CORRELATED RESPONSES AND PARAMETER CHANGES IN A BIDIRECTIONAL SELECTION EXPERIMENT FOR BODY WEIGHT IN CHICKENS

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

MASTER OF SCIENCE

in

POULTRY SCIENCE

December, 1965

Blacksburg, Virginia

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INTRODUCTION

In the study of the inheritance of quantitative traits, the development of theory and experimentation to test its validity are analogous to the two wheels of a cart. One wheel by itself cannot proceed a cart. Although in many cases, quantitative genetic theory has advanced ahead, only properly designed and conducted experiments can validate it. In addition, such experiments can suggest a re-examination of certain areas and provide data for further theoretical development. Selection experiments and validation of theory are important to industry because such knowledge is basic to the development of more effective breeding systems.

When two traits are genetically correlated, selection for one trait causes a direct change in the other. The correlated response is proportional to the response of selected trait and the regression coefficient of the breeding value of the unselected trait on the breeding value of the selected trait. Although this is quite clear, several important practical and theoretical problems still exist. For example, little is known either about the cause of asymmetry in correlated responses or the magnitude of the realized heritabilities of correlated traits when selection is practiced for a particular characteristic.

The investigation reported here involved truncation-type individual selection in divergent directions for body weight of chickens at eight weeks of age. Phenotypic changes were measured from generation to generation, within each line, for the selected trait and for unselected characteristics. Unselected traits were adult body weight at 24 and

38 weeks of age, age at sexual maturity, egg weight, and percentage hen-day egg production to January 1.

Expected secondary selection differentials for unselected traits were estimated each generation within lines by the phenotypic regression of unselected traits on body weight at eight weeks of age. Then, corrected realized heritabilities and corrected realized genetic correlations between the selected and unselected traits were obtained. To my knowledge this was the first time that this procedure had been used to calculate the realized heritability of a correlated trait in a selection experiment. Since the theory of this method was correct, if the results were in agreement with the value of heritabilities reported by others and consistent with those obtained by component analyses in the population under study, then this method may be utilized for the calculation of realized heritabilities of correlated traits. This procedure facilitates such advantages as: (1) Corrected realized genetic correlations between selected and unselected traits may be obtained without double two-way selection experiments, and (2) Corrected realized heritabilities may be obtained for many correlated traits from a selection experiment for a particular trait.

Predicted correlated responses using heritability estimates based on component analyses were evaluated in comparison with actual correlated responses. Such comparisons facilitated evaluation of the reliability of heritability estimates based on component analyses.

The information reported herein could be important in commercial poultry breeding because it provides geneticists with procedures for the prediction of the response of other traits to selection when direct selection is for a single trait. Extension of this theory to simultaneous direct selection for several traits would enable prediction of the aggregate responses to selection.

REVIEW OF LITERATURE

Heritability

Heritability (h^2) has been defined in several ways (Lush, 1948). The ratio of additive genetic variance to phenotypic variance is considered as heritability in the narrow sense and symbolically may be expressed as:

$h^2 = \sigma_G^2 / \sigma_P^2 = \sigma_G^2 / \sigma_G^2 + \sigma_I^2 + \sigma_E^2 + \sigma_{HE}^2$ where,

σ_G^2 are additive deviations, σ_P^2 is phenotypic variation, σ_D^2 are dominance deviations, σ_I^2 are epistatic deviations, σ_E^2 are environmental deviations and σ_{HE}^2 are deviations due to the joint effect of heredity and environment. The combination of σ_G^2, σ_D^2 and σ_I^2 are the total heritable deviations (σ_H^2) which yields heritability estimates in a broad sense and may be expressed symbolically as:

$$h^2 = \sigma_H^2 / \sigma_P^2 = \sigma_G^2 + \sigma_D^2 + \sigma_I^2 / \sigma_G^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2 + \sigma_{HE}^2$$

Lerner (1958) expressed phenotypic variance as:

$P^2 = \sigma_H^2 + \sigma_E^2 + 2\ \mathrm{Cov}_{HE} + f(HE)$ where,

covariance HE is a deviation due to genotype-environment correlations because Cov_{HE} is equal to $r_{HE}\sigma_H\sigma_E$, $f(HE)$ is a deviation due to genotype-environment interactions.

Heritability has also been expressed by Falconer (1960) as the regression of breeding value on phenotypic value ($h^2 = b_{GP}$) and as the square of the correlation between breeding values and phenotypic values ($h^2 = r_{GP}^2$).

Lerner (1950) described the estimation of heritability from a variance component analysis which utilized information based on full and half sib correlations. The statistical model appropriate to a heirarchial or nested type of classification is commonly used with chicken. The model is:

$X_{ijk} = u + S_i + D_{ij} + E_{ijk}$ where,

X_{ijk} is the record of the kth progeny of the jth dam mated to the ith sire. Heritability may then estimated from the variance components by use of 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 groups of full-sibs. The genetic interpretation of these variance component for chickens are:

S = 1/4 additive + 1/16 epistasis (additive x additive) + sex linkage (in female progeny only)

D = 1/4 additive + 1/4 dominance + 6/16 epistasis (3/16 additive x additive + 2/16 additive x dominance + 1/16 dominance x dominance) + maternal

E = 1/2 additive + 3/4 dominance + 41/16 epistasis (12/16 additive x additive + 14/16 additive x dominance + 15/16 dominance x dominance)

Heritability estimates based on full and half sib correlations may be overestimated because of the inclusion of sex-linked, maternal and non-additive effects which are multiplied by either two or four depending on the formula used.

A very reliable measure of additive gene action is heritability obtained by dividing the difference between the means of two lines selected in opposite directions by the cumulative selection differential (Student, 1934). The recent development of control populations enables the refinement of being able to calculate the heritability in both upward and downward directions and thereby minimize influences of asymmetry in response of the divergently selected lines. Falconer (1953) has also provided a very reliable method for two-way selection experiments by the regression of response on cumulative selection differentials. He has termed this the realized heritability. Other methods are available which yield estimations of heritability between the broad and narrow senses. Examples are regression of offspring on midparent and intrasire regression of offspring on dam.

Body weight:

Juvenile body weight: Siegel (1962a) reported realized heritabilities of body weight at eight weeks of age, based on a two-way selection experiment, of .23, .33, .35, and .31 for males and .21, .32, .27, and .28 for females in the F_1, F_2, F_3, and F_4 generations, respectively. He also summarized 176 published heritability estimates for the juvenile body weight of chickens and reported that the median heritability was .41 with an interquatile range of .29 to .54. Maloney et al. (1963a) reported from a two-way selection experiment for twelve-week body weight realized heritabilities of .34 for the high line, .07 for the low line, and .22 for the divergence of the lines. Recently, Kinney and Shoffner (1965) reported unweighted average estimates of heritability for juvenile body weight. Estimates based on 4S, 4D, 2(S + D) and 2(intrasire regression of offspring on dam), were .35, .52, .52, and .40 in males, .39, .71, .56, and .45 in females, respectively. These numerous reports indicate that the juvenile body weight of chickens is moderately heritable.

Adult body weight: A summary of heritability estimates for adult body weight by Soffner and Sloan (1948) showed a range from .22 to .75. Peeler *et al*. (1955) reported that heritability estimates of body weight at sexual maturity in Rhode Island Red pullets were .85, .71, and .72 based on 4S, 2(S + D), and 2(intrasire regression of offspring on dam), respectively. Nordskog *et al*. (1964) obtained realized heritabilities of .43 ± .04 and .48 ± .05 for adult body weight from selection experiments which lasted seven years. Kinney and Shoffner (1965) summarized the heritability estimates of this trait and obtained values of .54, .53, .46, and .54 for on 4S, 4D, 2(S + D), and 2(intrasire regression of offspring on dam), respectively. Estimates in these reports demonstrate the high heritability of adult body weight.

Egg weight:

King and Henderson (1954b) reported a mean of .57 for the previously reported heritability estimates of egg weight demonstrating that it was highly heritable. Nordskog and Festing (1962) computed realized heritabilities of .56 and .66 in lines selected for high and low egg weight, respectively. These values were from a four-generation selection experiment with White Leghorns. They subsequently (1964) reported after seven generations, in the same experiment, a realized heritability of .42 ± .06 and an estimate of .39 ± .04 from component analyses.

Sexual maturity:

Since sexual maturity is influenced largely by changes in photoperiod, this environmental effect would deflate the heritability through increases in the phenotypic variance. Thus when several hatches are involved corrections should be made to minimize this biasis. King and Henderson (1954b) summarized heritability estimates for age at sexual maturity and found a mean value of .27. Siegel (1963b) reported mean estimates of .39 and .49 for age at sexual maturity in lines selected in divergent directions for either eight-week body weight or breast angle for four generations. King (1961) found the heritability estimate based on sire component for sexual maturity was .26 for the Cornell randombred population. Heritability of this trait may also be influenced by heterosis (Ghostley and Nordskog, 1951; Glazener *et al*. 1952) and maternal effects (King, 1961; King *et al*., 1963). Kinney and Shoffner (1965) summarized the heritability estimates of this trait and reported values of .30, .53, .34, and .28 based on 4S, 4D, 2(S + D) and 2(intra-sire regression of offspring on dam), respectively.

Egg production:

The egg production of chickens has been measured in many different ways with the heritability estimates being consistently low. Oliver *et al*. (1957) reported heritability estimates of .14 to .15 for egg production based on five different measurements. Since in this thesis the data for egg production are obtained from the pullets hatched in March and terminated on January 1, the literatures cited are those where percentage egg production was measured for either four months of lay or to January 1. Jerome *et al.* (1956) obtained a heritability estimate of .29 for number of eggs laid during the first four months of lay. Oliver *et al.* (1957) and Yamada *et al.* (1958) estimated heritabilities of .15 and .19, respectively, for percentage egg production to January 1. A mean value of .36 for the data of two successive years was computed by King (1961). The above results were obtained from White Leghorns. In White Rocks, Siegel (1963) reported mean estimates of .21 and .22 for egg production to January 1 in the lines selected for eight week body weight and breast angle, respectively, for four generations.

The literature reporting heritability estimates of quantitative traits in chickens is voluminous. Since numerous methods for estimation have been employed with many different populations, the literatures provide only a crude criterion. Estimates of the heritability of body weight, age of sexual maturity, egg weight, and egg production reported in the literature have been summarized in several recent papers and only the more pertinent ones have been alluded to here.

Selection and the heritability of correlated traits:

A review of the selection differential and the heritability of correlated traits is necessary because they are concerned with the essential point of this thesis. Flower *et al.* (1964) indicated that to predict genetic change for any trait required simultaneous consideration of all traits under either direct or indirect selection. Harvey and Bearden (1962) presented procedures for the calculation of expected change for each trait in standard deviation units when selection was conducted for two traits. Magee (1965) investigated the same problem associated with phenotypic differences between the average of the parents ($\check{P}$) and the average of the population ($\bar{P}$) in which they were born. His conclusion was that in any case where selection is on the basis of more than one trait, e.g., trait 1 and trait 2, then the expected genetic change in trait 1 between one generation and the next (ΔG_1) is not equal to heritability 1 times ($\check{P}_1 - \bar{P}_1$), but rather is equal to $(b_1V(G_1) + b_2CovG_1G_2)(\check{P}_1 - \bar{P}_1)/b_1V(P_1) + b_2CovP_1P_2$. The bi values were determined by the index used in selection $I = b_1P_1 + b_2P_2$. He pointed out the difference between the selection differential for a directly selected single trait and the secondary selection differential for correlated traits, and proposed that the term selection differential should be reserved for the case where there was mass selection for only one trait. This was because the changes in correlated traits when selection was for a particular trait were not usually equal to heritabilities of correlated traits multiplied by $\check{P} - \bar{P}$ (average phenotype for correlated traits used as parents minus the average for correlated traits of the population in which the parents were born).

Yamada (1965) suggested that the expected secondary selection differential in unselected traits when selection was conducted for a particular trait was equal to the selection differential of selected trait multiplied by phenotypic regression coefficient of correlated traits on the selected trait only if selected and unselected traits were correlated with each other and the two variables were normally distributed. He gave the formula as follows:

$$iYx = iX\ b_{Pyx} = iX\ (\sigma G_{xy} / \sigma P_{x}^{2} + \sigma E_{xy} / \sigma P_{x}^{2})$$
$$= iX\ (b_{Gyx}\ h_{x}^{2} + b_{Eyx}\ (1 - h_{x}^{2}))$$ where,

iYx: expected secondary selection differential for unselected traits.

iX: selection differential for selected trait.

b_{Pyx}: phenotypic regression coefficient of Y on X.

b_{Gyx}: genetic regression coefficient of Y on X.

b_{Eyx}: environmental regression coefficient of Y on X.

h_{x}^{2}: heritability of selected trait.

Genetic Correlation

Correlated responses of unselected traits may result from genetic effects, environmental influences and a combination of the two. Although pleiotropy may be a permanent cause of a genetic correlation between two traits, linkage can be important as a transient effect, particularly in populations derived from crosses between divergent strains. The theory of genetic correlations has been discussed by Hazel (1943) and Lerner (1950). Falconer (1952) extended the theory of genetic correlation to include the interaction of the same trait of the same genetic groups to two different environments.

Recently Rendell (1963) discussed the various ways in which genetic correlations may be generated. He suggested that when the development of two characteristics was dependent upon common resources, it was reasonable to assume that a proportion of them would be used to develop one trait and the remainder would be used in the development of the other. Rendell explained that changes in common resources or in its proportion to the total resources or both could lead to a change in the genetic correlation between two traits.

Knowledge of the genetic correlation which is the association of breeding values between two traits is essential in the prediction of changes in a population under selection. Genetic correlations may be estimated from components of variance and covariance, regression of offspring on parent, iso-genic populations and two-way selection experiments. Computational procedures may be found in Becker (1964). Of the various methods for obtaining genetic correlations between two characteristics, properly designed selection experiments provide the most nearly valid estimates. The problems in sampling involved in the employment of the other methods have been discussed by Robertson (1959) and VanVleck and Henderson (1961).

Juvenile body weight and adult body weight:

Krueger (1952) observed in four breeds of chickens that a positive genetic relationship existed between body weight at ten weeks of age and at housing. Peeler et al. (1955) reported for Rhode Island Reds genetic correlations of .79 from sire variance and covariance and .68 from dam-offspring covariance between body weight at ten weeks of age and at sexual maturity. Hale (1961) obtained a genetic correlation of .60 ± .13 between body weight at eight weeks of age and at housing in White Wyandottes. A genetic correlation of .36 between body weight at eight and 24 weeks of age was obtained in a meat-type synthetic line by Jaap (1962). Realized genetic correlations between body weights at 24 and 38 weeks with body weight at eight weeks of age were reported in White Rocks by Siegel (1963b). Respective correlations between eight and 24-week weight in the F_1, F_2, F_3 and F_4 generations were .43, .87,

.42, and .84 while those between eight and 38-week weight were .48, 1.02, .32 and .71. Kinney and Shoffner (1965) reported genetic correlations between eight-week and mature body weights were .43 ± .12 in a meat line and .37 ± .12 in an egg production line. Both lines were developed from a synthesized meat-type population.

The genetic correlations between juvenile body weight and adult weight were consistently high in all published reports. This relationship would be expected as the correlations are part-whole. The fact that they were considerably less than unity, however, demonstrated that genes that influenced juvenile and post-juvenile body weight were not synonymous.

Juvenile body weight and egg weight:

A positive and moderately high genetic relationship between these two traits has been reported by several investigators. Estimates of this relationship ranged from .05 in White Wyandottes (Hale, 1961) to .65 in six different breeds (Ghostley and Nordskog, 1956). Jaap et al. (1962) obtained an estimate of .25 between these traits in a meat-type synthetic line. Genetic correlations of .40, .27, and .21 in 1958, 1959, and 1960, respectively were reported by Merrit and Gowe (1962) for a meat-type randombred population. Realized genetic correlations between eight-week body weight and egg weight of .57, .32, .18 and .24 for four generations of selection for the former trait were reported for White Rock chickens by Siegel (1963b).

Juvenile body weight and age at sexual maturity: A positive genetic correlation between body weight at 10 weeks of age and age at sexual maturity was found by Krueger _et al_. (1952) and Dillard _et al_. (1953). Krueger's experiments involved four different breeds of chickens and Dillard's was conducted with New Hampshires. Peeler _et al_. (1955) estimated the correlations between these traits in Rhode Island Reds was .26 and .33 from sire variance and covariance and from dam-offspring covariance, respectively. From dam-variance and covariance, however, the estimate was .14. Hale (1961) reported estimates, in Wyandottes, of .61 ± .18 and -.27 ± .21 from sire and from dam variance and covariance, respectively. Hatch effects were ignored in the analysis of his data. In contrast, Merrit and Gowe (1962) in a meat-type randombred population and Siegel (1963b) in White Rocks, found negative genetic correlations that ranged from -.11 to -.30 between these two traits.

King _et al_. (1963) reported in a randombred population of White Leghorns genetic correlations between juvenile weight and age at sexual maturity of 0, -.23 and -.17 based on paternal half sib, maternal half sib, and full-sib variances and covariances, respectively. Kinney and Shoffner (1965) obtained genetic correlations between these characteristics of -.81 ± .93 in a meat line and .21 ± .53 in an egg production line. Both lines has been developed from the same synthetic meat-type population. Although there were conflicting reports, there appeared to exist, in general, a negative genetic relationship between juvenile body weight and age at sexual maturity in most populations of chickens.

Juvenile body weight and egg production:

Among the literatures reported to date there were few estimates of the genetic correlations between juvenile body weight and part year egg production. The values, however, have been consistently negative. McClung (1958) reported a genetic correlation between body weight at eight weeks of age and egg production for four months of lay as -.04, -.15 and -.21 in three different lines of chickens. Siegel (1963b) obtained in White Rocks hatched in early March a realized genetic correlation of -.32 between body weight at eight weeks of age and egg production to January 1. A genetic correlation of -.26 ± .16 between body weight at eight weeks and short term egg production in meat-type New Hampshire was estimated by Enfield (1960). Kinney and Shoffner (1965) reported the correlations between these traits was -.40 ± .13 in meat and -.06 ± .26 in egg production lines of meat-type chickens.

Selection Experiments and Correlated Responses

Many selection experiments have been conducted with chickens in an effort to change the population means for particular quantitative traits. Unfortunately, however, precise interpretation of results from selection experiments has been hampered by a lack of estimation of genetic response independent of environmental trends and the effects of inbreeding. Dickerson (1960) summarized the theoretical bases, assumptions and limits of interpretation of several methods used to control environmental trends in successive generations. Randombred control populations have been recommended for this purpose in poultry (King _et al_, 1959; Gowe _et al_., 1959) while repeat mating systems have been suggested for both dairy cattle and poultry (Goodwin _et al_., 1960). Bray _et al_. (1962) studied 15 methods of maintaining control populations over eight generations using the flour bettle, Tribolium castaneum, and discussed the importance of genotype by environment interactions with reference to control populations. They concluded that genetic controls must be closely related to the selected lines in origin and time if their reactions to environmental shifts are to be similar to those of the selected lines.

The classical method of eliminating environmental bias from the response to selection in time is to conduct a two-way (bidirectional) selection experiment. Student (1934) presented a biometrical technique for this experiment and showed that the heritability of the trait selected for was obtained by dividing the difference between the means of the two selected lines by the cumulative selection differential. This was called a realized heritability and provided the most reliable measure of additive gene action.

Bidirectional selection, although enabling the measurement between lines, does not permit estimation of responses in one direction independent of the other. Asymmetry may thus introduce a bias in two-way selection experiments and a genetic control should be used to facilitate an evaluation of the response in both directions. A reliable control according to Bray et al. (1962) should be closely related to the selected lines. Falconer (1953) discussed the possible causes of asymmetrical response in selection experiments and concluded that unequal initial gene frequency and directional dominance, separately or together, were the principal causes. He also suggested that predicted rates of progress based on heritability estimates may overestimate the rate of progress in one direction when there was asymmetry.

Although the direct response of the selected trait is one of the main objectives in a single-trait selection experiment, another important objective is the direction and magnitude of the correlated responses of unselected characteristics. Reeve and Robertson (1953) and Falconer (1954) demonstrated the approach to obtain a valid estimate of genetic correlation from double two-way selection experiments using Drosophila and mice, respectively. This procedure requires, at the minimum, positive and negative selection solely for trait A in two lines and similar selection for trait B in another pair of lines. The response of both A and B must be measured in both pairs of lines. The formula for calculation of genetic correlation is:

$$\Delta G' \,/\, \sigma_G = r_G \, \Delta G \,/\, \sigma_G \qquad \text{or,}$$

$$r_G = \Delta G' \, h \, \sigma_P \,/\, \Delta G \, h' \, \sigma_P' \qquad \text{where,}$$

Δ G: genetic change in selected trait.

Δ G': genetic change in correlated trait.

σ G: genetic standard deviation of selected trait.

σ G': genetic standard deviation of correlated trait.

σ P: phenotypic standard deviation of selected trait.

σ P': phenotypic standard deviation of correlated trait.

r_G: genetic correlation between selected and correlated trait.

These formulas may be rewritten to predict the correlated response as:

$$\hat{\Delta} G' = \Delta G \; r_G \; h' \, \sigma_P' \,/\, h \, \sigma_P$$

Since bidirectional selection experiments are both expensive and time consuming, relatively few have been conducted. Recent ones reported in chickens are Siegel (1962a,b,c, 1963a,b), Maloney et al. (1963a,b) and Nordskog and Festing (1962, 1964). Siegel (1962a, 1963b) conducted a selection experiment for body weight at eight weeks of age using White Rocks and reported correlated responses in body weight at four, 24 and 38 weeks of age, feathering at eight weeks of age, sexual maturity, egg production to January 1, egg weight, Haugh units, specific gravity of eggs, semen volume, sperm concentration and motility of sperm in each of four generations. He (1962c, 1963a) also conducted a selection experiment for breast angle at eight weeks of age and reported the correlated response in the same traits described above. From these two selection experiments he obtained a realized genetic correlation between eight week weight and eight week breast angle and suggested a directionality of the genetic correlation (Siegel, 1962b). By using chicks selected divergently for body weight and breast angle at eight weeks of age, various types of correlated responses such as protein and energy requirements (Wisman and Siegel, 1962), influence of thiouracil (Washburn and Siegel, 1962), relative aggressiveness (Siegel and Siegel, 1963) embryonic development (Coleman _et_ _al_. 1963) and nucleic acid composition (Lepore _et_ _al_., 1965) were investigated.

Maloney _et_ _al_. (1963b) reported the results of ten years of two-way selection for body weight at 12 weeks of age in Silver Oklabars. They found a significant increase in six-week body weight in the high line and a significant decrease of March egg weight in the low line. Although they discussed other correlated responses these were the only ones in which were significant.

Nordskog and Festing (1962) and more recently Nordskog et al. (1964) reported the results of four years and seven years of single trait selection, respectively, in five lines of Leghorns and three lines of Fayoumis. The selected traits were rate of egg production, body weight and egg weight. For the latter two traits bidirectional selection was practiced. In former paper (1962) they reported both the direct and correlated responses in body weight, egg weight, egg production and the correlated response only for mortality, sexual maturity, fertility and hatchability. They obtained realized heritabilities and genetic correlations between body weight and egg weight. They noted an apparent discrepancy in the ratio of correlated response to direct response in the two traits and speculated on the directionality of genetic correlation as suggested by Siegel (1962b). In the latter paper Nordskog et al. (1964) pointed out asymmetrical responses in body weight, egg weight and decline of fitness traits in these lines.

EXPERIMENTAL

The Stocks

Foundation stock consisted of crosses of seven inbred lines of White Plymouth Rocks which had been developed at the Virginia Agricultural Experiment Station. Two lines were selected from this gene pool on the basis of individual body weight at eight weeks of age. The high weight line (HW) was developed by truncation-type selection for heavier body weight at that age whereas the low weight line (LW) was developed for lighter body weight at same age. The parents for each subsequent generation were chosen on a within line basis for the single trait, body weight at eight weeks of age.

The number of sires, dams and unselected female progeny used in the analyses are shown by generations in Table 1. The parents for each subsequent generation were chosen from the progeny of the preceeding generation in each line. Pullets were assigned at random to individual cockerels with the restriction that no half-sibs or matings of closer relationship were permitted. Under this procedure average percentage increase in inbreeding per generation was 1.50 in HW and 1.52 in LW lines.

Management Procedures

Progeny for each generation were obtained from two hatches, on the first and third Tuesday in March. Since under this procedure hatch effects were seldom significant, hatches were pooled for analyses.

On the 22nd day of incubation all chicks were removed from the hatcher, pedigreed and placed in floor pens with a hot air brooding system where temperature, humidity and lighting were regulated to provide similar environmental conditions among pens and generations. The same rations were used in all generations. They consisted of a starting ration fed from zero to eight weeks of age, a grower ration fed from eight to 24 weeks of age and a breeder ration that was fed thereafter. The formulation of these rations are presented in Table 2. Calculated analyses indicated that the percentage of protein was 20 for starter and 16 for both grower and breeder rations. All were considered to be medium energy rations.

Chicks from the Athens-Canadian Randombred population (Hess, 1962) were hatched each year and grown with birds from the selected lines except in the parental generation.

Table 1. Number of sires, dams and female progeny by generations.

		No. of		No. of Female Progeny Measured					
Gen.	Line	Sires	Dams	8 wk. Wt.	24 wk. Wt.	38 wk. Wt.	Egg Wt.	Age 1st Egg	Egg Prod.
P		11	71	269	263	247	241	269	269
F_1	HW	8	34	194	127	106	103	122	122
	LW	7	34	193	137	122	123	133	133
F_2	HW	8	28	167	90	87	90	90	90
	LW	7	28	140	65	62	65	65	65
F_3	HW	7	32	198	158	138	123	149	149
	LW	7	31	214	157	133	126	136	136
F_4	HW	8	27	137	115	105	80	104	104
	LW	8	36	203	150	132	125	140	140
F_5	HW	9	36	175	131	118	93	117	117
	LW	9	38	211	142	128	119	134	134
F_6	HW	10	43	161	128	112	85	129	128
	LW	12	50	259	190	170	151	182	181
F_7	HW	11	39	149	135	126	106	128	128
	LW	11	39	249	219	202	171	208	208

Table 2. Composition of the rations.

Ingredient	Period (Weeks)		
	0-8	8-24	24-
	(lbs)	(lbs)	(lbs)
Ground wheat	-	-	10
Ground yellow corn	43.75	51.35	50.3
Wheat flour middlings	10	6.25	5
Pulverized oats	5	15	10
Wheat bran	5	6.25	5
Alfalfa meal, 17% crude protein	5	2.5	2.5
Corn gluten meal	2.5	-	-
Soybean oil meal, 44% crude protein	21.25	13.75	8.75
Meat and bone scrap, 50% crude protein	2.5	2.5	5
Menadan fish meal	2.5	-	2
Iodized salt	.5	.5	.5
Deflorinated rock phosphate	.5	.78	.3
Ground limestone	1	1	.4
	g	g	g
Manganese sulfate, 70%	11	5.5	11
Vit. A suppl. 6,000 I.U./gm.	28	5.5	27.5
Vit. D_3 suppl. 3,000 I.C.U./gm.	9	11	27.5
B vitamin suppl.[1]	45	22	33
Choline Chloride, 25%	100	-	-
Vit. B_{12} suppl., 6 mgs./lb.	11	11	11
Chlortetracycline 10 gms./lb.	23	-	-
Total (lbs.)	100	100	100

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[1] Contained the following as grams per pound: 2 riboflavin, 3 calcium pantothenate, 12 niacin and 20 choline chloride.

Measurement of Traits

Body weights were obtained to the nearest gram at eight weeks of age for both males and females, and to the nearest 0.1 pound at 24 and 38 weeks of age for females only.

Egg weight was measured during the 35th week after hatching. Eggs laid by all pullets were saved overnight and measurements obtained the following morning. This procedure was repeated for a period of five days. The mean values obtained for three successive eggs per hen were used in analysis. When a hen failed to lay three eggs during that period, the average for the number of eggs laid was taken.

The age at sexual maturity of a female was measured as the number of days from hatching to the date of first egg. A pullet was considered sexually mature when at least two eggs were laid within a ten day period.

Egg production was measured from the date of first egg until January 1. Since sexual maturity has been shown to have an influence on egg production (Bray _et al_., 1960) percentage hen day egg production was used. The egg production data were based on a seven day trap-week through F_3 generation and on a five day trap-week thereafter.

Method of Analysis

Heritability estimates:

Selected trait. Realized heritabilities and estimates from variance component analyses based on full-sib correlations were obtained in all filial generations. For the P_1 generation the estimate was based on full-sib correlations only.

The variance component analysis employed was for unequal subclass numbers and followed the procedure given by King and Henderson (1954a). The sum of squares expectations were based on the following model for the phenotype of an individual:

$$P_{ijkl} = u + l_i + s_{ij} + d_{ijk} + e_{ijkl} \qquad \text{where,}$$

P_{ijkl}: the observed phenotypic value of the lth individual out of the kth dam mated to the jth sire of ith line.

u: the population mean.

l_i: an effect common to all individuals in ith line.

s_{ij}: an effect common to all individuals mated to the jth sire in ith line.

d_{ijk}: an effect common to all individuals out of the kth dam mated to the jth sire in ith line.

e_{ijkl}: a residual effect specific to the lth individual out of the kth dam mated to the jth sire in ith line.

All heritability estimates from component analyses were based on the combined sire and dam components $h^2 = 2(S + D)/(S + D + E)$. This type of estimate is actually an average of the 4S and 4D estimates and falls within the definition of broad and narrow heritability. In the case of this thesis the combined estimate should be superior to that based on either sire or dam components because of the small numbers of progeny within each generation. Robertson (1959) has shown that with a double classification of the sire and dam and equal intraclass correlations (t) the structure for optimum equal information on both correlations has three or four dams per sire and 1/2t offspring per dam. Since

$t = h^2 / 4$, under the assumption of $h^2 = .40$ the number of offspring per dam would be five. Table 1 shows that the requirement of dams per sire is adequately met while the number of progeny per dam was only 5.1.

The realized heritability of the selected trait was obtained by two different methods. One was obtained by dividing the difference between the means of the two lines by the cumulative selection differential (Student, 1934); the other was obtained from the regression coefficient of the difference between the means of the two lines on the cumulative selection differentials (Falconer, 1954). Data from the Athens-Canadian Randombred population were available as controls for the F_1 through F_7 generation. The realized heritability for each line was obtained by the regression of control-adjusted response from the F_1 through the F_7 generation on the cumulative selection differential. Although the lack of randombred control data for the parental generation may have caused a bias in the estimation of realized heritabilities based on the regression method, especially in a selection experiment of few generations, it may provide information on a asymmetry in the response of the selected lines.

Unselected traits. Realized heritabilities were obtained for unselected traits by dividing the difference between the means of the two lines by the cumulative expected secondary selection differential. This secondary selection differential was the cumulative product of selection differential of eight-week body weight multiplied by the regression coefficient of the unselected trait on eight-week body weight in each generation (Table 3). It is expressed symbolically as: $h^2 = HW - LW \ / \sum iYx = HW - LW \ / \sum iX \ \ b_{P_{yx}}$. From the same data another realized heritability was obtained for divergence based on the regression method. By using the same procedure employed with the selected trait, realized heritabilities were also obtained by the regression method based on the control adjusted data for each line. These values were compared with the heritability estimates from component analyses and the uncorrected realized heritabilities which were obtained from dividing the difference of means between the two lines by the difference between the average of the parents and the average of the population in which they were born. These comparisons facilitated an evaluation of the reliability of realized heritability based on the expected secondary selection differential.

Genetic correlation:

As described in the review of literature, the genetic correlation (r_G) between two traits may be estimated by several procedures. Since other methods include large sample variances of the estimate, genetic correlations between unselected traits and eight-week body weight were obtained from the formula $r_G = \Delta G' \ h \ \sigma_P \ / \ \Delta G \ h' \ \sigma_P'$. In the strict sense, the genetic correlation between two traits should be estimated from double two-way selection experiments in which bidirectional selection was made for one trait in a pair of lines and another in another pair of lines. Although this method is desirable, it is costly and time consuming. Double selection experiments may be conducted mainly to obtain unbiased heritability estimates and measure the symmetry of genetic

Table 3. Phenotypic regression coefficients (b) of unselected traits on eight-week weight, standard errors (s_b) and coefficients of determination (R^2) by generations.

		24 wk. wt.			38 wk. wt.			Egg wt.			Age at 1st egg			Egg production		
Line	Gen.	b	s_b	R^2	b	s_b	R^2	b	s_b	R^2	b	s_b	R^2	b	s_b	R^2
			(10^{-4})			(10^{-4})			(10^{-4})			(10^{-3})			(10^{-3})	
HW	P	28**	3	.24	26**	5	.12	15	28	.00	-58**	10	.11	+16	10	.01
	F_1	32**	7	.14	32**	7	.14	26	38	.01	-69**	21	.09	+ 9	19	.00
	F_2	24**	5	.19	25**	8	.11	86	43	.04	-65**	22	.09	+45*	17	.07
	F_3	32**	5	.19	45**	8	.19	71	37	.03	-61**	22	.05	-10	17	.00
	F_4	46**	1	.94	45**	8	.23	88	51	.04	-28	21	.03	+52	27	.03
	F_5	40**	5	.29	36**	7	.18	89	45	.04	-31	17	.03	-23	21	.01
	F_6	24**	6	.11	64**	8	.35	83	45	.04	-19	24	.01	- 1	20	.00
LW	F_1	40**	6	.26	40**	8	.24	79*	36	.04	-73**	18	.12	+43**	16	.05
	F_2	21**	5	.21	21**	8	.11	14	33	.00	-77**	18	.22	+30	27	.03
	F_3	34**	5	.25	41**	7	.22	114**	40	.06	-63**	21	.06	+28	16	.02
	F_4	49**	4	.55	16**	5	.08	131**	42	.07	-134**	26	.16	+16	18	.01
	F_5	20**	4	.12	15*	6	.04	80*	36	.04	-29*	12	.04	- 7	13	.00
	F_6	28**	4	.18	19**	6	.06	39	43	.01	-69**	15	.11	+ 6	14	.00

* Significant at 5% level.

** Significant at 1% level.

correlations. For practical and economical reasons single two-way selection experiments may be satisfactory if the heritability estimate of the unselected traits are reliable and if the genetic correlations obtained are consistent with those reported by others.

Phenotypic (r_P) and environmental (r_E) correlations:

The phenotypic correlation which is the association between two traits that can be observed directly, can be partitioned into two fractions, namely genetic and environmental. The former is the additive genetic component of the covariance while the latter includes the remainder of the covariance which includes non-additive genetic and environmental covariance. The relationship between the correlations may be expressed as:

$r_P = h_x \ h_y r_G + e_x e_y r_E$ where, e_x and e_y are the square roots of $1 - h_x^2$ and $1 - h_y^2$, respectively. When r_P, r_G, h_x and h_y are known, the formula to obtain r_E may be written as:

$$r_E = (r_P - h_x h_y r_G) / e_x e_y$$

Prediction of correlated response:

Prediction of correlated responses when selection is practiced for single trait may be made by the formula which is analogous to that used for the calculation of genetic correlations. The prediction formula is: $\hat{\Delta} G' = \Delta G \ r_G \ h' \ \sigma p' \ / \ h \ \sigma p$

Genetic correlations were obtained by using the realized heritability of the selected trait and the corrected realized heritabilities of unselected traits. Also heritability estimates based on full-sib correlations were used for prediction of the correlated responses and the results were compared with the actual correlated responses in terms of their regression on generation. When heritability estimates were negative, the predicted values were obtained by using the estimate of the previous generation.

RESULTS AND DISCUSSION

Selected Traits

Body weight at eight weeks of age:

The sole criterion of artificial selection in the development of these lines was body weight at eight weeks of age. Because the response of this trait may be associated with changes in unselected traits, a discussion of the direct response of body weight to artificial selection is pertinent to this thesis. The discussion of this response will be limited to females.

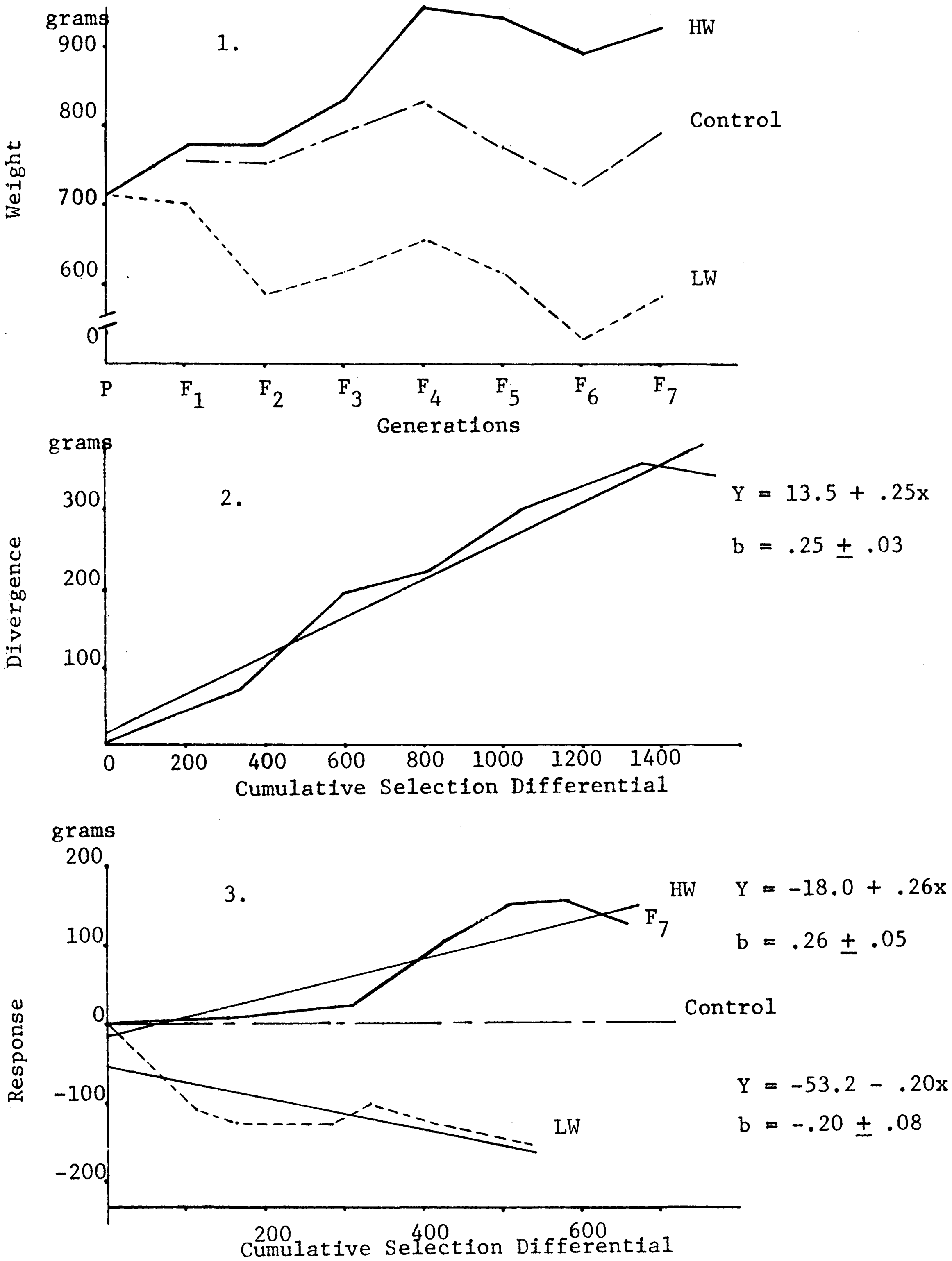
Means for eight-week weight by lines and generations are presented in Table 4 and Figure 1-1. The values of these parameters to the F_4 generation were the same for the HW and LW lines as those given in a prior report (Siegel 1962a). Selection for eight-week body weight in divergent directions resulted in a highly significant differences between selected lines in the first generation and the difference became progressively larger with each successive generation of selection. In the seventh generation the difference between lines was 344 g.

The coefficients of variation (CV) for the LW line were consistently larger than those for HW line. This result was consistent with that of Maloney et al. (1963a) who reported that in the first six generations of selection for 12-week body weight a larger CV for the LW line than for the HW line. This similarity

Table 4. Means ($\bar{x}$), standard deviations (s) and coefficients of variation (c.v.) of eight-week body weight in female by lines and generations.

	Control		High Weight Line		Low Weight Line	
Generation	$\bar{x} \pm s$	c.v.	$\bar{x} \pm s$	c.v.	$\bar{x} \pm s$	c.v.
P			715 ± 117	16.4	715 ± 117	16.4
F_1	759 ± 108	14.2	776 ± 100	12.9	705 ± 94	13.3
F_2	753 ± 82	10.9	777 ± 141	18.2	588 ± 132	22.4
F_3	795 ± 94	11.8	833 ± 87	10.4	615 ± 104	16.4
F_4	835 ± 85	10.2	951 ± 98	10.3	657 ± 112	17.0
F_5	772 ± 82	10.6	937 ± 96	10.3	618 ± 95	15.3
F_6	724 ± 75	10.3	894 ± 94	10.5	539 ± 93	16.2
F_7	791 ± 87	11.0	928 ± 73	7.9	584 ± 75	12.8

Figure 1. 8 Week Body Weight



in results is important because for juvenile body weight variance is usually proportional to the mean and thus one would expect selection differentials to be larger in the upward than in the downward direction.

The data presented in Table 4 indicated a reduction in the CV with each generation of selection. The regression coefficients of CV on generations were -1.13 ± .35 for HW and -.37 ± .46 for LW line. The former was significant at the 5 percent level of significance while the latter was comparable to that for the control population, which was -.43 ± .23. The negative sign of the regression coefficient for HW line showed that it was becoming phenotypically more uniform. This pattern may be expected to continue as selection proceeds toward its limits. However, since a decrease of heritability and of response to selection did not occur this decline may be due to a decrease of non-additive genetic variation. The negative regression, which was general for all lines, suggests further that the non-genetic variation may have been reduced in time.

Although, initially similar selection pressure for each line was desired within generations this was not always feasible. The reason was because the same number of chickens were selected to reproduce the lines from populations of different size. The variation in population size between lines was a result of the lower fecundity of the HW line. Expected (unweighted by number of offsprings) and effective (weighted by number of offsprings) selection differentials for body weight at eight weeks of age are presented in Table 5. Comparisons between expected and effective selection differentials provided information on whether natural selection had influenced artificial selection. This ratio of effective to expected selection differentials indicated that natural selection was not important in influencing the response to artificial selection for body weight at eight weeks of age. Although, the ratio was .79 for F_5 and F_6 generations in the LW and HW lines, respectively, the effect was probably temporary because the ratio was approximately unity in the succeeding generations.

Heritability estimates based on variance component analyses and realized heritabilities for eight-week body weight are presented in Table 6. Realized heritabilities were uniform, as would be expected, whereas the heritability estimates from component analyses were variable. The fluctuations of heritability estimates obtained from component analyses may be explained by small dam families. The number of dams per sire seems optimal. According to Robertson (1959) the optimal design for double classification of sires and dams is three to four dams per sire with the number of offspring per dam equal to $2/h^2$. Using the realized heritability 0.25 obtained from the regression of response on the cumulative selection differential, the optimal number of

Table 5. Comparisons of effective and expected selection differentials for body weight at eight weeks of age by generations.

Selection Differential	Line	F_1	sdu	F_2	sdu	F_3	sdu	F_4	sdu	F_5	sdu	F_6	sdu	F_7	sdu	Avg.	sdu
expected	H	+164		+144		+163		+117		+ 82		+ 84		+ 83		+119.6	
	L	-180		-109		- 45		-120		- 64		- 88		-110		-102.3	
	H-L	344		253		208		237		146		172		193		221.9	
effective (♀♀off-spring)	H	+163	(1.63)	+152	(1.08)	+153	(1.77)	+ 114	(1.16)	+ 85	(.89)	+ 67	(.70)	+ 84	(1.15)	116.9	(1.20)
	L	-175	(1.86)	-110	(.83)	- 51	(.49)	- 118	(1.06)	- 51	(.53)	- 93	(1.00)	-108	(1.44)	100.9	(1.03)
	H-L	338	(3.48)	262	(1.92)	204	(2.12)	232	(2.19)	136	(1.43)	159	(1.70)	192	(2.60)	217.7	(2.206)
cumulative effective (♀♀off-spring)	H	163		315		468		582		667		734		818			
	L	175		285		336		454		505		598		706			
	H-L	338		600		804		1036		1172		1332		1524			
effective/ expected (♀♀off-spring)	H	.99		1.05		.94		.97		1.05		.79		1.01		.971	
	L	.97		1.01		1.13		.99		.79		1.04		.98		.987	
	H-L	.98		1.04		.98		.98		.93		.92		.99		.974	

[1] Selection differential in standard deviation units (s.d.u.) is obtained from the selection differential divided by the standard deviation by lines and generations. Divergent selection differentials in standard deviations was obtained from the divergent selection differential divided by the pooled standard deviation of both lines by generations.

Table 6. Heritability estimates by generations for body weight at eight weeks of age.

	Generation								
h^2	P	F_1	F_2	F_3	F_4	F_5	F_6	F_7	$\bar{x}$
Realized[1]		.21	.32	.27	.28	.27	.27	.23	
2(S+D)	.52	.39	.06	.39	.56	.46	.29	.27	.37
4S	1.00	.13	.07	.02	.27	-.07	-.03	.29	.21
4D	.04	.65	.05	.76	.84	.99	.61	.25	.52
Realized[2]			.246 ± .025						
Realized[3]		HW	.259 ± .054						
		LW	-.203 ± .079						

[1] Difference between means of HW and LW lines divided by the cumulative selection differential by generations.

[2] Regression of the difference between means of HW and LW lines on the cumulative selection differential.

[3] Regression of control-adjusted response in each line on the cumulative selection differential in each direction. The negative value for the LW line denotes a positive heritability.

offspring per dam was eight. The mean number of offspring per dam was 5.1 in this experiment (Table 1) and therefore, an insufficient number of offspring per dam may have been a cause of the variability in heritability estimates for this particular characteristic.

Another possible bias could result from the use of selected parents in the variance component analysis. Even when selection is for only one or a few traits, correlated responses may introduce some bias into the estimates of the parameters of unselected traits. This is because the usual variance components analysis assumes unselected parents mated at random.

The realized heritabilities suggest the importance of additive gene action in the selection for large and small body weight. Another estimate of additive genic effects may be obtained from paternal half-sib correlations (4S in Table 6). The mean for eight generations was .21, a value very similar to the realized heritabilities. Heritability estimates obtained from maternal half-sib correlations provide information on dominance and maternal effects. The mean heritability estimate for eight generations based on maternal half-sib correlations was .52 and indicated that maternal effects and dominance deviations may have been important in the inheritance of juvenile body weight. Siegel (1962a) has discussed this in detail.

The consistency of the realized heritabilities for divergence of the lines as shown in Table 6 suggest that epistatic effects were not large. Some evidence, however, for their importance during the early generations is suggested from the data presented in Figure 1-3.

Realized heritabilities from the regression of response on cumulative selection differential are presented in Figure 1-2 and 1-3. The realized heritability was .26 ± .05 for the HW line, and .20 ± .08 for the LW line and .25 ± .03 for the divergence between lines. The line means for each direction were adjusted each filial generation according to fluctuations in the control population.

Since there was no difference between the magnitude of the regression coefficients in the upward and downward direction, no essential difference of selection differentials (Table 5), no scale effects (Table 4) and a comparable increase of inbreeding (Table 1), it can be concluded that to the F_7 generation the response in the two-way selection for body weight at eight weeks of age was symmetrical. Additional generations appear to be necessary to determine if and when asymmetry occurs.

Unselected Traits

<u>Correlated responses</u>:

Means, standard deviations and coefficients of variation of the unselected traits in selected and control lines are presented by generations in Table 7. The difference between means of selected

Table 7. Means ($\bar{x}$), standard deviations (s) and coefficients of variation (c.v.) of unselected traits in selected and control lines, by generations.

Gen.	Line	24 wk. wt. (lbs)			38 wk. wt. (lbs)			Egg wt. (g)			Age of 1st egg (days)			Egg prod. (%)		
		$\bar{x}$ ± s		c.v.	$\bar{x}$ ± s		c.v.	$\bar{x}$ ± s		c.v.	$\bar{x}$ ± s		c.v.	$\bar{x}$ ± s		c.v.
P	Cont.	5.1 ±	.6	11.8	6.9 ±	.8	11.6	52.3 ±	4.3	8.2	162 ±	17	10.5	64.6 ±	16.7	25.9
F_1	Cont.	5.5	.8	14.5	6.3	1.0	15.9	52.3	4.1	7.9	177	25	14.1	61.1	17.2	28.2
	HW	5.6	.7	12.5	7.0	.9	12.9	50.2	3.3	6.6	166	19	11.4	62.4	16.6	26.6
	LW	5.2	.7	13.5	6.5	.9	13.8	48.7	3.4	7.0	168	18	10.7	67.3	16.3	24.2
F_2	Cont.	4.9	.6	12.2	5.9	.7	11.8	51.7	4.2	8.1	175	25	14.3	64.9	20.9	32.2
	HW	5.4	.6	11.1	6.9	.8	11.6	50.4	4.5	8.9	182	23	12.7	67.7	18.1	26.7
	LW	4.7	.6	12.8	6.2	.8	12.9	48.1	3.1	6.4	190	20	10.5	67.9	20.8	30.5
F_3	Cont.	5.2	.5	9.6	6.1	.8	13.1	51.1	3.4	6.7	167	21	12.6	64.3	17.3	26.9
	HW	5.7	.6	10.5	7.1	.9	12.7	50.9	3.8	7.5	104	23	14.0	58.5	17.9	30.6
	LW	4.8	.7	14.6	6.1	.8	13.1	48.7	4.0	8.2	178	22	12.4	65.4	15.8	24.2
F_4	Cont.	5.2	.8	15.4	6.1	.9	14.8	53.2	4.1	7.7	165	21	12.7	66.1	16.1	24.4
	HW	6.0	.6	10.0	7.5	.8	10.7	51.6	3.7	7.2	160	17	10.6	57.4	22.4	39.1
	LW	4.7	.7	14.9	5.8	.5	8.6	47.4	3.8	8.0	175	31	17.7	67.1	18.1	26.9
F_5	Cont.	5.1	.5	9.8	6.0	.7	11.7	52.5	3.9	7.4	168	18	10.7	60.5	16.5	27.3
	HW	6.2	.6	9.7	7.8	.7	9.0	53.5	3.7	6.9	160	22	13.8	53.1	19.0	35.8
	LW	4.7	.6	12.8	5.7	.7	12.3	48.3	3.9	8.1	166	14	8.4	69.3	14.8	21.4
F_6	Cont.	5.0	.6	12.0	5.6	1.0	17.9	51.4	4.7	9.2	170	45	26.5	54.8	21.3	38.9
	HW	6.3	.5	7.9	7.9	1.0	12.7	52.0	3.4	6.5	161	20	12.4	47.3	19.0	40.2
	LW	4.5	.6	13.3	5.5	.7	12.7	46.7	3.2	6.9	175	18	10.3	63.9	16.1	25.2
F_7	Cont.	5.0	.8	16.0	5.4	1.2	22.2	51.6	7.4	14.3	167	22	13.2	53.2	21.1	39.7
	HW	6.2	.6	9.7	7.3	.8	11.0	50.9	3.8	7.5	162	20	12.4	53.2	16.9	31.7
	LW	4.1	.5	12.2	4.9	.7	14.3	45.7	4.8	10.5	185	24	13.0	61.1	17.4	28.4

lines in F_7 generation were 2.1 lbs., 2.4 lbs., 5.2 grams, 23 days and 7.9 percent for 24 and 38 week body weight, egg weight, age at first egg and hen-day egg production to January 1, respectively. All differences between lines were highly significant. Changes of these means in time are also presented in Figures 2-1 to 6-1. Significant differences between means of the HW and LW lines were first observed in the F_1 generation for 24 and 38-week body weight, egg weight and egg production and in the F_2 generation for age at first egg.

Realized heritabilities:

Realized heritabilities of unselected traits obtained from the difference of means between selected lines divided by the cumulative expected secondary selection differential $(\Sigma\, iYx)$ are presented in Table 8. Also presented for comparison are heritability estimates from full-sib correlations and uncorrected realized heritabilities. The latter were obtained by division of the difference of means between the two selected lines by the difference between the means of the parents and the means of the population in which they were born $(\check{P}-\bar{P})$. The $(\check{P}-\bar{P})$ of only dams were used in this investigation because $(\check{P}-\bar{P})$ for sires were not available for 24 and 38-week weight and egg weight, egg production and sexual maturity were sex-limited.

Figure 2. 24 Week Body Weight

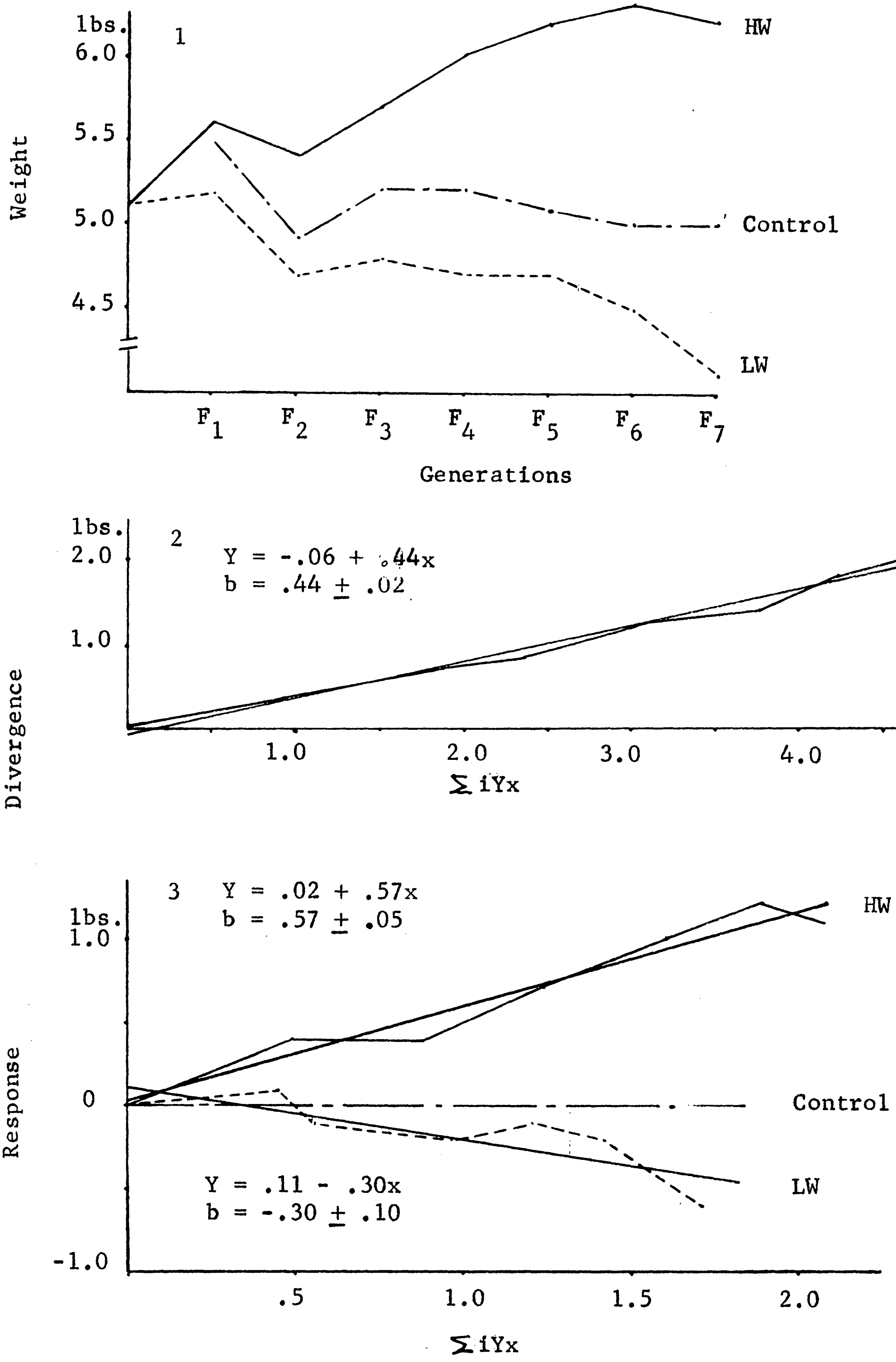


Figure 3. 38 Week Body Weight

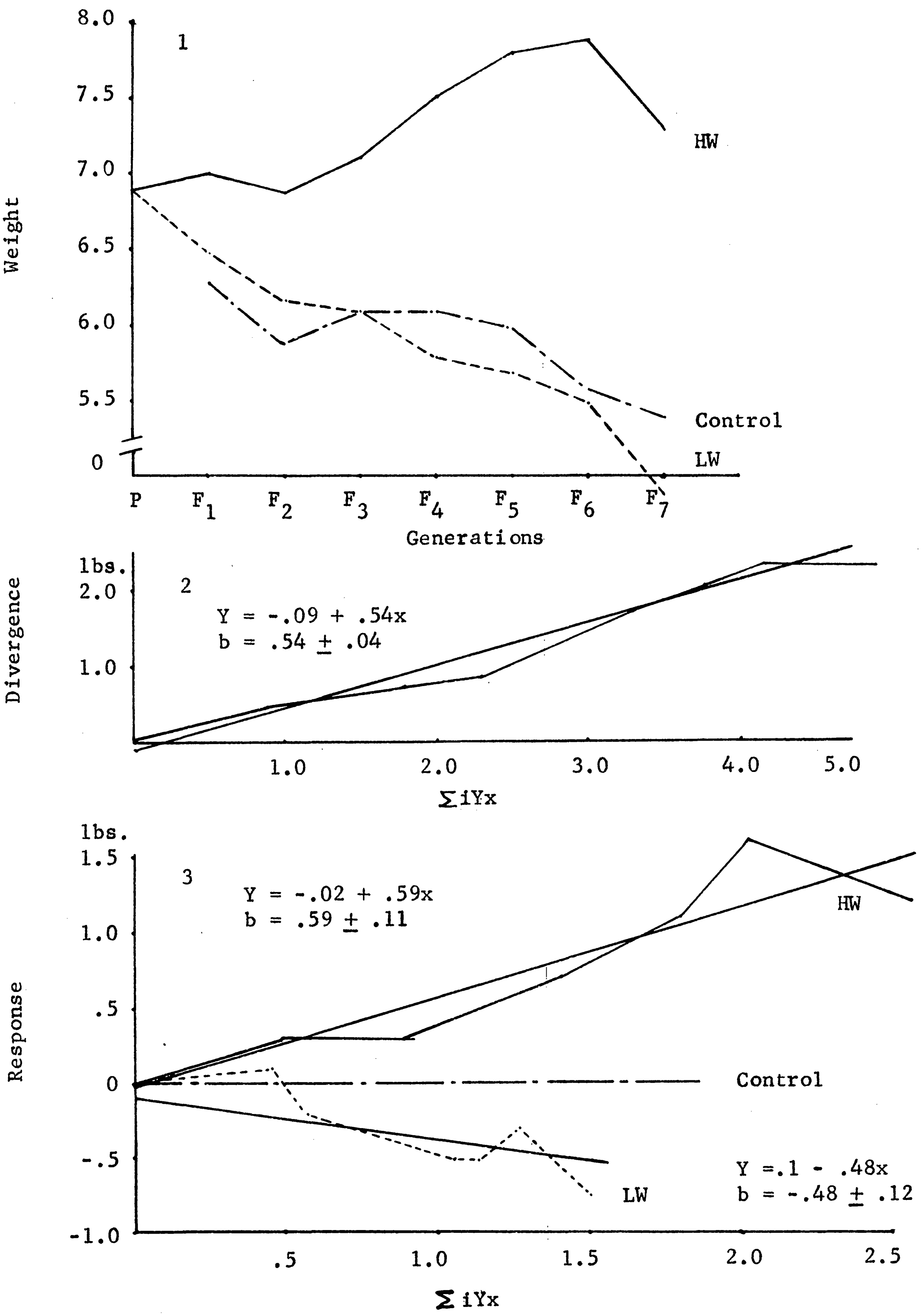


Figure 4. Egg Weight

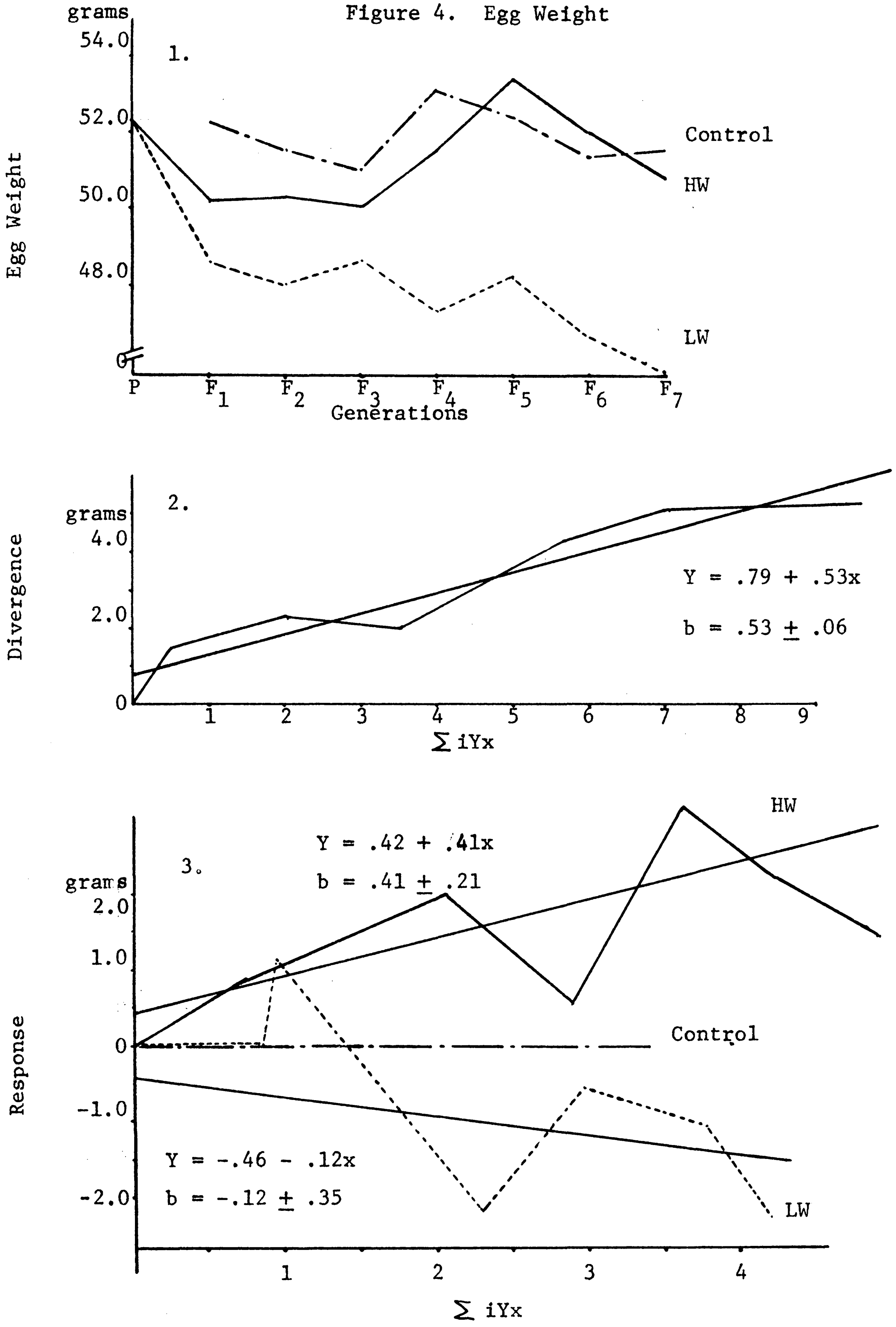


Figure 5. Age at First Egg

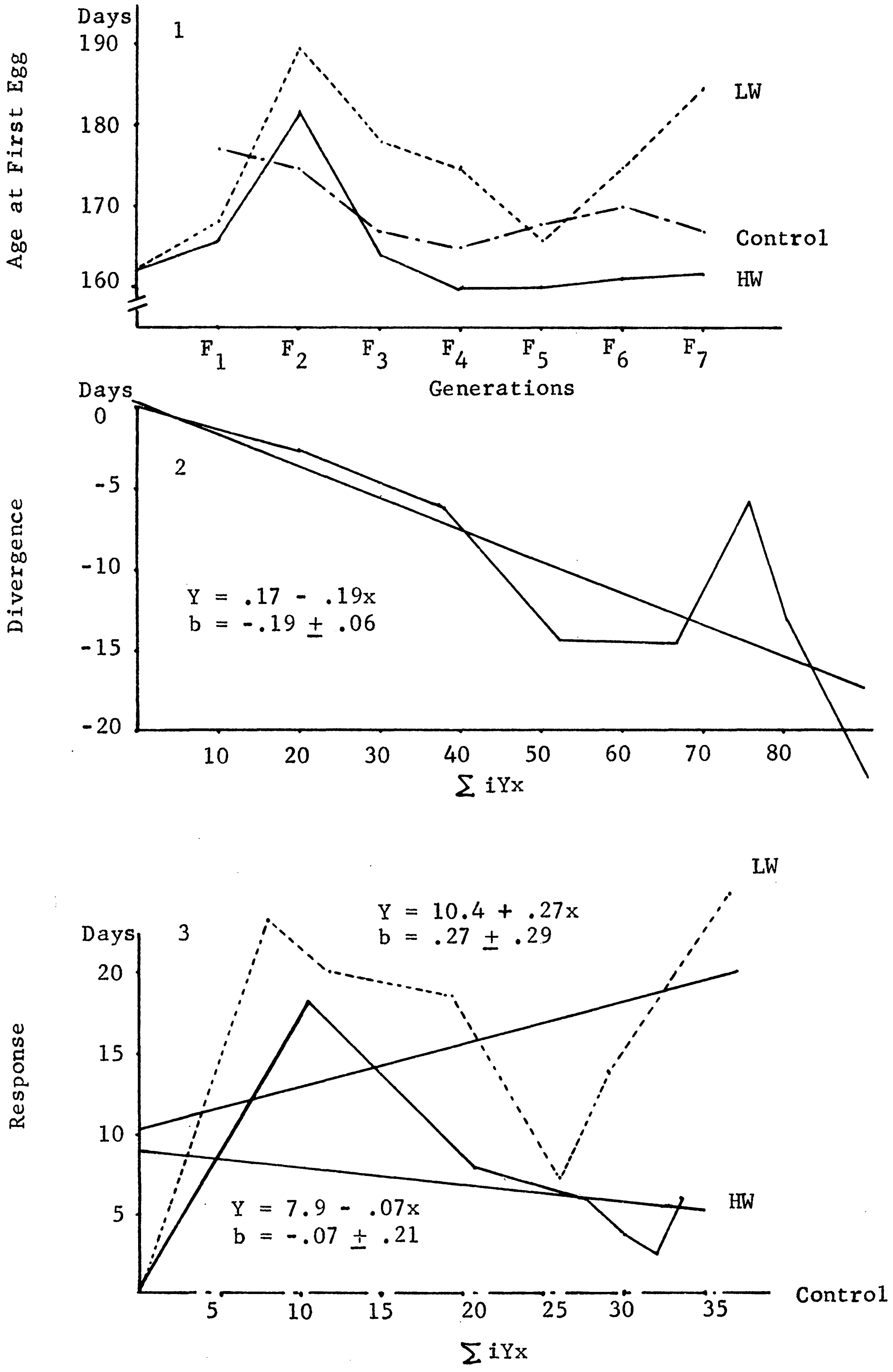


Figure 6. Percentage Egg Production

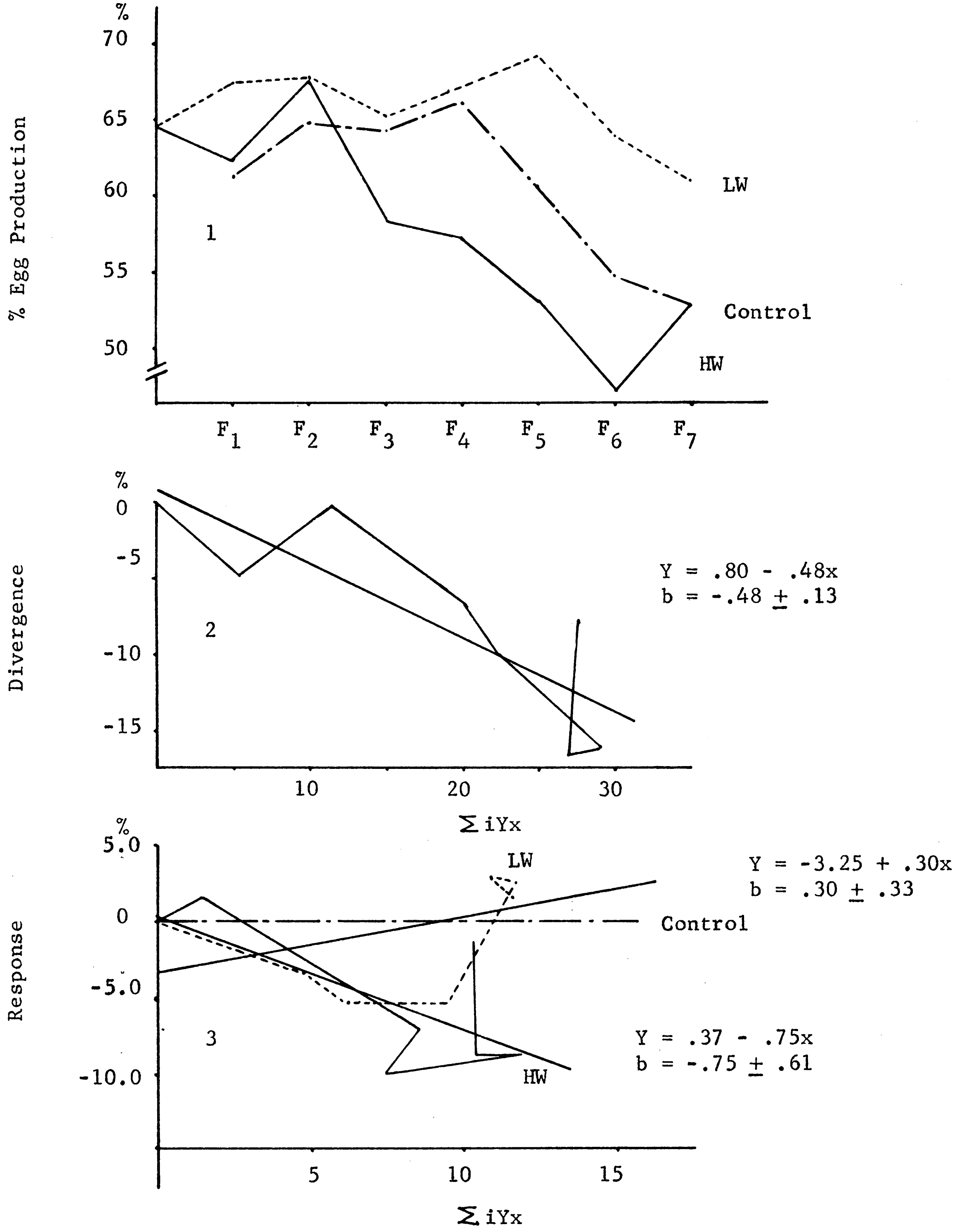


Table 8. Comparisons of uncorrected and expected selection differentials in unselected traits and of subsequent realized heritabilities to heritability estimates based on full-sib correlations.

		Cumulative secondary selection differential				Heritability Estimates			
Trait	Gen.	Uncorrected $\Sigma(\check{P}-\bar{P})$ dam	sire+dam	Expected (ΣiYx)	Response (HW-LW)	Uncorrected dam	sire+dam	Corrected[1]	2(S+D)
24-wk. wt.	P								.64
	F_1	.45	.45	.93	.37	.82	.82	.40	.58
	F_2	.77	.80	1.86	.73	.95	.91	.39	.36
	F_3	1.19	1.16	2.35	.85	.71	.73	.36	.52
	F_4	1.62	1.32	3.11	1.29	.80	.98	.42	.22
	F_5	1.88	1.51	3.75	1.44	.77	.95	.38	.30
	F_6	2.16	1.68	4.18	1.85	.86	1.10	.44	.30
	F_7	2.28	1.82	4.68	2.09	.92	1.15	.45	.23
								$\bar{x}$ =	.38
38-wk. wt.	P								.19
	F_1	.41	.34	.87	.45	1.10	1.33	.51	.48
	F_2	.68	.61	1.79	.73	1.07	1.20	.41	.13
	F_3	1.23	1.12	2.29	.89	.72	.80	.39	.60
	F_4	1.65	1.44	3.29	1.72	1.04	1.19	.52	.49
	F_5	1.67	1.61	3.76	2.05	1.23	1.27	.55	.24
	F_6	1.86	1.77	4.14	2.38	1.28	1.38	.57	.46
	F_7	2.11	2.13	4.88	2.35	1.12	1.10	.48	.27
								$\bar{x}$ =	.36

Table 8. (Continued)

egg weight	P								1.06
	F_1	.55	.38	.49	1.52	2.74	4.00	3.10	.25
	F_2	.94	.64	2.06	2.25	2.39	3.52	1.09	.53
	F_3	2.21	2.08	3.49	2.20	1.00	1.06	.63	.49
	F_4	3.01	2.37	5.65	4.22	1.40	1.77	.75	.81
	F_5	2.60	3.04	7.06	5.16	1.99	1.70	.73	.77
	F_6	3.12	3.56	8.39	5.23	1.68	1.47	.62	.46
	F_7	4.00	4.91	9.51	5.23	1.31	1.06	.55	.98
									$\bar{x}$ = .66
age at 1st egg	P								.55
	F_1	8.52	9.10	19.4	-2.32	.27	.25	.12	.53
	F_2	17.33	15.41	37.9	-7.20	.42	.47	.19	.29
	F_3	21.90	29.94	52.1	-14.36	.66	.48	.28	.39
	F_4	34.34	24.75	66.5	-14.63	.43	.59	.22	.13
	F_5	37.90	27.22	75.7	-5.9	.16	.22	.08	.04
	F_6	40.30	28.69	80.4	-13.41	.33	.47	.17	.07
	F_7	45.70	28.42	89.5	-22.44	.49	.79	.25	.23
									$\bar{x}$ = .28

Table 8. (Continued)

percent egg	P								.07
	F_1	1.30	3.54	5.39	-4.87	3.74	1.37	.91	.19
	F_2	.76	4.07	11.51	-.24	.32	.06	.02	.54
	F_3	3.29	5.26	20.12	-6.90	2.10	1.31	.33	.14
	F_4	8.50	3.88	22.31	-9.80	1.15	2.53	.44	.10
	F_5	8.46	6.24	28.98	-16.20	1.91	2.59	.56	-.01
	F_6	12.24	11.60	26.79	-16.27	1.35	1.43	.61	.0
	F_7	16.33	18.57	27.55	-7.87	.53	.47	.29	.11
								$\bar{x}$ =	.14

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[1] Corrected realized heritabilities were obtained from the responses divided by expected secondary selection differentials.

Uncorrected secondary selection differentials ($\check{P}-\bar{P}$) were obtained by two different procedures. One was based on the deviations of dam means from population mean weighted by the number of dam progeny. The second procedure was based on the deviations of the average of the combined means of dams and the full-sisters of sires from the population mean. Under this procedure both were weighted by the number of progeny.

Expected secondary selection differentials (iYx) were obtained by multiplication of selection differential for the selected trait, eight-week body weight (Table 3) with the regression coefficients (b's) of unselected traits on selected trait (Table 4). This adjustment was made within lines and generations. Regression coefficients (Table 3) for 24 and 38-week body weight on the selected trait were positive and significant. For age at first egg on the selected trait, all b's were negative and significant except for the last three generations in the HW line. Although the b's that involved egg weight were consistently positive, few were significant. The sign of the b's were not same in each generation for percentage egg production. Since iYx is expressed as follows:

$$iYx = b_{Pyx}\ iX = iX\ (b_{Gyx}\ h_x^2 + b_{Eyx}\ (1-h_x^2) = iX\sigma P_y\ (r_G h_x h_y + r_E e_x e_y)\ /\ P_x$$

then b_{Pyx} is a function of the genetic and environmental correlations between the selected and unselected traits, their phenotypic standard deviations, the square root of the heritabilities and $1-h^2$ for both traits. This shows how the genetic and environmental causes of correlation and the phenotypic variance may combine to give a phenotypic regression of an unselected trait on the selected trait. When the both traits are lowly heritable and their phenotypic variances are constant, regression is determined chiefly by the environmental correlation. The importance of the genetic correlation will increase with the magnitude of the heritability.

Realized heritabilities based on the regression of divergence on $\sum iYx$ and realized heritabilities based on regressions of control-adjusted responses on $\sum iYx$ are presented for the HW and LW lines in Figures 2-2, 3 to Figures 6-2, 3.

The data presented in Table 8 indicated that uncorrected realized heritabilities based on $(\breve{P}-\bar{P})$ of unselected characteristics were generally inflated and were frequently greater than unity. The exception for the traits studied here was age at first egg and even those values were consistently inflated. The data also show that for each trait heritability estimates based on full-sib correlations were very variable whereas the realized heritabilities based on the iYx were comparatively uniform.

The $(\check{P}-\bar{P})$ were obtained from the dam side only. The inflated heritabilities based on $(\check{P}-\bar{P})$ for the unselected traits may be attributed to the lack of $(\check{P}-\bar{P})$ for the sires. The iYx were obtained from the effective selection differential of the selected trait which was the average of selection differentials of the sires and dams, iX, multiplied by the phenotypic regression coefficients of the unselected traits on the selected trait.

When the selection differential of unselected traits $(\check{P}-\bar{P})$ for either the sire or dam are not available due to a trait being sex-limited or the lack of a population mean due to selection at an earlier age the selection differential of one sex would not be equal to the expected secondary selection differential iYx unless the selection differentials for both sexes were equal. In general, the selection differential for sire when selection could apply to both sexes is far larger than that of dam because the number of sires selected is considerably less than that for dams. In this study the effective selection differential of eight-week body weight for sires was larger than those of dams in all generations by an average magnitude of three times. The effective selection differential of eight-week weight was therefore about twice that of the dams. This relationship is indicated in Table 8 by the uncorrected $\Sigma(\check{P}-\bar{P})$ and expected (ΣiYx) secondary selection differentials. Subsequently, the values of the uncorrected realized heritabilities were about twice those of corrected realized heritabilities.

Body weight at 24 and 38 weeks of age: Realized heritabilities based on the regression for divergence on iYx were .44 ± .02 and .53 ± .04 for body weight at 24 and 38 weeks of age, respectively. The range of realized heritabilities by generations were .36 to .45 for 24-week weight and .39 to .57 for weight at the latter age. These values were consistent with those reported by others, Shoffner and Sloan (1948), Nordskog *et al*.(1964), and Kinney and Shoffner (1965) but lower than those reported by Peeler *et al*. (1955).

Realized heritabilities for 24-week body weight, based on the control-adjusted data, were .57 ± .05 and .30 ± .09 in the HW and LW lines, respectively. The values for 38-week weight were .59 ± .11 for the HW line and .48 ± .12 for the LW line. Although heritability was higher in the HW line than in the LW line at each age the confidence interval for the regressions overlapped and there was no difference between them. Σ iYx for these traits, however, were different in each line. The Σ iYx for the LW line through the F_7 generation was 82 and 58 percent of that in the HW line for 24 and 38-week body weight, respectively. Since the selection differential for body weight at eight weeks of age in LW line was 86 percent of that in the HW line through the F_7 generation (Table 5), then the lower ΣiYx for 38-week weight in the LW line was influenced by the smaller regression coefficients of 38-week weight on eight-week weight. This indicates that selection for eight-week weight in LW line caused a smaller secondary selection differential for 38-week weight than selection for eight-week weight in the HW line. This may have been due to either a lower genetic, and a lower environmental correlation or a combination of both in this particular line.

One possible cause of bias may be the control population which was from a different gene pool than the selected lines. Body weight at 24 and 38 weeks of age may be considered to be the weight at sexual maturity and mature weight, respectively. If the control line was not closely related to the selected lines or if the selected lines were greatly divergent, body weights at these chronological ages may not reflect comparable physiological ages. For example, if egg production, the rate of additional fat disposition and other physiological characters in selected and control lines were different, control-adjusted 38-week body weight of selected lines could include a bias. Furthermore, there may be genotype-environment interactions between selected and control lines.

Egg weight: The realized heritability of egg weight based on the regression for divergence on iYx was .53 ± .06 with a range from .55 to 3.11, by generations (Table 8). The inflated heritabilities in the F_1 and F_2 generations may be attributed to linkage. The mean of the heritability estimates for the seven filial generations based on full-sib correlations was .66. The realized heritability for divergence from regression was .53, a value consistent with those reported by King and Henderson (1954) and Nordskog and Festing (1962). Realized heritability from the regression of control-adjusted data was .41 ± .20 for the HW line and .12 ± .35 for the LW line. Neither heritability was significant. Maloney et al. (1963) in a two-way selection for 12-week body weight, reported a significant decrease of March egg weight in the low line and no significant increase in the high line. Although their data were neither adjusted to controls to remove environmental fluctuations nor were secondary selection differentials in each directions known, their data may suggest the possibility of different correlated responses in each direction.

Sexual maturity: The realized heritability of sexual maturity based on the regression for divergence on iYx was .19 ± .06 with a range from .08 to .28, by generations (Table 8). The average of the heritability estimates for seven generations based on full-sib correlations was 128. Realized heritabilities based on iYx were slightly lower than those reported by King and Henderson (1954), King (1961), Siegel (1963) and Kinney and Shoffner (1965). Realized heritability from control-adjusted data was .07 ± .21 for the HW line and .27 ± .29 for the LW line and neither was significant. The correlated response of sexual maturity to selection for juvenile body weight was consistent with that of Maloney _et_ _al_. (1962) who observed a 54.7 days difference between HW and LW lines after ten generations of selection.

Egg production: Realized heritability of egg production based on the regression for divergence on iYx was .48 ± .13 with a range from .02 to .91, by generations (Table 8). These values were higher than those reported with egg production stocks (Jerome _et_ _al_., 1956; Oliver _et_ _al_., 1957; and Yamada _et_ _al_., 1958). The mean value of .36 obtained by King (1961) was also lower than the values obtained here. Most egg production stocks, however, have a prior history of selection for egg production and hence may have less additive gene action than meat-type stocks such as White Rocks. This may explain the discrepancy. The mean heritability estimate for the seven filial generations based on full-sib correlations was .14.

The phenotypic regression coefficients of egg production on eight-week body weight fluctuated in magnitude and sign from generation to generation (Figure 6-2, 6-3; Table 3) and were not significant. This suggests high standard errors of the iYx estimates, which in turn resulted in high standard errors of the corrected realized heritabilities based on iYx. However, the regression for divergence on iYx (equal to realized heritability) was highly significant which indicated that the divergence between the selected lines had increased significantly for egg production concomitant to selection for eight-week weight. Furthermore, the fact that the genetic correlation between eight-week weight and percentage egg production obtained by using the corrected realized heritabilities were consistent with those in the literature may indicate that the high heritabilities were reasonable for the lines studied in this thesis. The realized heritability of each line based on control-adjusted data, however, was highly variable (Figure 6-3) and not significant.

Genetic correlations between eight-week body weight and unselected traits:

Genetic correlations between eight-week body weight and unselected traits were obtained from:

$$r_G = \Delta Y_x \, h_x \, \sigma_{px} / \Delta X \, h_y \, \sigma_{Py}$$

These correlations were calculated each generation from realized heritabilities of the selected trait (h_x^2), corrected realized heritabilities of unselected traits (h_y^2), pooled phenotypic standard deviations of selected and unselected characteristics in HW and LW lines (σP_x and σP_y) and the phenotypic response of the selected (ΔX) and unselected (ΔYx) trait. The results are presented in Table 9.

Body weight at 24 and 38 weeks of age: The genetic correlations between eight-week and adult (24 and 38-week) weight were comparatively uniform for all generations. The mean genetic correlation was .62

Table 9. Realized genetic correlation (r_G) between selected and unselected traits based on realized heritability of selected trait and corrected realized heritability of unselected trait.

	r_G between 8 week body weight and				
Generations	24 wk. wt.	38 wk. wt.	Egg wt.	Age at 1st egg	Egg prod.
F_1	.52	.47	.29	-.22	-.20
F_2	.85	.58	.23	-.31	-.04
F_3	.50	.38	.16	-.27	-.16
F_4	.60	.68	.25	-.23	-.14
F_5	.61	.60	.25	-.18	-.20
F_6	.68	.45	.27	-.23	-.17
F_7	.57	.49	.17	-.21	-.09
Mean	.62	.52	.23	-.24	-.14

with a range from .52 to .84 for a 24-week body weight. The mean genetic correlation for 38-week body weight was .52 with a range from .38 to .68. These values were consistent with those obtained by Peeler _et al_. (1955), Hale (1961), but higher than those obtained by Jaap (1962) and Kinney and Shoffner (1965). Siegel (1963) reported genetic correlations of .43, .87, .42 and .84 and .48, 1.02, .32 and .71 in the F_1, F_2, F_3 and F_4 generations between the selected trait and 24 and 38-week weight, respectively. These correlations were for the same lines used in this thesis. His values were obtained from realized heritabilities of eight-week weight and heritabilities estimates based on full-sib correlations for the unselected traits. Thus, differences between his values and those obtained here stemmed from differences between the heritabilities estimated by full-sib correlations and those from corrected realized heritabilities of unselected traits. The high genetic correlation between eight-week and adult body weight demonstrates the difficulties of the development of breeding stocks which have large broiler and small adult weights.

Egg weight: The genetic correlations between eight-week weight and egg weight were also relatively uniform for all generations. The mean value was .23 with a range from .16 to .29. These values were consistent with those reported by Jaap (1962), Merrit and Gowe (1962), and Siegel (1963), but higher than those obtained by Hale (1961) and lower than those of Ghostley and Nordskog (1956). The magnitude of the genetic correlation between these characteristics indicates the selection for large broiler weight may result in increased egg weight. Egg weight is a trait in favor of intermediate size from the view point of natural selection and hatchery management. The sign and size of the genetic correlation between broiler weight and egg weight should be considered in the maintenance of uniform egg size in meat-type chickens.

Sexual maturity: The genetic correlations between eight-week weight and age of first egg were relatively uniform for all generations. The means was -.24 with the range from -.18 to -.31. These values were consistent with those reported by Merrit and Gowe (1962), King *et al*. (1963) but lower than those of Kinney and Shoffner (1965). The moderately negative genetic correlations indicate that selection for increased juvenile body weight will result birds commencing egg production at an earlier age. Since it is desirable to have a reasonable age of first egg for the practical reasons of large egg size and subsequent egg production, age at first egg should be controlled by management procedures. When this is done consideration should be given to the magnitude and sign of the environmental correlation between these traits.

Egg production: The genetic correlations between eight-week body weight and percentage hen-day egg production to January 1 were relatively uniform. The mean of -.14 with a range of -.04 to -.20 was consistent with those reported by McClung (1958), Enfield (1960) and Kinney and Shoffner (1965). The mean was lower than those reported in a meat line by Kinney and Shoffner (1965) and Siegel (1963). Although the later report involved the early generations of the lines used here, the heritability estimates of percentage egg production were based on full-sib correlations.

Phenotypic and environmental correlations between eight-week body weight and unselected traits:

Phenotypic (r_P) and environmental (r_E) correlations between eight-week weight and unselected traits are presented in Table 10. Environmental correlations were obtained from the formula $r_E = (r_P - r_G h_x h_y) / e_x e_y$ using the square roots of realized heritability of the selected trait (h_x) and the corrected realized heritabilities of unselected traits (h_y).

Phenotypic correlations between body weight at eight weeks of age with egg weight were positive and increased at a non-significant rate of .06 per generation. The negative and high environmental correlations between eight-week weight and age at first egg indicate that an environment which causes heavier broiler weights would also result in earlier sexual maturity. No consistent pattern of change in correlations was observed during the course of selection.

Phenotypic correlations between body weight at eight weeks of age with body weight at 24 and 38 weeks of age increased

Table 10. Phenotypic (r_P) and environmental (r_E) correlations between body weight at eight weeks of age and unselected traits.

	Unselected Trait									
Generation	24 wk. wt.		38 wk. wt.		Egg wt.[1]		Age at first egg		Percent Egg prod.	
	r_P	r_E	r_P	r_E	r_P	r_E	r_P	r_E	r_P	r_E
P	.48		.33		.03		-.33		.10	
F_1	.50	.51	.50	.56	.23	-	-.29	-.88	.07	.07
F_2	.63	.52	.49	.44	.28	-	-.38	-.41	.17	.21
F_3	.67	.76	.61	.73	.34	.53	-.37	-.41	-.12	-.10
F_4	.75	1.02	.48	.46	.52	1.15	-.62	-.91	-.03	.04
F_5	.79	.88	.84	1.07	.11	0	-.05	-.03	-.31	-.41
F_6	.86	1.01	.82	1.15	.59	.91	-.39	-.44	-.43	-.65
F_7	.86	1.06	.78	.97	.58	.88	-.43	-.50	-.24	-.29

[1] No r_E was calculated in the F_1 and F_2 generations because the heritability of egg weight was greater than unity.

significantly in time. The rate of increase per generation was .06 for the correlation between eight and 24-week weight and .08 for the correlation between eight and 38-week weight. The phenotypic correlation between the selected trait and percentage hen-day egg production increased significantly at a rate of -.07 per generation. In the present experiment the realized heritabilities of selected and unselected traits and the respective genetic correlations were relatively uniform throughout the generations as discussed previously (Tables 8 and 9). Therefore, the significant increase of the phenotypic correlations was primarily due to the significant increase in the environmental correlations between the selected and these three unselected traits in time. A change in the environmental correlation can cause a concomitant change in the phenotypic correlation because the latter consists of the sum of $r_G h_x h_y$ and $r_E e_x e_y$.

The significant increase in the environmental correlations between the selected and certain unselected traits in time should be noted because it indicates that the degree which two traits were influenced by environmental conditions increased during selection. This may be explained from genotype-environment correlations. These data demonstrate the importance of such factors and suggest that they may complicate the breeding of meat-type chickens. Environments that favor genotypes for larger juvenile body weights could result in individuals with heavier post-juvenile weights and poor rates of egg production. This effect could become magnified in subsequent generations of selection. In other words, environmental correlations in these traits tend to increase the effect of genetic correlations between them as selection is continued. This may cause further difficulties in the development of a breeding stock possessing a large broiler weight, small adult weight and high egg production. The time trends of phenotypic and environmental correlations in further generations in this experiment may provide more information concerning genotype-environment correlations.

Prediction of correlated responses:

Prediction of correlated responses were obtained by a formula analogous to that for obtaining the genetic correlation $\Delta G' = \Delta G \, r_G h' \sigma'_P / h \, \sigma_P$, using the realized heritability of selected trait and heritability estimates of unselected traits based on full-sib correlations. This was because the genetic correlations were obtained from this formula using the realized heritability of the selected trait and the corrected realized heritabilities of unselected traits. Therefore, the only differences between the actual and predicted responses were different heritability estimates of unselected traits, i.e., 2(S + D) and the corrected realized heritability.

Predicted and actual correlated responses are presented in Table 11. It may be observed that in the F_7 generation the predicted

Table 11. Prediction of correlated response using heritability estimates based on full-sib correlations for the unselected trait and realized genetic correlations

Gen.	24 wk. wt.		38 wk. wt.		Egg wt.		Age at 1st egg		Egg prod.	
	Predict.	Actual	Predict.	Actual	Predict.	Actual	Predict.	Actual	Predict.	Actual
F_1	.33	.37	.32	.45	.56	1.52	-3.6	-2.3	-1.6	-4.87
F_2	1.62	.73	.96	.73	3.80	2.25	-20.6	-7.2	-2.9	-.24
F_3	.85	.85	.92	.89	1.61	2.20	-14.1	-14.4	-3.7	-6.9
F_4	.66	1.29	1.18	1.72	3.11	4.22	-7.9	-14.6	-3.3	-9.7
F_5	.98	1.44	1.04	2.05	4.06	5.16	-3.0	-5.9	-4.9[1]	-16.1
F_6	1.47	1.85	2.07	2.38	4.34	5.23	-8.3	-13.4	-6.4[1]	-16.6
F_7	1.38	2.09	1.73	2.35	6.45	5.23	-22.0	-22.4	-4.6	-7.9
95% C.I. of the regression coefficient of the prediction on generation	.11 ± .22		.22 ± .15		.76 ± .62		-.70 ± 4.0		-.61 ± .43	
95% C.I. of the regression coefficient of the actual response on generation	.29 ± .04		.36 ± .10		.72 ± .27		-2.30 ± 2.46		-1.82 ± 2.34	

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[1] In the case of negative heritability estimates, the predicted value was calculated by using the heritability estimate in previous year.

values for body weight at 24 and 38 weeks of age and hen-day egg production were only 65, 69 and 58 percent of the actual response. This may reflect the genotype-environment correlations discussed in the previous section of this thesis. Comparisons were also made in terms of the regression of response on generation. The results indicate that regression coefficients of predicted response on generations were not different from those of the actual response. This, however, was primarily because of the high standard errors, especially in the predicted response. Although the standard error of the predicted egg production was smaller than that of the actual response, it should be noted that for predictive purposes there was a substitution for the negative heritability estimates in the F_5 and F_6 generations. The substituted values used were those of the previous generation. These results may suggest that when heritability estimates based on sib correlations and genetic correlations based on variance and covariance components are used for the prediction of correlated responses, the predicted response will be variable because of the large variation in both estimates. A further complication could, perhaps, be due to the directionality of genetic correlations between selected and certain unselected characteristics. Therefore, the prediction of response is no more reliable than the poorest estimate of any of the parameters involved in its calculation.

SUMMARY AND CONCLUSIONS

The investigation reported here involved truncation-type individual selection in divergent directions for body weight at eight weeks of age in White Rocks. Phenotypic changes, from generation to generation within lines, were measured and analyzed for the selected and unselected traits. Unselected traits were body weight at 24 and 38 weeks of age, age at sexual maturity, egg weight and percentage hen-day egg production to January 1. Only female chickens were used in this study which included the parental and seven selected generations.

The direct response of selection for body weight at eight weeks of age were discussed in detail. The divergence between means of the HW and LW lines was significant in all filial generations for the selected trait. The coefficient of variation in each line decreased with selection with the CV for LW line being consistently larger than that for HW line. Through the F_7 generation the response to bidirectional selection for eight-week body weight was symmetrical. This was concluded from the lack of a difference between the regressions of the control-adjusted response on the selection differential for each line, selection differentials of a similar magnitude in both lines, lack of scale effects, and the same rate of inbreeding in the selected lines.

Heritability estimates of body weight at eight weeks of age were obtained each generation from full-sib correlations. Realized heritability was obtained from the divergence between lines divided by the cumulative selection differential by generations; the regression of divergence on cumulative selection differential; and the regression of the control-adjusted responses in each line on the cumulative selection differentials. The realized heritabilities were consistent with the mean of heritability estimates based on paternal half-sib correlation for eight generations whereas the mean of heritability estimates based on maternal half-sib correlation were larger and thus indicated the possible importance of either maternal effects, dominance deviations, or both.

The correlated responses of unselected traits were consistently large and all differences between lines were highly significant. Realized heritabilities of the unselected traits were obtained from the divergence between lines divided by the uncorrected $(\check{P}-\bar{P})$ and by the expected (iYx) secondary selection differential by generations. iYx were obtained by multiplication of the selection differential of eight-week body weight with the regression coefficient of the unselected trait on the selected trait within lines and generations. Realized heritabilities of unselected traits were also obtained from the regression of divergence on iYx and the regression of control-adjusted response on iYx for each line. The corrected realized heritability based on iYx were comparatively uniform and consistent with those reported by other investigators with the exception of percentage egg production. The uncorrected heritabilities based on $(\check{P}-\bar{P})$ however, were inflated and frequently more than unity. This was due to lack of sire selection differential.

Genetic correlations between eight-week body weight and the unselected traits were obtained from the formula using the realized heritabilities of selected trait and the corrected realized heritabilities of unselected traits. Genetic correlations obtained were relatively uniform throughout all the generations and were consistent with those reported in the literature.

Phenotypic and environmental correlations between eight-week body weight and unselected traits were presented and discussed. Phenotypic correlations between the selected trait and body weight at 24 and 38 weeks of age increased significantly in time, whereas those with percentage egg production increased significantly in a negative direction. These increases were primarily due to significant increases in the environmental correlation between these traits during the course of selection. The significant increase in environmental correlation during selection may indicate a genotype-environment correlation. The importance of this factor in the breeding of meat-type chickens was discussed.

Prediction of correlated responses were obtained by a formula which is analogous to that of genetic correlation using the heritability estimates of unselected traits based on full-sib correlations instead of the corrected realized heritability. Predicted and actual correlated responses were compared in terms of the regression of response on generations. The large discrepancy between the predicted and actual correlated response for 24 and 38-week body weight and egg production might reflect genotype-environment correlations. The reliability of the prediction of correlated responses was discussed.

ACKNOWLEDGEMENTS

The author wishes to express his sincere thanks and appreciation to Dr. Paul B. Siegel, Professor of Poultry Genetics and major advisor, for his suggestions, guidance and encouragement throughout the course of this study.

Appreciation is also expressed to Dr. Y. Yamada, Poultry Geneticist, for his suggestions, especially on expected secondary selection differentials.

Thanks are expressed to Dr. C. E. Howes, Head, Department of Poultry Science, and Dr. C. E. Holmes, Department of Poultry Science, for their advice and help in reviewing this thesis.

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ABSTRACT

The investigation reported here involved truncation-type individual selection in divergent directions for body weight at eight weeks of age in White Rocks. Phenotypic changes of selection and unselected traits within lines were measured for females from the P_1 through the F_7 generation. Unselected traits were 24 and 38-week body weight, egg weight, age at first egg and percentage egg production to January 1.

The following were analyzed and discussed:

1. Direct response of eight-week body weight to selection,
2. Correlated responses and estimates of realized heritabilities,
3. Genetic correlations between the selected and unselected traits,
4. Phenotypic and environmental correlations between selected and unselected traits, and
5. The prediction of correlated responses.

The realized heritabilities of unselected traits based on the expected secondary selection differential were relatively uniform and consistent with those reported in the literature. Genetic correlations obtained from realized heritabilities of the selected and unselected traits were uniform and consistent with those of others.

The significant increase of environmental correlations between selected trait and 24 and 38-week weight and percentage egg production during the eight generations indicated genotype-environment correlations. Such correlations may cause further difficulties in the development of a breeding stock possessing a large broiler weight, small adult weight and high egg production. Predicted correlated responses of these three traits were lower than the actual responses and may reflect these relationships.