

Results and Discussion

It is well known that male chickens are heavier than females. This experiment was designed to determine whether this sexual dimorphism is comparable in different lines and its mode of inheritance.

Response to Selection

Means, standard deviations, and coefficients of variation for body weight at eight weeks of age by lines, sexes, and generations are presented in Table 12. Analysis of variance of these data are shown in Table 13. The divergence between the HW and LW lines in the F_{10} generation was 563 g for males and 501 g for females. All main effects, as expected, were highly significant. The first order interactions were the sources of variation that were of particular interest. All were highly significant. The generation-line interaction was, of course, expected because selection was in divergent directions. That divergence occurred is shown in Figure 9. The significant generation-sex interaction resulted from a greater response of males ($b = 5.6 \pm 4.3$) than females ($b = 0.4 \pm 2.5$) to selection (Figure 9). The highly significant line-sex interaction was of particular interest because it was concerned with both the genetic correlation between sexes and the heritability of sex dimorphism for body weight which will be referred to subsequently.

The coefficients of variation in the HW line decreased significantly with selection ($b = -.80 \pm .17$ for males and $-.80 \pm .40$ for females) demonstrating a reduction in phenotypic variation. The coefficients of variation for the LW line did not follow this pattern ($b = -.08 \pm .19$ for males and $.27 \pm .29$ for females). Further evidence of differences

Table 12. Means ($\overline{x}$), standard deviations (s), and coefficients of variation (cv) %, for body weight at eight weeks of age by lines, sexes and generations.

	HW[1]				LW[1]			
	♂♂		♀♀		♂♂		♀♀	
Gen.	$\overline{x} \pm s$	cv	$\overline{x} \pm s$	cv	$\overline{x} \pm s$	cv	$\overline{x} \pm s$	cv
P_1	879 ± 123	14	715 ± 117	16	879 ± 123	14	715 ± 117	16
F_1	945 ± 120	13	776 ± 100	13	879 ± 113	13	697 ± 94	13
F_2	980 ± 158	16	766 ± 141	18	784 ± 152	19	631 ± 132	21
F_3	1040 ± 105	10	795 ± 87	11	757 ± 104	14	612 ± 104	17
F_4	1100 ± 114	10	853 ± 98	11	780 ± 98	12	620 ± 112	18
F_5	1221 ± 101	8	921 ± 96	10	810 ± 110	14	597 ± 95	16
F_6	1194 ± 114	10	927 ± 94	10	741 ± 106	14	572 ± 93	16
F_7	1136 ± 94	8	891 ± 73	8	697 ± 105	15	543 ± 75	14
F_8	1192 ± 119	10	935 ± 90	10	695 ± 97	14	529 ± 79	15
F_9	1272 ± 92	7	961 ± 89	9	687 ± 96	14	499 ± 101	20
F_{10}	1207 ± 126	10	947 ± 118	12	644 ± 91	14	446 ± 88	20

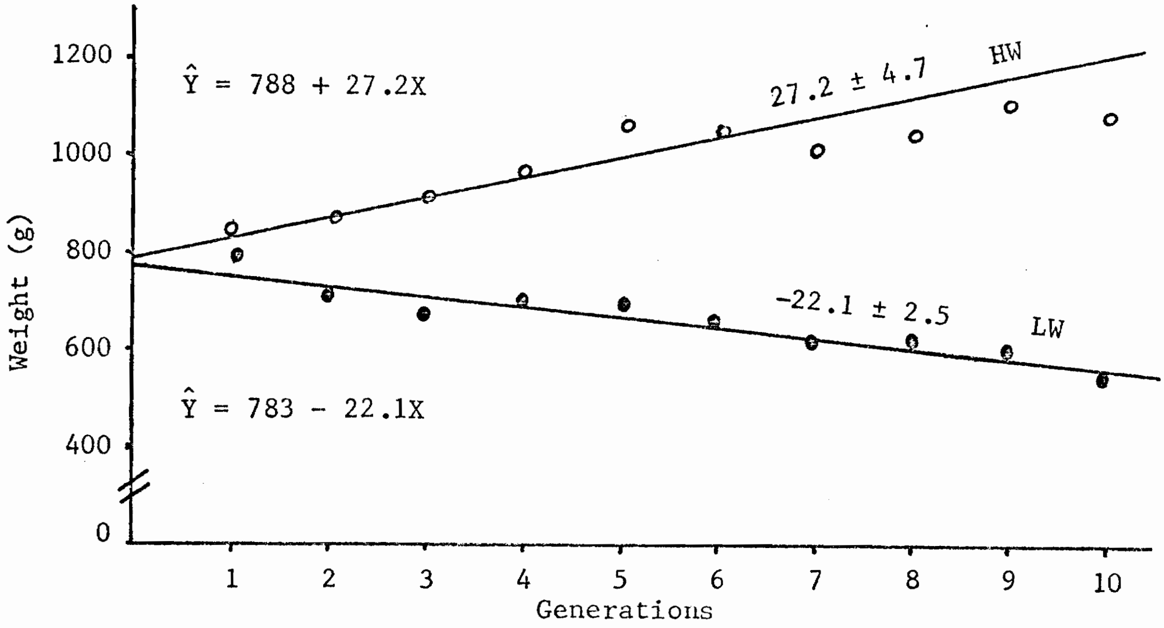
[1] HW - High weight line.
LW - Low weight line.

Table 13. Analysis of variance for generations, lines sexes and their first order interactions for body weight at eight weeks of age.

Source of var.	degrees of freedom	mean squares
Generations (G)	9	1.39 **
Lines (L)	1	204.78 **
Sexes (S)	1	59.15 **
G x L	9	3.50 **
G x S	9	.08 **
L x S	1	2.01 **
Error[1]	7419	.02

[1] The second order interaction was pooled with the error term.

** $(P \leq .01)$.



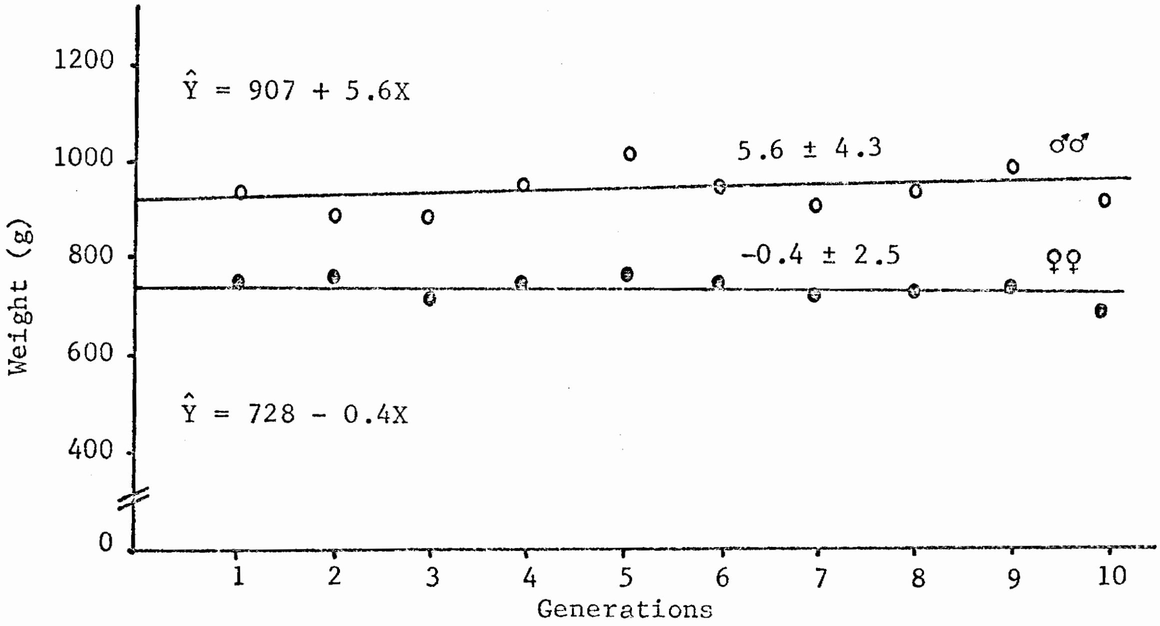


Figure 9. Line-generation (top) and sex-generation (bottom) interaction for body weight at eight weeks of age.

in phenotypic variation was the highly significant difference between lines from an analysis of variance of the coefficients. The larger coefficients of variation in the LW line than the HW line was in agreement with the results of Maloney *et al.* (1967). They are, however, opposite to what one normally thinks of in domestic animals in that the mean and variances are usually positively correlated. This suggests that the percentage of the population as parents from the HW line will decrease and lessen the reproductive capabilities of the line with continued selection. In the LW line, with the large amount of variation remaining, retardation of reproduction should not be realized with increased selection pressure.

Genetic correlations between sexes and the heritability of sexual dimorphism for body weight:

Genetic covariances between sexes for body weight, genetic variances for males and females, and genetic correlations between males and females for body weight at eight weeks of age are shown in Table 14. The genetic correlation was essentially unity for each generation with some minor variations and the pooled values over all generations was 1.00 which was similar to the .98 value obtained by Robertson's (1959) method from the analysis in Table 13. Although these estimates are high they cannot be considered as unity because the line-sex interaction was highly significant. The sizes of these values were consistent with those

Table 14. Male-female genetic covariances[1], male genetic variances[2], female genetic variances[3], and genetic correlations between males and females[4] for body weight at eight weeks of age.

Gen.	σG_{12}	$\sigma^2_{G_1}$	$\sigma^2_{G_2}$	$r_{G_{12}}$ [5]
F_1	1,318	1,022	1,498	1.06
F_2	8,552	9,421	7,562	1.01
F_3	15,476	20,599	11,912	0.99
F_4	20,372	25,057	16,457	1.01
F_5	33,271	42,126	26,162	1.00
F_6	39,302	50,000	30,804	1.01
F_7	38,157	47,814	29,983	1.01
F_8	44,675	53,407	37,286	1.00
F_9	60,529	76,534	47,775	1.00
F_{10}	65,676	73,845	58,227	1.00
Total	327,328	399,785	267,716	1.00

[1] σG_{12}

[2] $\sigma^2_{G_1}$

[3] $\sigma^2_{G_2}$

[4] $r_{G_{12}}$

[5] Calculated from the covariance analysis.

of other investigators. Becker _et_ _al_. (1964) reported a genetic correlation of .80 between sexes for body weight in Leghorn chickens. They also reported values of .91 for 24-week body weight in turkeys and 1.00 for body weight at four weeks in _Coturnix_. Yoshida and Collins (1967) obtained a genetic correlation of .90 between sexes for four-week weight in _Coturnix_ and Eisen and Legates (1966) reported a value of .90 for six-week weight in mice. By contrast, Horton and McBride (1964) obtained considerably lower values of .52 for four-week body weight and .48 for eight-week body weight in chickens.

Heritability estimates for body weight at eight weeks of age are presented in Table 15 by sexes and generations. Mean realized heritabilities (cumulative divergence ÷ cumulative selection differential) for males and females were .28 and .24, respectively. Estimates from maternal half sib and full sib correlations were somewhat larger than the realized heritabilities whereas those based on paternal half sib correlations were comparable to the realized values for males and considerably less than those for females. The main point of interest, however, is the difference between the heritabilities in males and females. This can best be compared from the realized heritabilities based on the regression of divergence on the selection differential because such estimates have standard errors. This enables one to determine if the regressions are different from each other. The heritability

Table 15. Heritability estimates of body weight at eight weeks of age by sex and generation.

Sex	Gen.	Realized[1]	4S/(S+D+E)	4D/(S+D+E)	2(S+D)/(S+D+E)
♂♂	P_1	--	.90	.52	.71
	F_1	.23	.26	.48	.37
	F_2	.33	.21	.48	.34
	F_3	.35	.24	.78	.51
	F_4	.31	.45	.65	.55
	F_5	.34	.36	.32	.34
	F_6	.34	-.19	.85	.33
	F_7	.28	.18	.34	.26
	F_8	.28	.41	.17	.29
	F_9	.30	-.06	.74	.34
	F_{10}	.28	.61	.09	.35
	$\bar{x}$		.31 ± .22	.49 ± .23	.40 ± .13
♀♀	P_1	--	-1.01	.04	.52
	F_1	.21	.13	.65	.39
	F_2	.32	.07	.05	.06
	F_3	.27	.02	.76	.39
	F_4	.28	.21	.84	.56
	F_5	.30	-.07	.99	.46
	F_6	.27	-.34	.61	.29
	F_7	.23	.29	.24	.27
	F_8	.23	.40	.48	.44
	F_9	.25	.72	-.06	.33
	F_{10}	.24	.05	.30	.18
	$\bar{x}$		.04 ± .29	.44 ± .32	.35 ± .14

Realized[2]
♂ .28 ± .02
♀ .22 ± .01

---

[1] $\Sigma(\bar{x}_{HW} - \bar{x}_{LW}) \div \Sigma ix$

[2] $b(\bar{x}_{HW} - \bar{x}_{LW}) \cdot \Sigma ix$

was .28 ± .02 for males and .22 ± .01 for females with the difference being significant. Thus we can say with confidence that the heritability of eight-week weight is higher for males than for females.

Theoretically the difference between heritabilities for the males and females should be an estimation of the genetic variation for sexual dimorphism. The difference between heritabilities for males and females were .04, .06, .05, .05 and .27 for the realized^1, realized^2, full sib, maternal half sib, and paternal half sib procedures, respectively. The first four values were in excellent agreement whereas the difference between estimate based on paternal half sib correlation was inconsistent. There was considerable variation among generations for estimates based on paternal half sib correlations and the difference of .27 was probably an overestimate. It may be assumed that for juvenile body weight male heritabilities are about .05 higher than those for females.

Heritability estimates of the sex dimorphism for body weight at eight-weeks of age _per se_ were calculated by taking the difference between the male and female full sib family means. This procedure considered sexual dimorphism as a single trait and two heritability estimates were obtained, one in the broad sense that was estimated by the between and within line procedure of Falconer (1960) and the other in the narrow sense from paternal half sib correlations as outlined by King and Henderson (1954). The estimate in the broad sense for the ten generations was .17 whereas the one in the narrow sense was .02. The latter which measures additive gene action per se is in good agreement with the estimates of .01, .08, and .14 for sex dimorphism of mice at 3, 6, and 8 weeks of age, respectively, (Eisen and Legates, 1966). Further, the broad and narrow heritabilities obtained here bracketed the value of .09 reported by Yoshida and Collins (1967) for four week body weight in Coturnix. The difference between the broad and narrow estimates suggests that the heritability of the nonadditive genetic effects influencing sex dimorphism was about .15.

Although, these heritability estimates suggests that additive genetic variation for sex dimorphism of body weight at eight weeks of age is low, it may be considered real because of the highly significant line-sex interaction (Table 13 and Figure 10). A biological hypothesis for the cause of the significant line-sex interaction is necessary and one concerning the genetic mechanism involved for sex dimorphism will be presented later in this dissertation.

The comparison of the predicted and actual genetic response to selection should be close if the parameters for prediction are good estimates. Presented in Table 16 are the predicted (selection differential in g times the heritability in the narrow sense) and actual responses obtained for sex dimorphism of eight-week body weight. The ratios of

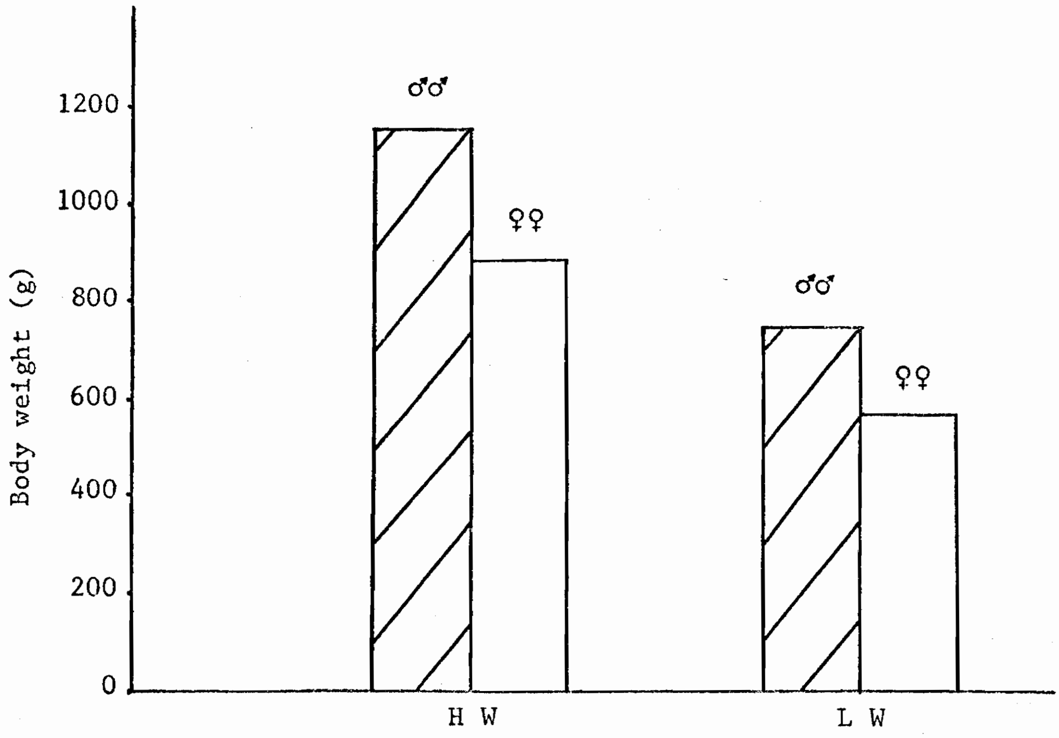


Figure 10. Body weight response by sexes for the HW and LW lines.

Table 16. Predicted[1] and actual response of sex dimorphism of eight-week body weight and the ratio of actual to predicted response.

	Response					
	HW[3]			LW[3]		
Gen.	Predicted	Actual	Ratio[2]	Predicted	Actual	Ratio[2]
F_1	167	169	1.01	167	182	1.09
F_2	172	214	1.24	184	153	0.83
F_3	217	245	1.13	153	145	0.95
F_4	247	247	1.00	147	160	1.09
F_5	249	300	1.20	161	213	1.32
F_6	301	267	0.89	215	169	0.79
F_7	269	245	0.91	171	154	0.90
F_8	247	247	1.00	156	166	1.06
F_9	249	311	1.25	168	188	1.12
F_{10}	310	260	0.84	190	198	1.04

[1] (Selection differential times the heritability in the narrow sense)

[2] Ratio of actual to predicted response of sex dimorphism of eight-week body weight.

[3] HW - High weight line.
LW - Low weight line.

of actual to predicted were essentially unity for both the HW and LW lines demonstrating the reliability of the estimated parameters.

General

The estimation of additive genetic variance for sexual dimorphism of eight week body weight showed that this was a measurable trait with a low heritability. The demonstration that sexual dimorphism is a genetic trait is consistent with the conclusions of Horton and McBride (1964) who interpreted a strain-sex interaction to indicate that sexual dimorphism was a quantitative trait in chickens. They explained the sex dimorphism as being due to higher selection intensities for sires than dams. This hypothesis is probably incorrect, because, although the selection applied to sires is more intense than for dams the contribution of the sire is equal for male and female progeny. Weighting of the selection differentials by the number of male and female offspring (the effective selection differential) will be essentially equal unless natural selection favors one sex over another.

To demonstrate this point, selection intensities (selection differentials ÷ phenotypic standard deviations), weighted for male and female progeny by lines and generations are presented in Table 17. During ten generations of selection the selection intensities for body weight at eight weeks

Table 17. Selection intensities[1] of body weight at eight weeks of age weighted by male and female progeny.

	HW[2]		LW[2]	
Gen.	Males	Females	Males	Females
F_1	1.39	1.64	1.48	1.84
F_2	0.95	1.08	0.74	0.83
F_3	1.48	1.76	0.59	0.49
F_4	1.04	0.86	1.10	1.05
F_5	0.79	0.92	0.45	0.54
F_6	0.63	0.70	0.85	0.99
F_7	0.88	1.15	1.00	1.44
F_8	0.76	1.00	1.13	1.40
F_9	0.89	0.88	1.16	1.07
F_{10}	0.57	0.56	0.99	1.04
$\bar{x}$	0.94	1.07	0.93	1.04

[1] (Selection differential ÷ the standard deviation)

[2] HW - High weight line.
LW - Low weight line.

of age were slightly higher for female than for male progeny. Thus, Horton and McBride's (1964) hypothesis was not a valid explanation for the results of this study and the change in sexual dimorphism was due to something other than higher selection intensities for sires than for dams.

What then caused the line-sex interaction? If male and female progeny received an equal allotment of chromosomes from their parents, one would expect the ratio of male to female body weight not to change over a given number of generations. This hypothesis is based on the assumption that the genes for body weight are randomly distributed among chromosomes. In the chicken, the male is the homogametic sex and receives two complete sex chromosomes, one from each parent. Ohno _et al_. (1960) presented evidence of positive heteropycnosis in the female, and Shoffner (1965) and Zervas (1962) suggested that the heteropycnotic sex chromosome was not inert. Since the W chromosome is only a small fraction of the size of the X chromosome it is doubtful that a comparable compliment of (compared to the X chromosome) genes would be carried on the W chromosome. This has in fact been demonstrated in qualitative studies with the barring and late feathering genes (Hutt, 1949; Siegel, 1957). Therefore, it is proposed that the line-sex interaction resulted from the genes affecting body weight located on the extra X chromosome possessed by the male. These genes probably acted in an additive manner because the additive estimate of sex dimorphism for eight week body weight was a good estimator when tested in predicted responses of sex dimorphism.

The argument for sex-linked additive genetic effects for body weight can be further strengthened by looking at the heritability estimates of body weight based on maternal half sib correlations calculated on a within sex basis (Table 16). Since the dam contributes an X chromosome to her male progeny and a W chromosome to her female progeny, the 4D/(S + D + E) estimate for body weight should be greater for male than female progeny if additive sex-linkage is present, i.e., more additive genetic variability for eight week body weight in her male progeny than in her female progeny. The 4D/(S + D + E) heritability for male progeny was .05 higher than that for female progeny (Table 15). More conclusive evidence is available from the data in Table 15, namely that the realized heritability for weight was significantly higher for males than females with the difference between heritabilities being .06.

There is one more avenue to possibly strengthen the the hypothesis for the role of sex-linked additive genetic effects on sex dimorphism in chickens. Shoffner (1965) reported that the number of macrochromosomes detectable in the domestic fowl was 6 to 8 pairs, depending on the author. If one assumes an average of seven pairs then the diploid number of chromosomes would be 14 in the male and 13 in the female. Assuming equal effects of each chromosome there should be seven percent more genetic variation in males than females. Since the realized heritability for 8-week body weight of females was .22, seven percent of this would be .015, i.e., a heritability of .015 for sexual dimorphism in the narrow sense. This value was essentially the same as the .02 obtained for the heritability of sexual dimorphism in the narrow sense (pg. 68). This reasoning supports the hypothesis for additive sex linkage as an explanation of genetic changes in sex dimorphism of eight week body weight in chickens.

It is interesting to note that the realized heritability of breast angle was .21 for males and .17 for females in Experiment 1 (Table 6). Applying the same reasoning for this trait of a seven percent difference in favor of males yields a comparable situation to breast angle as with body weight.

The finding of additive sex-linked effects in this experiment was consistent with the speculations of Beilharz (1960) who found in both rabbits and chickens that there was more genetic variability in progeny with sex opposite to that of the parent. Siegel (1962a) also suggested that additive sex-linked effects were present for body weight on the basis of higher heritabilities for males than females for eight week body weight. In this dissertation the realized heritability of body weight was .28 for males and .22 for females. The difference of .06 was in close agreement with the estimate of .02 for sexual dimorphism <u>per se</u>. Thus, although both Beilharz (1960) and Siegel (1962a) were apparently correct neither examined either the genetic correlations between sexes or the genotype-sex interaction to support their suppositions.

If more genetic progress can be obtained from the second X chromosome in selecting for body weight it should appear in homogametic female mammals. This has been shown in cattle by Stonaker (1963) who reported that weaning weights of Herford female calves were greater than those of bulls. Although male cattle are heavier than females, the physiological environment of the sexes are genetically fixed and this allows for larger adult body weight of males. A comparable physiological environment exists for chickens. However, the ratio of male to female body weight as such is not an indication of the degree of sex-linked additive genetic effects present. Instead it is the change of this ratio that is important when one considers the quantitative inheritance of characters affected by additive sex-linked genes.

In summary it appears, from the literature and the present experiment, that there is a high genetic correlation between body weights of males and females. This correlation is not unity because genotype-sex interactions can be demonstrated and these interactions are apparently caused by additive sex-linked genes.

SUMMARY AND CONCLUSIONS

This dissertation consisted of two phases. One phase was to study the realized heritabilities of correlated traits and the second was to investigate the inheritance of sexual dimorphism of body weight.

The first phase involved data from four generations of a double two-way selection experiment for body weight and breast angle at eight weeks of age. Phenotypic changes in both traits were measured in each subpopulation. Breast angle was considered a correlated trait in the weight subpopulation and body weight a correlated trait in the angle subpopulation.

There was a significant divergence between lines for both selected traits. The divergence of body weight in the angle population was significant in the F_1, F_3, and F_4 generations. Divergence of breast angle in the weight subpopulation was significant in the F_2 and subsequent generations. There was asymmetry of response to direct selection for breast angle, with the response in the narrow direction being greater than that in the broad direction. Through four generations of selection for body weight the response in the high and low directions was symmetrical.

Heritabilities of body weight and breast angle were obtained each generation in each subpopulation. Realized heritabilities of body weight were .28 for males and .24 for females. Realized heritabilities for breast angle were .21 for males and .17 for females.

Heritabilities of the unselected traits were obtained by the cumulative difference between lines $\div \Sigma iY_X$ and the regression of divergence on ΣiY_X. Validity of this procedure was tested by comparisons of correlated realized heritabilities with the heritabilities obtained when the traits were under direct selection. The correlated realized heritability of breast angle in the weight lines was greater than it was for body weight in the angle lines. Examination of the components of the correlated realized heritability showed that they were the ratio of the genetic to the phenotypic covariances of the two traits. Therefore the procedure for estimation of correlated realized heritabilities may contain random biases. These would be minimized by regression of the cumulative divergent response on ΣiY_X.

A second experiment involved ten generations of data from a bidirectional selection experiment for body weight at eight weeks of age. The data were subjected to an analysis of variance considering lines, sexes, and generations as main effects. As expected all main effects and first order interactions were significant. The genetic correlation obtained between sexes for eight week body weight from this analysis was .98.

The heritability of sex dimorphism for body weight was .02. Predicted response of sex dimorphism using the .02

heritability yielded estimates very near the actual response obtained by selection. The realized heritability for divergence of selected lines was .28 ± .02 and .22 ± .01 for males and females, respectively. These biological evaluations demonstrated the reliability of the heritability estimate of sex dimorphism and the procedures for obtaining it.

The genetic changes in sex dimorphism for body weight, as shown by a slightly greater response of males than of females, were due to additive sex-linked genes. Several lines of evidence were presented to support this hypothesis.

VITA

The author, Ira Franklin Carte, was born in Fayette County, West Virginia, January 21, 1938, the first child of Dova Wesly and Mary Lee Carte. He was reared in Botetourt County, Virginia and attended Buchanan High School. He received his high school diploma from the U.S.A.F.I. while serving in the U.S. Navy from 1955 to 1959. He entered Virginia Polytechnic Institute in September, 1959 and received the Bachelor of Science Degree in Poultry Science in June, 1964 and the Master of Science Degree in Poultry Science in June, 1966. He is a member of the American Genetic Association, Genetics Society of America, Poultry Science Association, Alpha Zeta, Phi Sigma, Sigma Xi, and Masonic Lodge. He is married to the former Miss Gayle Patricia Spencer of Lithia, Virginia and has one son, Ira Cameron.

Ira F. Carte

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CORRELATED RESPONSES AND SEXUAL DIMORPHISM IN BIDIRECTIONAL SELECTION EXPERIMENTS

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Abstract

This dissertation involved two experiments, (1) the study of realized heritabilities of correlated traits, and (2) the study of the inheritance of sexual dimorphism of body weight.

The first experiment included data from four generations of double two-way selection for body weight and breast angle at eight weeks of age. Breast angle was considered a correlated trait in the weight subpopulation and body weight a correlated trait in the angle subpopulation. There was a significant divergence between lines for both selected traits. The response to direct selection for breast angle was asymmetrical with the response in the narrow direction being greater than that in the broad direction. The response of body weight to two-way selection was symmetrical through the F_4 generation.

Divergence of body weight between the lines selected for breast angle was significant in the F_1, F_3, and F_4 generations. Divergence of breast angle between the lines selected for body weight was significant in the F_2 and subsequent generations.

Heritabilities of the unselected traits were obtained by the cumulative difference between lines divided by the expected secondary selection differential and by the regression of the cumulative difference between lines on expected secondary selection differential. The correlated realized heritability of breast angle was greater in the weight lines than was the correlated realized heritability for body weight in the angle lines. Examination of the components of the correlated realized heritability showed that they were the ratio of the genetic to phenotypic covariances of the two traits.

The second experiment involved the investigation of sex dimorphism for body weight at eight weeks of age. The heritability estimate for sex dimorphism of this trait was .02, and the genetic correlation of it in males and females was .98. The genetic variability (.02) in sex dimorphism was evidenced by a greater response in males to selection for eight-week body weight than in females. The biological reason for this was additive sex-linkage.