THE EFFECTS OF SELECTION FOR TWELVE-WEEK BODY WEIGHT ON JUVENILE BODY WEIGHT AND OTHER TRAITS OF ECONOMIC IMPORTANCE IN THE DOMESTIC FOWL

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CHAPTER I

INTRODUCTION

Since the beginning of the twentieth century, great advancements have been made in the development and utilization of genetic principles in plant and animal breeding. With the application of the laws and theories related to population genetics, the broiler segment of the poultry industry has become one of the most dynamic and competitive segments in the area of animal industry. Under the pressures of economic necessities, the broiler breeders are constantly confronted with the challenge of further requirements. Their basic objective is the development of broiler chickens which will produce a large amount of meat with a relatively low intake of feed per pound of meat produced. Although there are several factors which are of primary concern, probably the most important single factor is growth rate. In broilers this trait is usually measured by the body weight attained at broiler age.

The attainment of a specific broiler weight in a minimum amount of time does not constitute the entire problem facing the breeder. The broiler breeder stock also must have a relatively efficient reproductive rate. This is usually measured by the number of eggs laid per bird and the hatchability of those eggs.

The development of these qualities in the broiler strains rests primarily with the breeders of these strains. The genetic characters that concern the poultry breeders are usually quantitative in nature;

that is, they depend upon many pairs of genes, and characteristicly exhibit a continuous variation when observed. Thus, the development of an efficient breeding system would be greatly facilitated by knowledge of the mode of inheritance of these traits.

Probably the most important statistics from the breeder's standpoint are the degree of heritability of each trait considered in his breeding program and the correlations which exist among those traits. Other factors which are also important are the types of gene action involved and the relative importance of non-additive gene effects and maternal effects with respect to the traits with which the breeder is working.

Even though several studies have indicated that body size in the young chicken is highly influenced by selection, there is very little information on the effects that long term selection may have upon the response of a single trait and upon the interrelationships among traits of economic importance.

This thesis is a summary of several experiments conducted to determine some of the influences of long term selection for body weight at twelve weeks of age, and the effects of this selection on other traits of economic importance. The objectives were as follows:

1. To determine the response to selection for high and low twelve-week body weight over a period of fifteen generations.
2. To determine the response to relaxed selection during a period of ten generations in two lines of chickens which were previously selected for high and low twelve-week body weight for five generations.

3. To determine the progeny response to reciprocal cross matings between two lines previously selected for high and low body weight at twelve weeks of age over a period of ten generations.
4. To determine the influence of an incomplete negative assortive mating system on traits related to fitness when applied to a strain of chickens selected for high twelve-week body weight over a period of twelve generations.

Discussion of the Problem

The purpose of this investigation was to study the nature of the various sources of variation that are observed in some traits in chickens under various breeding regimes. The different regimes studied will be presented as four separate phases. Phase I will present the results of an experiment conducted to determine the effect of long term divergent selection for body weight at twelve weeks of age. In the fifth generation of selection in the divergent selection program, a relaxed-selected line was initiated from each of the two divergent lines. The results of this breeding system will be discussed in phase II. The response of progeny produced from reciprocal cross matings between the two divergent selected lines during the eleventh generation of selection will be presented in phase III of this thesis. Phase IV will consist of a report on the effects of an incomplete negative assortive mating system involving individuals produced from the high selected line on several traits of economic importance.

Since there are several types of variance which are likely to be involved, a section of this thesis is devoted to a discussion of the types of variance. This will be presented in a general review of literature common to all of the phases being presented.

CHAPTER II

GENERAL LITERATURE REVIEW

Types of Variance

The traits which are of most importance economically in a poultry breeding program are generally classified as quantitative or metric characters. A quantitative character is defined as a trait exhibited by individuals in a population which will not allow a breeder to classify the individuals into distinct classes. These characters thus exhibit a continuous variation, and their study depends on a quantitative measurement rather than a qualitative measurement. The reasons which cause these traits to fail to exhibit the discontinuous variation caused by genetic segregation have been reported by Lush (1945), Li (1955) and Falconer (1960). These authors suggest two reasons for this phenomenon, namely, the simultaneous segregation of many genes with small effects and the superimposition of truly continuous variation arising from nongenetic causes.

The phenotypic variance observed among individuals may be due to genotypic differences and to differences produced by environmental effects on the individuals. The variance due to genetic differences can be further subdivided into the additive genetic variance, (V_A), dominance deviations, (V_D), and epistatic or interaction deviations (V_I). The total variance or phenotypic variance (V_P) can be then represented by the formula: $V_P = V_A + V_D + V_I + V_E$, where V_E is the variance due to the environmental deviations.

The additive variance is the most important component since it is the chief cause of the resemblance between relatives. It is therefore the chief determinant of the observable genetic properties of the population and of the response of the population to selection. Moreover, as pointed out by Falconer (1960), it is the only component that can be readily estimated from observations made on the population. Dominance deviations are characteristics of gene combinations and are not transmitted as such from parent to offspring. Thus, they would tend to reduce heritability estimation.

Heritability of Traits

The degree of heritability for each trait is of exceedingly great importance. It influences the amount of gain which selection can accomplish in a breeding program and dictates the choice of an efficient breeding system.

All methods of estimating heritability depend in one way or another on how closely the phenotypic resemblance parallels the genetic resemblance between individuals. That is, they are based on the correlation between the genotype and the phenotype. Because it is usually difficult to calculate this directly, analysis of variance is usually used to separate the variance into its components to obtain the correlation indirectly.

Several methods of estimating heritability are outlined by Li (1955) and Falconer (1960). These methods depend upon different kinds of relatives for estimating either the additive genetic variance from the covariances of the relatives or the heritability from the regression or correlation coefficients between relatives. Generally, the half-sib correlation and the regression of offspring on father are the most reliable, since the covariance is least likely to be augmented by an environmental component. The regression of offspring on mother is sometimes liable to be overestimated due to the effects of maternal influences. The full-sib correlation, which is the only relationship for which an environmental component of covariance is likely to occur, is the least reliable of all.

In experimental and domesticated populations the parents are often a selected group and consequently the phenotypic variance among the parents is less than that of the population as a whole and less than that of the offspring. Falconer (1960) suggested that under these circumstances a regression of offspring on parent be used for estimating heritability. This regression is not affected by the selection of parents because the covariance is reduced to the same extent as the variance of the parent. Therefore, the slope of the regression line is unaltered. The regression of offspring on one parent is a valid measure of one-half of the heritability. This author (Falconer, 1960) further suggested that since in most populations each male is mated to several females, an intra-sire regression should be utilized. In this method the heritability is estimated from the average regression of offspring on dams, calculated within sire groups. The validity of the estimate is dependent on the absence of maternal effects contributing to the resemblance between the daughters and dams. Falconer (1960) also pointed out that if an inequality exists in the variance of the male and female progeny, then an adjustment in the heritability, as estimated from the intra-sire regression of male offspring on dams, should be made. This adjustment is accomplished by multiplying the regression coefficient by the ratio of the phenotypic standard deviation of the females to that of the males.

Heritability of Juvenile Body Weight: Much of the early work on the inheritance of body weight was designed to show that inherent differences do exist. Punnett and Bailey (1914) were two of the early workers to demonstrate that inherent differences exist. These workers concluded that size in poultry depends upon definite factors and that these factors segregate in gametogenesis. One of the most extensive early studies was reported by Waters (1931). From the data collected it was concluded that weight differences were dependent primarily upon two pairs of genes each with equal and cumulative effects. It further suggested that possibly other genes of lesser influence were also expressed.

Many other studies such as these have been reported in the early work of investigators, and studies involving the estimation of heritability were not prevalent until the early 1940's.

Lerner et al. (1947) determined heritability estimates for 12-week body weight in a randomly selected sample of New Hampshire chickens. The heritability was based on the methods of Whatley (1942) and Hazel et al. (1943) with a few modifications. The heritability for 12-week body weight based on the sire's contribution was 0.42; based on the dam's contribution the estimate was 0.60; and a combination of the two gave an estimate of 0.51. El-Ibiary and Shaffner (1951) criticized these workers for using only 230 birds and for combining the sexes. They stated that under normal conditions there would be a 15 to 20 percent sex difference in body weight.

Shoffner and Sloan (1948) calculated heritability for 300-day body weight among inbred lines of chickens. The method of analysis was that of an intra-sire regression proposed by Lush (1940). When the estimate was corrected for 16.2 percent inbreeding, h^2 equaled 0.75. This estimate appears to be high in comparison to other estimates of heritability for body weight. A large part of the data was derived from crosses of breeds differing considerably in body weight. Segregation in succeeding generations probably would provide a larger portion of genetic variance than normally observed in the case of closed flocks.

El-Ibiary and Shaffner (1951) calculated heritability estimates for body weight in New Hampshires at 2, 4, 6, 8, and 10 weeks of age. These estimates were based on data collected from two randomly distributed groups of chicks treated differently. One group was fed an adequate ration plus 0.2 percent of thiouracil and the other group received the same ration without the thiouracil. Only dams having at least two male or two female chicks and sires with chicks from at least two dams were used in the analysis. These data were analyzed separately by sexes by means of an analysis of variance and covariance. Heritability estimates were calculated from the sire's contribution to the genetic variance (g^2) and from the combined contribution of sire and dam (h^2). Their estimates for g^2 at two weeks of age ranged from zero to 0.056; 0.055 to 0.217 at four weeks; 0.033 to 0.194 at eight weeks and 0.038 to 0.231 for body weight at ten weeks of age. The estimates reported for h^2 ranged from 0.314 to 0.574 at two weeks of age; 0.255 to 0.381 at four weeks of age; 0.270 to 0.374 at eight weeks of age and 0.210 to 0.540 at ten weeks of age. The authors stated that

g^2 is heritability in a rather narrow sense, and that h^2 is heritability in a broad sense. This is not an estimate in the narrow sense as used by Lerner (1950) to include only additive genetic variance. Lush et al. (1948) stated that the combined estimates lead to a smaller sampling error since sampling errors due to sire and dam contributions tend to cancel each other. Lush et al. (1948) also pointed out that the combined estimates include one-fourth of the variance from dominance deviation in the component which he calls "extra variance" within groups of paternal half-sibs. In addition, this component contains likeness between full-sibs caused by similarity of this environment. More confidence can be placed in the estimate from the sire's contribution when the data are numerous enough to make sampling errors small.

When the available estimates of heritability for body weight in young chickens are considered as a group, there is considerable variation among them. Various types of error such as sire's sampling error may be operating in the reported studies. This considerable variation in estimates can be expected. Other discrepancies might arise from using different stocks and from using different methods of calculation. It seems that estimates from several sources would tend to give a rather reliable estimate of heritability.

Reported estimates of heritability of body weight in chickens have been based on weight of birds at various ages. Estimates have also been published only in tabular form with no description as to the method of calculation or source of data. Because of these reasons, some of these estimates have not been reviewed but will be presented in a tabular form. Some of the available estimates of juvenile body weight in chickens are shown in Table I.

TABLE I

HERITABILITY ESTIMATES BY VARIOUS AUTHORS OF JUVENILE BODY WEIGHT

Investigators	Year	h^2_S	h^2_D	h^2_{S+D}	b_{OD}	Unk.	Sex
Comstock *et al.*	1947					0.52*	Comb.
Lerner *et al.*	1947	0.42	0.60	0.51			Comb.
El-Ibiary and Shaffner	1951	0.13*		0.21*			Male
El-Ibiary and Shaffner	1951	0.26*		0.54*			Female
Godfrey and Williams	1952					0.30*	Comb.
Martin *et al.*	1953			0.29*			Comb.
Wyatt	1954			0.40			Comb.
Peeler *et al.*	1955				0.27*		Comb.
Goodman and Godfrey	1956			0.43			Comb.
Thomas *et al.*	1958	0.47*	0.80*				Male
		0.91*	0.65*				Female
Goodman and Jaap	1960	0.32*	0.25*				Male
		0.25*	0.63*				Female
Moyer *et al.*	1962	0.38*	0.60*				Male
		0.38*	0.68*				Female
Siegel	1962	0.29	0.60	0.44	0.22		Male
		0.12	0.58	0.35	0.36		Female
Amer	1965	0.67	0.84	0.76			Comb.
Merritt	1966	0.40	0.81		0.56		Male
		0.44	0.49		0.47		Female
Average		0.33	0.61	0.33	0.39	----	Male
		0.39	0.61	0.46	0.42	----	Female
		0.39	0.63	0.44	0.38	0.41	Comb.

* Simple average of estimates calculated from estimates reported.

The average of these estimates indicates that a very close agreement exists between the two sexes when the estimates were obtained from the dam component. It was also noted that the estimates obtained from the sire components of variance were consistently lower than those estimated for the dam's component. This would tend to indicate that maternal and other non-additive effects were being measured in the dam's contribution to the total variance.

Heritability of March Egg Weight: Waters (1941, 1945) suggested that the inheritance of egg weight was predominantly maternal while other workers (Hutt and Bozivich, 1946; Ghigi, 1948; Osborne, 1953; Hogsett and Nordskog, 1956, 1958; Fuchs and Krueger, 1957; Hicks, 1958; and Goodman and Jaap, 1961) have found evidence of sex-linkage. It was indicated by Benjamin (1920) and Hurst (1921) that small egg size is dominant. Evidence found by Waters and Weldin (1929) was indicative of dominance of large egg size. On the other hand, Roberts et al. (1952) found that egg weight was influenced equally by the male and the female since no evidence of dominance or sex-linkage was observed.

Among this array of data, there has also been a wide variation in the heritability estimates presented for the trait. Some of the heritability estimates of March egg weight range from 0.12 reported by Redman and Shoffner (1961) for the dam component to an estimate by Hogsett and Nordskog (1958) of 1.15 for the sire component. The heritability estimates of various authors are presented in Table II.

Because each method of analysis takes into account different sources of variation, it was felt that only those estimates obtained by the same method could be compared. Considering the probable high sampling variance of the various estimates cited, it is not surprising

TABLE II

HERITABILITY ESTIMATES BY VARIOUS AUTHORS OF MARCH EGG WEIGHT

Investigator (s)	Year	h^2_S	h^2_D	h^2_{S+D}	b_{OD}	Unk.
Comstock *et al.*	47					0.58*
Shoffner *and* Sloan	48				0.61	
Lerner and Cruden	51	0.73		0.47		
Krueger *et al.*	52				0.39	
Scheinberg *et al.*	53			0.54**		
				0.33**		
				0.56**		
Wyatt	53			0.52	0.52	
King and Henderson	54	0.39	0.49		0.60*	
Wyatt	54			0.52**	0.23	
Dickerson	55					0.59*
Farnsworth and Nordskog	55a			0.50		
Farnsworth and Nordskog	55b			0.51		
Ghostley and Nordskog	56			0.72	0.46	
Hogsett and Nordskog	56			0.68	0.43	
Jerome *et al.*	56	0.62	0.56	0.59		
Lowry *et al.*	56			0.42*		
Abplanalp	57			0.49		
Dickerson	57	0.50		0.47		
Fuchs and Krueger	57			0.45		
Hicks	58	0.53*	0.25*	0.39*		
		0.68*	0.58*	0.63*		
Hogsett and Nordskog	58	0.36	0.45	0.50**	0.44**	
Crittenden and Bohren	61	0.35*	0.53*			
Goodman and Jaap	61	0.66*	0.34*	0.51*		
Hicks *et al.*	61				0.14	
King	61	0.60	0.73	0.24		
Manson and Abplanalp	61			0.42*		
Redman and Shoffner	61	0.36*	0.12*	0.25*		
Ideta and Siegel	66a		0.69*	0.67*		
Average		0.53	0.47	0.49	0.42	

* Simple average of estimates, calculated from estimates reported.

** Corrected for inbreeding.

to see a fairly wide range in the estimates of heritability.

Assuming that the heritability estimates presented are unbiased, an unbiased estimate of the mean heritability may be obtained by taking the simple average of those cited. Thus, the average estimate of heritability of March egg weight would be 0.53 for the sire component of variance, 0.47 for the dam component and 0.49 for the estimate from the combined sire and dam component of variance. These would compare to 0.42 obtained from the intra-sire regression method of estimation. These estimates would tend to indicate that sex-linked effects may be operating, since the sire component of heritability is higher than the dam component estimate.

Heritability of Sexual Maturity: The heritability of sexual maturity seems to have been studied less extensively than has March egg weight. This could be due to the possible inaccuracy of data collected. Shoffner and Sloan (1948) estimated that at least fifteen percent of the pullets in any given flock have been laying for varying lengths of time before the "first egg" is recorded.

Pearl (1912) was the first to suggest that age at sexual maturity was sex-linked. Goodale and MacMullen (1919) and Hurst (1921), however, failed to substantiate this theory. Evidence presented by Hays (1924) and Warren (1934) indicated that age at sexual maturity was dependent upon autosomal as well as sex-linked genes, with early sexual maturity being a dominant factor. Heritability estimates ranged from 0.04 as reported by King (1961) to 0.54 as given by King and Henderson (1954). The reviewed estimates of heritability for sexual maturity are presented in Table III.

The estimates of Bray et al. (1960) and King and Mitchell (1959)

TABLE III

HERITABILITY ESTIMATES BY VARIOUS AUTHORS OF SEXUAL MATURITY

Investigator (s)	Year	h^2_S	h^2_D	h^2_{S+D}	b_{OD}	Unk.
Lerner and Taylor	43	0.20				
Lerner	45			0.24		
Comstock *et al.*	47					0.27
Hazel and Lamoreaux	47	0.27				
Shoffner and Sloan	48				0.25	
Lerner *et al.*	49			0.31		
Lerner and Cruden	51	0.24		0.31		
Krueger	52			0.20	0.07	
Dillard *et al.*	53			0.16	0.19	
King and Henderson	54	0.38	0.54			
Farnsworth and Nordskog	55b			0.40		
Peeler *et al.*	55	0.21		0.39	0.40	
Yamada	55			0.48		
Jerome *et al.*	56	0.35	0.23	0.30		
Lowry *et al.*	56			0.17*		
Abplanalp	57			0.12		
Dickerson	57	0.22		0.31		
King	61	0.26	0.54	0.04		
Manson and Abplanalp	61			0.17*		
Ideta and Siegel	66a		0.39*	0.47*		
Average		0.27	0.43	0.27	0.23	0.27

* Simple average of estimates, calculated by author.

are not included in the table. Bray et al. re-analyzed data previously presented by King and Henderson (1954), and the report by King and Mitchell (1959) was a preliminary report of that published by King (1961). The overall average estimate of heritability was 0.27 for the sire component of variance, 0.43 for the dam component of variance, and 0.27 for the combined sire and dam component of variance. A very close agreement was indicated between the estimate obtained from the sire component and the combined component of sire and dam with that obtained from intra-sire regression, the latter value being 0.23.

Heritability of Egg Production: Pearl (1912) was one of the earliest investigators of the inheritance of egg production in the domestic fowl. From the studies the author concluded that differences in egg production resulted from the action of two pairs of genes, one of which was autosomal and the other was sex-linked. Goodale and MacMullen (1919) reported that their data indicated that both pairs of genes were autosomal and showed that Pearl's data could also be explained on that basis.

With the development of more advanced statistical analysis and the development of new breeding schemes by Wright (1921), reported estimates of heritability for egg production have become quite numerous. The review of heritability in this thesis will deal mainly with those estimates related to percentage production, since this measurement was utilized in the experiments to be reported.

Using an analysis of variance, Shoffner (1946) estimated the heritability of percentage egg production as 0.34 when estimated from the full-sib correlation. This estimate was very similar to those reported by Lerner and Cruden (1948). Both of these estimates are higher than most of those reported in Table IV.

The estimates vary from 0.43 reported by Lerner and Cruden (1948) to 0.04 reported by King (1961). In almost all cases reported, the heritability estimated for the sire component is higher than that estimated for the dam component, thus indicating that egg production may be at least to some degree controlled by sex-linked genes. This source of variation was considered significant by Goodman and Jaap (1961) and King (1961). The overall average heritability for egg production estimated from the sire component of variance was 0.21, from the dam component 0.18 and 0.20 from the combined sire and dam component. The average calculated from the intra-sire regression method was 0.16.

Correlations Between Traits

The relationship or correlation between traits may be due to genetic and/or environmental forces. Falconer (1960) stated that genetic causes of correlation are chiefly pleiotropy, though linkage is a cause of transient correlation particularly in populations derived from crosses of divergent strains. Pleiotropy is simply the property of a gene whereby it affects two or more characters. If this type of gene is segregating, it would cause simultaneous variation in the characters which it affects. Falconer (1960) also pointed out that the environment may cause a correlation if two characters are similarly influenced by the same environmental conditions.

The amount and degree of correlation between traits may be measured by several different methods. Phenotypic correlation coefficients are usually the simplest to estimate. The general procedure as outlined by Snedecor (1959) for calculating simple correlation coefficients was

TABLE IV

HERITABILITY ESTIMATES BY VARIOUS AUTHORS OF EGG PRODUCTION

Investigator (s)	Year	h^2_S	h^2_D	h^2_{S+D}	b_{OD}
Lerner and Cruden	1948	0.36	0.43	0.39	
Krueger *et al.*	1952		0.28		0.17
Dillard *et al.*	1953			0.12	0.20
King and Henderson	1954	0.14	0.20		
Farnsworth and Nordskog	1955b			0.34	
Yamada	1955			0.15	
Jerome *et al.*	1956	0.13	0.11	0.12	
Oliver *et al.*	1957	0.16	0.15	0.15	
Yamada *et al.*	1958	0.14	0.24	0.19	
Yao	1958			0.10	
Hicks	1958			0.25	
Goodman and Jaap	1961	0.28	0.05	0.17	
King	1961	0.16	0.04		
Wheat and Lush	1961	0.23	0.14	0.18	0.12
Jaap *et al.*	1962	0.28			
Average		0.21	0.18	0.20	0.16

utilized in most of the early genetic studies in poultry. The method developed by Hazel et al. (1943) enabled investigators to estimate genetic, environmental and phenotypic correlation coefficients between traits.

The early work on phenotypic correlations has been reviewed in detail by Jull (1940). Most of these studies indicated that a negative relationship exists between rate of egg production and egg weight. Jull (1940) further concluded that age at sexual maturity was not correlated with egg weight, but seems to have negative relationship with rate of production. The early studies also indicated that body weight was correlated with egg weight and age at sexual maturity but not with egg production.

In more recent studies both phenotypic and genetic correlations have been estimated in the domestic fowl. In studies conducted by Blyth (1952), Waters (1953) and Farnsworth and Nordskog (1955b) the phenotypic correlation between egg weight and rate of egg production was estimated to be near zero. The genetic correlations were found to range from -0.43 to -0.07. These estimates are lower than the values reported by Quinn (1963) for the genetic and phenotypic correlations. The values reported by Quinn were 0.31 and 0.11, respectively. In a study conducted by Hicks (1958) the data indicated that the phenotypic correlation was -0.07, which is considerably lower than most of the values reported in recent studies. This value is consistent with the studies reviewed by Jull (1940).

There seems to be good reason to believe that a positive phenotypic correlation exists between body weight and egg size. This is based on the estimates reported in recent studies and the early studies as reported by Jull (1940). Both positive and negative correlations between body weight and egg production have been reported.

In studies reported by Wyatt (1953), Jerome et al. (1956) and Mostageerand Kaman (1961), the genetic and phenotypic correlations between body weight and egg size were positive. These estimates averaged 0.27 and 0.50 for the genetic and phenotypic correlations, respectively. The genetic correlation between body weight and egg production was estimated to be -0.31 and -0.51 by Wyatt (1953) and Jerome et al. (1956). These estimates are considerably different than the values estimated by McClung (1958) and by Ideta and Siegel (1966). The estimates of the genetic correlation between egg production and body weight reported by McClung (1958) ranged from -0.21 to 0.19. The unweighted average of these estimates was about -0.13 which compares to -0.14 reported by Ideta and Siegel (1966).

Although the early studies reported (Jull, 1940) seem to indicate that body weight is positively correlated with age at sexual maturity, more recent investigations indicate that a negative relationship may exist. Hazel and Lamoreaux (1947) and Peeler et al. (1955) estimated the phenotypic correlation between these two traits to be -0.44 and -0.18, respectively. The genetic correlations reported by these authors were -0.32 and 0.26. The latter estimated reported by Peeler et al. (1955) does not compare with that reported by Jerome et al. (1956) and Ideta and Siegel (1966) who reported the values to be -0.53 and -0.24.

Jerome et al. (1956) reported that sexual maturity was negatively correlated with egg weight and rate of egg production. A negative correlation between sexual maturity and egg production was also reported by Bray et al. (1960). This value was -0.17. These authors further reported that the phenotypic correlation between these two traits was near zero. The genetic relationship between sexual maturity and egg weight was reported as 0.78 by King (1961). This value was estimated from the eggs produced during the first month of production and this may result in an overestimation.

CHAPTER III

GENERAL EXPERIMENTAL PROCEDURES

Since this thesis reports the findings of four different experiments, the experimental procedures which were common to all of the phases are presented in this section. The procedures which are related to a specific phase of the study will be presented in the respective phase.

The stock used in this investigation was from the Oklahoma Agricultural Experiment Station. The Silver Oklabar breed used in this study was developed over a period of several years by Dr. R. G. Jaap, who was poultry geneticist at the Oklahoma State University from 1935 to 1946. The first step in its development was the crossing of White Plymouth Rocks with Rhode Island Reds. This was initiated in 1936. The red, barred males produced from the first cross were then back-crossed to Rhode Island Red females. The progeny which were proven to be free of recessive white were then mated together. The female progeny from these matings were mated to Dark Cornish males to improve their body conformation. The final cross of these progenies to Silver-Laced Wyandottes was made to introduce the dominant silver gene. After the breed was "purified" for the silver gene, the resulting chickens were named Silver Oklabars. This latter stage in their development was completed in 1940. A more detailed discussion on the development of this breed was reported by Godfrey, 1953.

Following the development of the Silver Oklabar chicken, a large population of these birds was maintained under a closed-flock random breeding program, until the initiation of the two-way selection program in 1950.

In this study each generation consisted of a 500-day test period for the selected parental stock in each of the developed lines. Individual male mating pens were used in order to maintain pedigree records of all progeny produced within the lines. Approximately ten females were utilized in each mating pen. This number varied from one generation to another, depending upon the number and relationship of the females available for breeding purposes. A double shift of males was also utilized in order to minimize the amount of inbreeding. These procedures were followed in Phases I, III and IV.

In Phase II, however, a flock mating system was used to propagate the relaxed-selected lines. Approximately 50 females and five males within each line were randomly assigned to each mating pen. The number of pens used varied among generations, depending upon the number of females available in each line.

After the matings were made, seven days were allowed to assure good fertility. Two weeks were allowed between shifts of males in order to insure correct pedigree of offspring.

Individual trapnest records were maintained to provide an accurate measure of egg production and correct pedigree of eggs laid. All pedigreed eggs were collected daily and held at a temperature of 50 to 55 degrees Fahrenheit. The eggs were set at 14-day intervals to allow for the maximum number of chicks per hatch without a serious decline in hatchability due to the age of the egg.

Eggs were trayed according to individual pedigree. On the 18th day of incubation, all eggs were candled and infertile and dead germs removed. The remaining eggs were placed in wire pedigree baskets according to dam number and transferred to the hatcher. The infertile eggs were "broken out" to detect any sign of embryonic development, and those eggs showing signs of development were recorded as fertile.

On the day of hatching, all chicks were wing-banded and pedigreed by sire and dam. At this time they were vaccinated intranasally against Newcastle disease and infectious bronchitis with a live-virus vaccine. All offspring of a specific hatch were brooded together in the same house insofar as possible. The offspring produced from each breeding system were brooded together in the same pens. The breeding system which is presented in Phase I, however, produced progeny during the fourth generation which could not be brooded together because of the difference in size. In order to minimize environmental differences, each hatch of progeny from the divergent lines (Phase I) was brooded in adjacent pens within the same house. Each brooding pen was 30 ft. x 15 ft. in dimensions and one square foot per bird was allotted to insure optimal performance. Uniform brooding conditions were maintained for all groups of chicks within each generation.

The starter and grower rations fed during this experiment were the same insofar as possible within and among generations. The ration was changed once during this study. In an effort to provide a more efficient grower ration, an improved formula was used at the beginning of the fourth generation growth period during Phase I of this study.

Gravity-type, gallon-capacity waterers were used during the first two weeks of the brooding period. Automatic waterers were utilized after the second week of brooding.

At six and at twelve weeks of age the birds were weighed to the nearest tenth of a pound. After the twelve-week weights were recorded, the selected progeny were placed on range at the University Poultry Farm at Perkins, Oklahoma. The birds were vaccinated against fowl pox and Newcastle disease during this period. At the same time all male birds were separated from the females and dubbed.

At approximately 16 to 18 weeks of age, the females were housed. Each hen was wing-badged to enable easier and more accurate recording of trapnested egg production. Artificial lights were used, starting about October 1, to provide 14 hours of continuous light per day. These lights were continued until spring, when normal day-length provided 14 hours of natural light per day.

In December of each year, the males and females were assigned to single-male mating pens according to their pedigree within each line. This assignment was based upon the pedigree relationship of the male to the female in each pen, in order to minimize inbreeding.

The layer-breeder ration fed during the laying and breeding seasons was changed at the beginning of the sixth generation of the Phase I experiment. This change consisted of a slight increase in the energy level and in the percentage of protein. All other management practices were the same, insofar as possible, within and among generations.

Age at sexual maturity was recorded as the number of days from date of hatch to date of first egg laid. To obtain percentage egg production, the age at sexual maturity was subtracted from the smaller of two numbers, either the number of days lived or 500 days. This value was termed production days. This value was then divided into the total number of eggs laid by the individual female and the percentage recorded.

During the first ten days of March, all pedigreed eggs were weighed to the nearest tenth of a gram. From these weights the individual female's average egg weight was calculated.

CHAPTER IV

PRESENTATION OF THE LITERATURE REVIEW, THE EXPERIMENTAL PROCEDURES, THE RESULTS AND DISCUSSION, AND THE SUMMARY ASSOCIATED WITH PHASE I, PHASE II, PHASE III, AND PHASE IV OF THE STUDY

Phase I. Differential Selection for Twelve-Week Body Weight in the Domestic Fowl

The breeder of broiler stock chickens must maintain and utilize an efficient breeding system in order to meet the keen competition of the industry. The breeder must have basic information concerning the traits for which he is selecting. Probably one of the most important factors from the breeder's standpoint is the degree of response he will obtain for a given amount of selection. Other useful information includes the interrelationship among traits of economic importance, the type of gene action involved and the relative importance of the non-additive gene effects.

Compared to such laboratory animals as rats, mice and fruit flies, there is little basic information on the effects of long-term selection for body size in the young chicken, especially as broiler age. Even though body size is highly influenced by selection, there is very little information available to suggest the response in body size which might be obtained by selection over a period of several generations.

This phase of this thesis is a summary of an experiment conducted to determine some of the effects of long-term selection for body size at twelve weeks of age and its effects on other economic traits. The objectives were as follows:

1. To determine the response to selection over a period of fifteen generations of selection for high and low twelve-week body weight.
2. To determine the effect of long-term selection for body weight at twelve weeks of age on other traits of economic importance.
3. To determine the effect of long-term selection for body weight at twelve weeks of age on estimates of heritability.

Review of Literature

Because this investigation deals with several problems, this specific review of the literature will be divided into the following areas: measurement of response, asymmetry of response, effectiveness of selection for body size, correlated response of non-selected traits and the effects of inbreeding.

Measurement of Response: When one or more generations of selection have been made, the measurement of the response actually obtained introduces several problems. Falconer (1960) discussed these problems and classified them into two main groups; the first group dealt with variance due to the sampling variation and the second group with variance due to environmental changes. Sampling variation depends primarily on the number of individuals measured. The best measure of the average response per generation is obtained from the slope of a regression line fitted to the generation means. The assumption being made is that the true response is constant over the period. Variation due to changes of environment may be overcome, or at least reduced, by the use of a control population. Falconer (1960) suggested that the measurement of response could be improved in precision if the "control" is not an unselected population but is selected in the opposite direction.

The use of two-way selection was made in poultry as early as 1913 by Hall and Marble (1930) in selecting for high and low annual egg production in White Leghorns. More notable examples of such studies with the use of laboratory animals are those of Kyle and Chapman (1953) with rats, Falconer (1953) with mice, and Robertson and Reeve (1952) with Drosophila melanogaster. This type of study is generally used for a long-term selection experiment, and consequently is not used to a great extent in poultry. However, it was used by Schnetzler (1936) in the development of fast and slow growing lines of Barred Plymouth Rock chickens. Knox and Godfrey (1940) also used this system of selection in selecting for high and low percentage of thick albumen in the eggs of Rhode Island Reds. Hutt and Cole (1948) demonstrated the ability to develop strains of poultry genetically resistant to avian lymphomatosis with the use of the two-way selection system. Since the initiation of this current program, a similar program has been reported by Siegel (1962) where selection was based on individual body weight at eight weeks of age.

Asymmetry of Response: Inequality of the response to selection in opposite directions has been found in many two-way selection experiments. MacArthur (1949), Falconer (1953) and Robertson (1955) reported that the response in a two-way selection experiment tends to be asymmetrical. The asymmetry was considered to be due to the selection producing a greater change in the small line than in the large line. Although the causes of this asymmetry are not understood, some possible explanations are discussed by Falconer (1960). The selection differential may differ between the lines selected upward and downward due to natural selection aiding artificial selection in one direction or hindering it in the other. Also, the fertility may change so that a higher intensity of selection is achieved in one direction than in the other.

There are two genetic properties in the initial population that could give rise to asymmetry of the response to selection, according to Falconer (1954). These concern the dominance and gene frequencies of the loci associated with the character. The dominant alleles at each locus may be mostly those that affect the character in one direction, instead of being more or less equally distributed between those that increase and those that decrease it. If the initial gene frequency were about 0.5, the response would be expected to be greater in the direction in which the alleles tend to be recessive.

If selection in one direction favors heterozygotes at many loci, or at a few loci with important effects, the response would become slow as the gene frequency approached this equilibrium value, according to Lerner (1954). However, the response in the opposite direction would be rapid until the favored alleles approach fixation. This situation would also be expected to give rise to an asymmetric response.

Falconer (1955) found that asymmetry of response may also be associated with the maternal effects in selection of six-week weight in mice. The character selected, weight at six weeks of age, was divided into two components, weaning weight at three weeks of age and growth between three weeks and six weeks of age. The first may be determined mainly by the mother and the second mainly by the individual. The anatomical component, or simply the size of the mammary glands, was found to be associated with body size. It increased continuously as size increased in the large line, and decreased in the same manner in the small line. This would tend to aid selection in both directions. It was further noted that as selection continued the increase in mammary gland growth increased at a decreasing rate in the large line, as compared to the small line in which the mammary gland continued to decrease at about the same rate as the decrease in body size.

Effectiveness of Selection for Body Size: Some of the most extensive selection experiments in body size have been reported in laboratory animals. MacArthur (1944) found mice to be highly responsive to selection for large and small body size at sixty days of age. Body size was selected on the basis of progeny test, sib likeness and individual phenotype. MacArthur (1949) reported that mice were still responding to selection for large and small body size after 21 generations of selection. Falconer (1953) reported similar response to selection for large and small body size in mice. In this study the large line reached its limit of response at about the 22nd generation, whereas the low line reached its limit of response in the 17th generation. Falconer based his selection experiment on the within-litter variation for body weight at six weeks of age. Both Falconer (1953) and MacArthur (1949) reported that the effectiveness of selection was greater in both of the divergent lines during the first ten generations, and it steadily decreased as the trait under selection approached its limit. These authors also indicated that their experiments showed the same trend in the effect of selection on the phenotypic variation, in that the variance increased in the large line and decreased in the small line. On the other hand, the coefficient of variation was equal in both lines until near the end of the period of selection.

In a study using *Drosophila melanogaster*, Robertson (1955) noted that the response to selection for large and small body size was similar to that reported by MacArthur (1949) and Falconer (1953). The actual units of size at which the corresponding lines stabilized were approximately the same, 8 to 10 units of increase for the large line and 14 to 17 units of decrease for the small line.

Krider *et al.* (1946) selected for rapid and slow growing lines of Hampshire swine during four generations. The most effective selection was at 180 days of age, since the weight was influenced only slightly by maternal effects. Dickerson and Grimes (1947) reported selection in swine based on high and low feed efficiency to be nearly as effective as the criterion of improved gains based on individual weight.

Waters (1931) reported one of the most extensive early experiments in selecting for body weight in chickens. This study extended over a period of ten generations and included some 3,000 birds. Waters stated that his data gave evidence of genetic as well as phenotypic differences, and that it was certain that segregation for large and small size took place during the experiment. A study was made by Asmundson and Lerner (1933) of the genetic difference in growth rate of White Leghorns. In this study an attempt was made to divide more or less closely-related families into rapid, intermediate and slow-growing lines. A comparison among the progenies revealed no significant difference in growth rate.

Some of the factors which may influence initial selection were studied by Gyles *et al.* (1955). Over a period of eight generations, the size of the selection differentials for individual performance was determined in standard deviation units. The authors stated that automatic selection, due to association with family size, was significant only for total viability. The relative intensity of selection was less among cockerels than among pullets. The author further stated that initial selection was not reduced by the number of eggs set, progeny housed or mating of progeny selected as breeders. These workers concluded that a genetical difference in growth rate was evident, and that this difference was dependent upon multiple factors.

Martin et al. (1953) studied the efficiency of selection for broiler growth at various ages in Rhode Island Red chickens. These workers found that dominance effects did not show statistical significance in this study. The authors stated that the best index from this study was secured on the basis of the six- and twelve-week body weight, and estimated the index to be four percent more efficient as a criterion of genetic gain to twelve weeks than any single weight.

An experiment was reported by Siegel (1962) which was designed to measure the short-term response of individual selection in divergent directions for body weight at eight weeks of age. In this study the difference between the two lines was significantly different after the first generation of selection. These differences became progressively larger with each successive generation. The response to selection as exhibited by the high line males and females was greater than that exhibited by the low line offspring. The author also reported that a difference in rate of response per generation was different for the two sexes in each of the selected lines. The male responded more rapidly to selection than did the female.

Correlated Response of Non-Selected Traits: The relationship between two or more traits is of importance in any breeding program because it may influence the effectiveness of selection. If simultaneous improvement occurs in a trait other than the one under selection, then a positive correlation may be present. A negative correlation may exist in cases where improvement in one character brings about an opposite effect in another character.

In some cases traits may be correlated because of their relationship to fitness. Robertson (1955) presented a discussion on the relationship of several traits and fitness. The author stated that natural forces caused several effects in variation between traits. Each character has its place in one of a series of chains of causation converging toward fitness. These chains of causation interconnect. In mice, body weight, for example, influences not only litter size but also lactation, longevity and probably many other characters. Thus, according to the author, the relationship between any particular character and fitness is important in any breeding program.

In a study by Robertson (1957), a moderate phenotypic correlation was found to exist between body size and egg production among individuals in a wild population of Drosophila melanogaster. The author also reported that selection for large and small body size did not change the egg production in any of the lines studied. Thus, relatively little or no correlation occurred under artificial selection.

A high association between early sexual maturity and rapid early growth was reported by Hays (1951). In this study Rhode Island Red chickens were selected for high body weight at twelve weeks of age.

Schierman et al. (1959) reported on a correlated response in selecting for egg production, egg weight and body weight. In this study a correlated response in body weight or egg weight was not observed in the line selected for high egg production. A correlated response in egg weight was observed in two divergent lines selected for high and low body weight. The author also noted that in two Leghorn lines selected in opposite directions for egg weight, a correlated response in body weight was evident.

The effects of selection for growth rate at nine weeks of age and the interrelationship between growth rate and other economic traits were reported by Singh _et al._ (1960). Females of the growth selected line reached sexual maturity earlier than the random-bred control pullets. The author also stated that the selected females were larger in body weight at all ages than those of the unselected line. It was further noted that the selected line maintained a higher rate of egg production during the first month of lay. The average egg weight for the selected line was larger than that of the unselected line.

Correlated responses, as measured by differences between lines, were determined by Siegel (1963) for unselected characteristics during the course of a two-way selection experiment for body weight at eight weeks of age. This author reported that selection for divergent body weight resulted in correlated changes in body weight at 4, 24, and 38 weeks of age. Other traits such as age at sexual maturity, percentage egg production and egg weight also indicated a correlated response to selection. A more detailed analysis of this study was reported by Ideta and Siegel (1966b). In this report, the authors stated that the phenotypic correlation between body weight at eight weeks of age and percentage egg production increased significantly in the negative direction. These increases were primarily due to significant increases in the environmental correlations between these traits during the course of selection. The rates of change per generation in the unselected traits, as measured by the regression of response on generations, were 0.72 for egg weight, -0.30 for age at sexual maturity and -1.82 for percentage egg production.

The Effects of Inbreeding: Although general agreement exists that inbreeding has a depressing influence on performance, the level of this depression for different characters may vary considerably. The effects of inbreeding on characters of economic importance influence the relative emphasis that should be placed on various traits in a breeding program. In most breeding programs the size of the population sample which comprises the selected parents is usually relatively small. The breeder must be aware of the effects of inbreeding even though it is not intended to be an integral part of the breeding program or selection experiment. It is important then to know something of the amount of response which might be expected in the traits due to inbreeding.

Numerous studies have been conducted on the effects of inbreeding on the fowl. Dunn (1923), Hays (1924, 1934), Goodale (1927), Jull (1929a, 1929b, 1933), Dumon (1930), Waters and Lambert (1936) and Waters (1945a, 1945b, 1945c) have investigated the response in poultry to inbreeding. These workers generally agreed that inbreeding has a depressing effect, although their studies indicate that different characters did not respond to the same degree. The above investigations indicated that egg production declined, number of days to sexual maturity increased, hatchability and adult mortality were affected adversely.

There seemed to be no apparent decline in egg weight or adult body weight.

Shoffner (1948) was first to demonstrate the effect of inbreeding on the performance of specific characters in poultry by computing the regression of performance of various characters on the degree of inbreeding. The relative effects were greatest in hatchability and egg production, intermediate for sexual maturity, while body weight and egg weight exhibited no significant change with an increase in inbreeding. A decline in egg production rate of 0.14 percent for each percent increase in inbreeding was obtained by Wilson (1948a). Wilson (1948b) found that the hatchability of fertile eggs was apparently affected to a greater extent by the inbreeding of the dam than by the inbreeding of the embryo. Shoffner (1948) indicated that the inbreeding of the offspring was the significant factor, while the inbreeding of the dam had no significant effect on the hatchability of fertile eggs. Stephenson and Nordskog (1950) reported a regression of 0.29 and -0.43 on the coefficient of inbreeding for days to sexual maturity and percentage egg production, respectively.

Glazener _et al._ (1951) reported a decrease of 0.13 pound per each ten percent of inbreeding in body weight at twelve weeks of age. Blow and Glazener (1953) determined the regression coefficient associated with the effect of inbreeding on egg weight, sexual maturity, egg production and percentage fertility. These regression coefficients were -0.02 grams, 0.32 days, -0.17 percent and -0.37 percent for every one percent increase in inbreeding.

It has also been reported that inbreeding may affect the rate of mortality of chickens at various ages (Duzgunes, 1950). These authors stated that inbreeding tends to reduce the number of offspring of a mating which survive until breeding age. Based on this report it would seem that inbreeding would affect the selection applied in a selection study by changing the expected selection differential when selection is made at early ages.

Experimental Procedure

The study reported in this phase involves fifteen generations of selection for high and low body weight at twelve weeks of age. This experiment was initiated in January of 1950. Selection was based on individual body weights at twelve weeks of age. From the original population, two groups of birds were selected. One group consisted of all individuals having body weights greater than one standard deviation above the population mean. This group was designated as the high line parents. All individual birds which had weights greater than one standard deviation below the population mean were designated as the low line parents. Selection was not changed until the tenth generation, at which time selection was changed to a percentage fraction of the population. This percentage value was the upper seventeen percent in the high line and the lower seventeen percent in the low line. This change was made because the number of parents selected in the low line based on the standard deviation method of selection was becoming too small to prevent the probable effects of close inbreeding.

The procedure followed in measuring the various traits observed in this experiment and the management practices have been previously outlined in the general experimental procedure section of this thesis.

Since this experiment is based on individual selection, and each selected male is mated to several selected females, the intra-sire regression of offspring on dam was utilized to estimate the heritability of six and twelve-week body weight. Details of this method are outlined in Appendix A.

The theoretical values of the expected selection differential (S) were estimated from the formula $S = K \sigma_p$, where (K) is a constant and σ_p is the phenotypic standard deviation of the population. This formula and the values of the constant (K) were developed by Lush (1945). Estimates of the actual weighted selection differentials in this study were obtained by weighting the actual differential obtained for each mated pair by the number of offspring that was measured in the next generation. This procedure is discussed by Falconer (1960).

The regression of six-week body weight on twelve-week body weight for each generation was computed using the method of linear regression as outlined by Snedecor (1959). The phenotypic correlation coefficients obtained between these two traits were estimated by using the IBM 650 computer program, "Beaton Correlation Routine". This program was designed by Beaton (1957).

Results and Discussion

The response in twelve-week body weight to the divergent selection program over a period of fifteen generations is shown in Figure 1 for male offspring and in Figure 2 for the female offspring. The points utilized in these figures are the generation's twelve-week body weight mean as exhibited by the respective sexes. These figures also show a straight line regression fitted to the generation means. The results show the effectiveness of selection in increasing and in decreasing

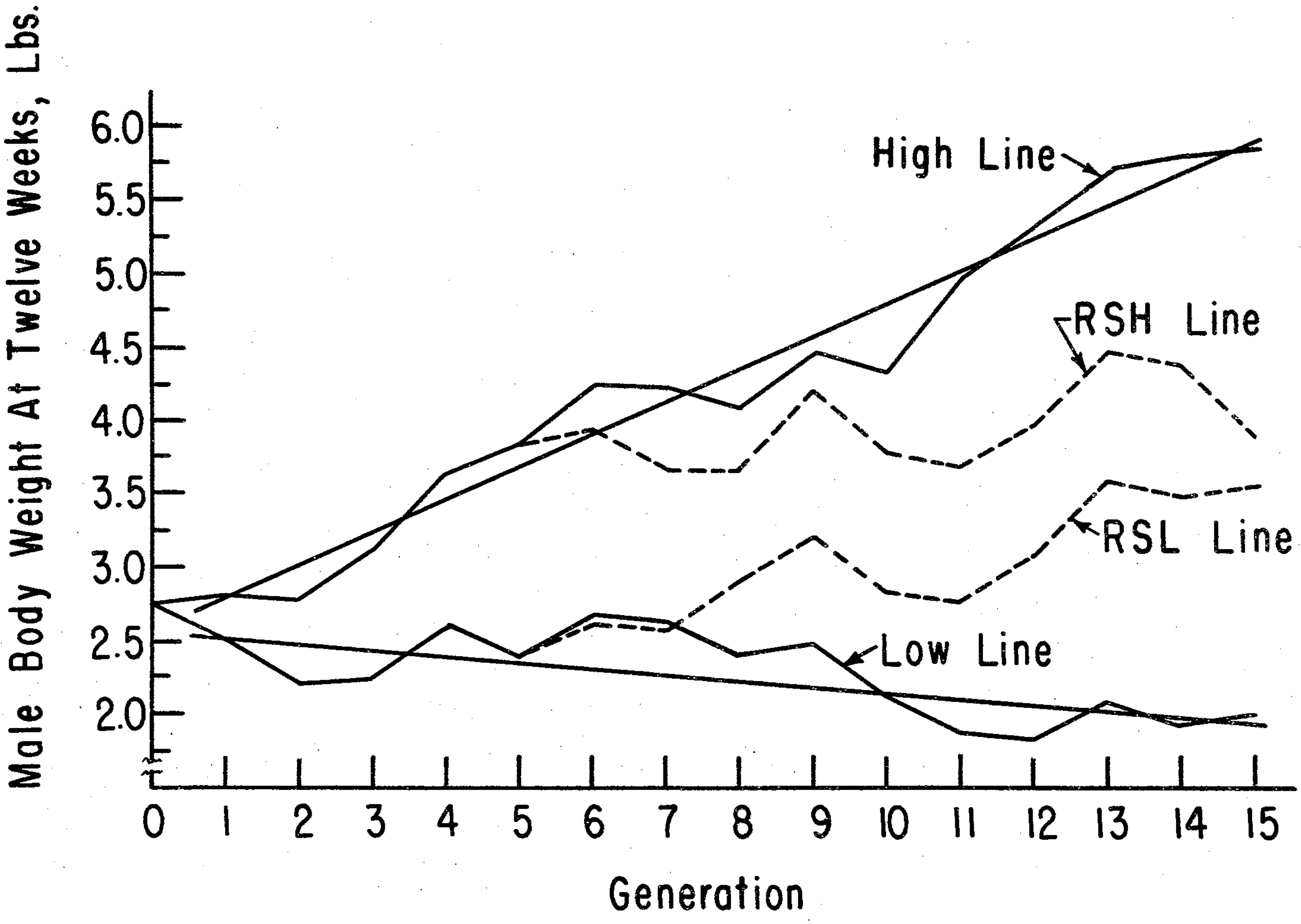

Figure 1. Male Offspring Twelve-week Body Weight Means by Generation. (Solid Lines Represent the Divergent Selected Lines and the Broken Lines Represent the Relaxed-Selected Lines.)

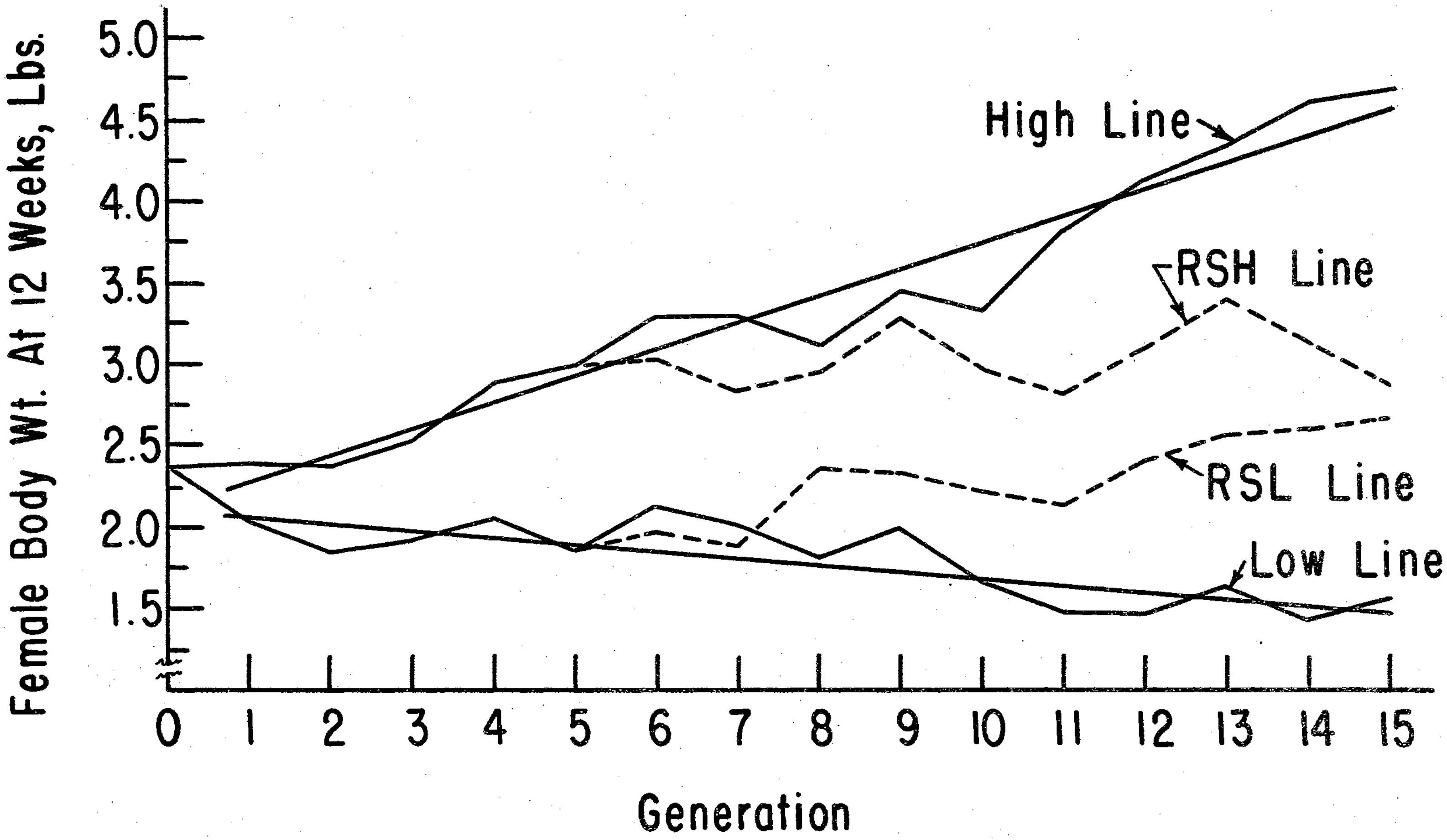

Figure 2. Female Offspring Twelve-week Body Weight Means by Generation. (Solid Lines Represent the Divergent Selected Lines and the Broken Lines Represent the Relaxed-Selected Lines.)

body weight at twelve weeks of age in both sexes. The difference between lines after fifteen generations of selection was 140 percent of the initial weight in the males and 133 percent in the females. Progress in both lines appears erratic. This irregularity is similar to that reported in other selection experiments.

For the purpose of analysis, the true response was regarded as a straight line about which the observed generation means fluctuate. Regression lines were fitted to the generation means, and the error of variance about the regression line was estimated. The assumption that the responses were essentially linear, upon which the regression analysis depends, appears to be justified by actual observation throughout the experiment.

The regression analysis of the two lines for each sex is given in Table V. The calculations were based on the fifteen generations of selection from generation zero to generation fifteen. The response in the high line males was 0.22±0.012 pound per generation, and the low line male response was 0.045±0.013 pound per generation. The response exhibited by the female progeny in the study was 0.16±0.010 in the high line and 0.047±0.001 in the low line.

By using the analysis of covariance as outlined by Snedecor (1959) a test was made to determine the statistical significance of the differences obtained between the various regression coefficients. This analysis indicated that a highly significant difference occurred in the rate of response to selection between the high line and low line for both sexes and between the high line males and the high line females. The difference between the rate of response per generation between the low line males and the low line females was not statistically significant

TABLE V

LINEAR REGRESSION ANALYSIS OF TWELVE-WEEK BODY WEIGHT RESPONSE TO SELECTION AND REALIZED HERITABILITY IN THE HIGH AND LOW LINES BY SEX OVER ALL GENERATIONS

	High Line		Low Line		Difference(1)	
Parameter	Male	Female	Male	Female	Male	Female
Response						
β(2)	0.220**	0.160**	-0.045**	-0.047**	0.266**	0.208**
V (β)(3)	0.00014	0.00010	0.00017	0.00006	0.00021	0.00016
st. er.(4)	0.012	0.010	0.013	0.00775	0.01449	0.01265
Realized Heritability (%)						
h^2(2)	47.2	35.1	12.3	12.7	35.6	27.8
V (h^2)(3)	9.00	7.29	18.49	8.24	5.62	4.08
st. er.(4)	3.00	2.70	4.30	2.87	2.37	2.02

1 - Difference between generation means of the two selected lines.
2 - Slope of the regression line expressed in pounds change per generation.
3 - Variance of parameter estimated.
4 - Standard error of parameter estimated.
** - Significant at the 1 percent level of probability.

at the five percent level of probability.

All of the regression coefficients were significantly different from zero. It was suggested by Nordskog (personal communication) that the standard error of the regression coefficients may be biased downward since a control population was not utilized to correct the generation means.

The point of intersection of the two regression lines, when extrapolated backwards, provides an estimate of the means of the unselected population. This was demonstrated by Falconer (1953). These lines intersect at a weight of 2.55 pounds for the male response to selection and 2.13 pounds for the female response. These values are very close to the observed mean of generation zero which was 2.75 pounds for the males and 2.36 pounds for the females. The means of each of the selected populations in the final generation lie close to their respective regression lines. Thus, it would seem that the preliminary judgment based on the total response in the two selected lines was substantially correct. The total change in the high and low lines reflects a real difference in the rate of response to selection in the two directions.

The difference obtained between the two selected lines in each generation for each sex was utilized to measure the response to the divergent selection program. The response to divergent selection for twelve-week body weight exhibited a fairly steady increase through the tenth generation of selection, but during the eleventh and twelfth generations the response was increased sharply. The reasons for this increase in response are unknown. The results of the linear regression analysis of the divergence response (Table V) indicated that the rate of response for the two sexes was significantly different from zero. The rate of response observed in the male offspring was 0.266±0.015 pound per generation and 0.208±0.013 pound per generation for the female progeny. The analysis of covariance used to test the difference noted between these two slopes indicated that they were statistically significant at the one percent level of probability. Since the rates of response were significantly different from zero, it may be concluded that the response to selection proceeded almost unchanged. This may mean that the heritability remained substantially unaltered by continuous selection through the fifteen generations. These findings concur with those obtained by Falconer (1953) and Robertson (1955) in selecting for body size in laboratory animals.

Since the progress made through selection depends upon the magnitude of the selection applied, a critical analysis of the selection differentials was obtained on the basis of a normal distribution. Table VI presents the expected and actual weighted selection differentials obtained in this study for the high line and those obtained for the low line are given in Table VII. In order to compare the selection applied in the high line with that applied in the low line, the intensity of selection was also determined. This value is actually the standardized selection differential (i) obtained by dividing the actual weighted selection differential attained in each generation by the phenotypic standard deviation of the population from which the individuals were selected.

The intensity of selection (i) given in Tables VI and VII was compared to determine if selection pressure was applied equally to sexes within each line and between lines. The analysis of the intensity values associated with the male and female selection within the high

TABLE VI

ESTIMATES OF PARAMETERS ASSOCIATED WITH THE AMOUNT OF SELECTION APPLIED IN THE HIGH LINE FOR TWELVE-WEEK BODY WEIGHT BY SEXES

	Selection Differential (s)(1)				Actual Weighted	
	Expected		Act. Weighted(2)		Intensity (i)	
Gen.	Male	Female	Male	Female	Male	Female
1	0.67	0.48	0.70	0.46	1.52	1.39
2	0.72	0.49	0.55	0.30	1.10	0.88
3	0.64	0.43	0.71	0.28	1.61	0.93
4	0.57	0.38	0.58	0.32	1.49	1.23
5	0.58	0.39	0.56	0.30	1.40	1.11
6	0.71	0.48	0.49	0.34	1.00	1.03
7	0.57	0.42	0.64	0.48	1.64	1.66
8	0.61	0.33	0.28	0.23	0.68	1.00
9	0.59	0.57	0.21	0.20	0.51	0.51
10	1.10	0.48	0.88	0.39	1.16	1.18
11	0.74	0.32	0.67	0.29	1.31	1.30
12	0.68	0.55	0.74	0.60	1.57	1.50
13	0.78	0.58	0.82	0.61	1.50	1.54
14	0.43	0.72	0.35	0.50	1.17	1.00
15	1.39	0.45	0.91	0.35	0.95	1.13
	10.78(3)	7.07(3)	9.09(3)	5.65(3)	1.241(4)	1.159(4)

1 = Given in pounds.
2 = The actual weighted selection differential.
3 = Total.
4 = Mean.

TABLE VII

ESTIMATES OF PARAMETERS ASSOCIATED WITH THE AMOUNT OF SELECTION APPLIED IN THE LOW LINE FOR TWELVE-WEEK BODY WEIGHT BY SEXES

	Selection Differential (s)(1)				Actual Weights	
	Expected		Act. Weighted(2)		Intensity (i)	
Gen.	Male	Female	Male	Female	Male	Female
1	0.67	0.48	0.97	0.51	2.11	1.55
2	0.67	0.48	0.27	0.22	0.59	0.67
3	0.61	0.38	0.63	0.17	1.50	0.65
4	0.72	0.48	0.66	0.32	1.32	0.97
5	0.74	0.57	0.44	0.19	0.86	0.49
6	0.62	0.39	0.52	0.18	1.21	0.67
7	0.67	0.54	0.37	0.30	0.80	0.81
8	0.51	0.41	0.56	0.47	0.63	1.68
9	0.39	0.36	0.35	0.28	1.30	1.12
10	0.41	0.36	0.28	0.19	1.00	0.76
11	0.43	0.36	0.37	0.34	1.19	1.31
12	0.31	0.39	0.25	0.33	1.14	1.18
13	0.59	0.48	0.51	0.42	1.21	1.24
14	0.55	0.59	0.38	0.38	0.97	0.90
15	0.88	0.88	0.47	0.43	0.75	0.68
	8.77(3)	7.15(3)	7.03(3)	4.73(3)	1.11(4)	0.98(4)

1 = Given in pounds.
2 = The actual weighted selection differential.
3 = Total.
4 = Mean.

line and within the low line indicated that the differences observed were not significant at the five percent level of probability. The difference between the selection intensity in the high line and the low line was also determined to be non-significant. It may be concluded that the differences in response obtained between the two sexes in the high line and the asymmetrical response observed for the two-way selection were probably not due to a difference in the selection applied.

In comparing the expected and actual weighted selection differentials calculated for each generation in the high line, it was noted that a difference of 0.11 pound occurred in the males and 0.09 pound occurred in the females. An analysis indicated that these values were not statistically significant at the five percent level of probability.

The difference observed in the low line males was also found to be non-significant. The difference obtained in the low line females between the expected selection differential and the actual weighted value was significant at the one percent level of probability. Falconer (1960) suggested two possible reasons for these differences. The difference may be due mainly to selected parents failing to produce an average number of offspring because of late sexual maturity. Secondly, there may be differential fertility between different phenotypes by weight. Both of these factors may have been operating in the low line females, but probably the most important single factor was extremely low egg production by various females observed in the low line. This factor will be discussed in more detail in the presentation of the effects of selection on percentage egg production.

The average of the actual weighted selection differential obtained for the two sexes for each generation was used to estimate the amount of selection applied, since the sire and the dam contribute equally to the genetic make-up of the individual offspring. These values are shown in Table VIII for the high line and in Table IX for the low line. The responses for each generation for the two sexes are also given in these tables. By dividing the selection differential into the amount of response, the realized heritability for twelve-week body weight can be obtained. As indicated in Tables VIII and IX, these values are quite variable and are probably influenced by a large amount of sampling variation for any one given generation. It was noted that the females exhibited a consistently lower degree of heritability than the males in the high line. The low line females as indicated in Table IX were slightly higher in heritability than the low line males. These differences were not significant.

Since the realized heritability is the ratio of the response (R) to the selection differential (S), then the best estimate of this type of heritability may be obtained by calculating the slope of the regression line where the cumulated response per generation is plotted against the cumulated selection differential. The slope of the regression line measures the average value of (R/S) realized heritability. This was discussed in more detail by Falconer (1960).

The estimates of the realized heritability obtained in this study are given in Table V. The regression analysis indicated that the realized heritability was 47.2±3.0 percent in the high line males and 35.1±2.7 percent in the high line females. This seems to indicate a definite difference in heritability between the two sexes, which was indicated by the difference in response to selection. The analysis

TABLE VIII

RESPONSE AND REALIZED HERITABILITY BY GENERATION AND SEX ASSOCIATED WITH THE AMOUNT OF SELECTION APPLIED IN THE HIGH LINE

	Selection	Response (R)(2)		Heritability(3)	
Gen.	Differential (S)(1)	Male	Female	Male	Female
1	0.58	0.05	0.02	0.086	0.034
2	0.43	-0.01	-0.02	-0.023	-0.047
3	0.50	0.35	0.17	0.700	0.340
4	0.45	0.51	0.36	1.130	0.800
5	0.43	0.20	0.09	0.465	0.209
6	0.42	0.39	0.31	0.929	0.738
7	0.56	-0.02	0.01	-0.036	0.018
8	0.26	-0.12	-0.18	-0.462	-0.692
9	0.21	0.36	0.33	1.714	1.571
10	0.64	-0.12	-0.11	-0.188	-0.172
11	0.48	0.65	0.48	1.354	1.000
12	0.67	0.36	0.31	0.537	0.563
13	0.72	0.35	0.22	0.486	0.306
14	0.43	0.08	0.25	0.186	0.581
15	0.63	0.07	0.08	0.111	0.127
	7.41(4)	3.10(4)	2.32(4)	0.418(5)	0.313(5)

1 - Average actual weighted selection differential, in pounds.
2 - Amount of change observed in the 12-week body weight mean, in pounds.
3 - Realized heritability estimated by the formula $h^2 = R/S$.
4 - Total.
5 - Heritability estimated from total selection and total response.

TABLE IX

RESPONSE AND REALIZED HERITABILITY BY GENERATION AND SEX ASSOCIATED WITH THE AMOUNT OF SELECTION APPLIED IN THE LOW LINE

Gen.	Selection Differential (S)(1)	Response (R)(2)		Heritability(3)	
		Male	Female	Male	Female
1	0.74	0.25	0.32	0.338	0.432
2	0.25	0.29	0.19	1.160	0.760
3	0.40	-0.04	-0.07	-0.100	-0.175
4	0.49	-0.35	-0.13	-0.714	-0.265
5	0.32	0.22	0.18	0.688	0.563
6	0.35	-0.28	-0.24	-0.800	-0.686
7	0.34	0.03	0.10	0.088	0.294
8	0.52	0.25	0.20	0.481	0.385
9	0.32	-0.09	-0.18	-0.281	-0.563
10	0.24	0.36	0.33	1.500	1.375
11	0.35	0.23	0.18	0.657	0.514
12	0.29	0.04	0.01	0.138	0.034
13	0.47	-0.25	-0.16	-0.532	-0.340
14	0.38	0.15	0.19	0.395	0.500
15	0.45	-0.06	-0.11	-0.133	-0.245
	5.91(4)	0.75(4)	0.81(4)	0.127(5)	0.137(5)

1 - Average actual weighted selection differential, in pounds.
2 - Amount of change observed in the 12-week body weight mean, in pounds.
3 - Realized heritability estimated by the formula $h^2 = R/S$.
4 - Total.
5 - Heritability estimated from total selection and total response.

of the low line male and female offspring indicates that the heritabilities were very similar, 12.3±4.3 percent in the males and 12.7±2.9 percent in the females. An analysis of the difference obtained between the two selected lines with respect to the total cumulated selection differential indicated that the realized heritability of twelve-week body weight for the two-way selection program was 35.6±2.4 percent in the males and 27.8±2.0 percent in the females. These values compare reasonably well with those shown in Table X for the heritability estimated for the total selection and total response. Table X also shows the heritability estimates obtained in each generation for the two-way selection experiment. These values do no indicate any particular trend during the fifteen generations of selection. When one considers the effects of the cumulated selection upon any specific generation as compared to the cumulated response for that generation, then an estimate of the realized heritability to that point can be calculated. These estimates are shown in Table XI. The values noted seem to show a slight increase during the study as well as indicating a consistently higher value for the males than for the females.

Since the realized heritability varies considerably from generation to generation, reports on short term experiments do not generally give these values. In order to obtain heritability estimates which would have comparative value, an intra-sire regression method was used within each generation. These values are shown in Table XII. The intra-sire regression heritabilities are fairly consistent with those reported in selection studies pertaining to body weight at broiler age and with the exception of two or three values, they are reasonably consistent. The difference due to sex was not as large as that obtained

TABLE X

ESTIMATES OF PARAMETERS ASSOCIATED WITH THE TWO-WAY SELECTION FOR BODY WEIGHT AT TWELVE-WEEKS OF AGE BY GENERATION

		Response(2)		Heritability(%)(3)	
Gen.	Act.Wt.S. D.(1)	Male	Female	Male	Female
1	1.32	0.30	0.34	22.7	25.8
2	0.68	0.28	0.17	41.2	25.0
3	0.90	0.31	0.10	34.5	11.1
4	0.94	0.16	0.23	17.0	24.5
5	0.75	0.42	0.27	56.0	36.0
6	0.77	0.11	0.07	14.3	9.1
7	0.90	0.01	0.11	1.1	12.2
8	0.78	0.13	0.02	16.7	2.6
9	0.53	0.27	0.15	50.9	28.3
10	0.88	0.24	0.22	27.3	25.0
11	0.84	0.88	0.66	104.8	78.6
12	0.96	0.40	0.32	41.7	33.3
13	1.19	0.10	0.06	08.4	5.0
14	0.81	0.23	0.44	28.4	54.3
15	1.08	0.01	-0.03	0.9	-02.8
Total	13.33	3.85	3.13	28.9(4)	23.5(4)

1 - Sum of the actual weighted selection differential for each selected line for each generation, in pounds.
2 - Measured as the difference obtained between the two selected lines for the specific generation, in pounds.
3 - Ratio of the response to the selection differential.
4 - Estimated from the total selection applied and the total difference obtained.

TABLE XI

REALIZED HERITABILITY ESTIMATED FROM THE CUMULATED SELECTION AND THE CUMULATED DIFFERENCE OBTAINED BETWEEN THE TWO SELECTED LINES IN TWELVE-WEEK BODY WEIGHT BY GENERATION

Gen.	C. S. D.(1)	Response(2)		Heritability (%)	
		Male	Female	Male	Female
1	1.32	0.30	0.34	22.7	25.8
2	2.00	0.58	0.51	29.0	25.5
3	2.90	0.89	0.61	30.7	21.0
4	3.84	1.05	0.84	27.3	21.9
5	4.59	1.47	1.11	32.0	24.18
6	5.36	1.58	1.18	29.5	22.0
7	6.26	1.59	1.29	25.4	20.6
8	7.04	1.72	1.31	24.4	18.6
9	7.57	1.99	1.46	26.3	19.3
10	8.45	2.23	1.68	26.4	19.9
11	9.29	3.11	2.34	33.5	25.2
12	10.25	3.51	2.66	35.5	26.0
13	11.44	3.61	2.72	31.6	23.8
14	12.25	3.84	3.16	31.3	25.8
15	13.33	3.85	3.13	28.9	23.5

1 - Cumulated selection differential as a sum of both selected lines over all previous generations, in pounds.

2 - Cumulated difference obtained between the two selected lines summed over all previous generations, in pounds.

TABLE XII

HERITABILITY ESTIMATES (h^2) OF TWELVE-WEEK BODY WEIGHT RESPONSE TO SELECTION IN THE HIGH LINE FOR EACH SEX BY GENERATION

	h^2 ± Standard Error(1)		
Gen.	Male(2)	Female	Combined
2	---------(3)	---------	0.38±0.24
3	---------	---------	0.64±0.22
4	---------	---------	0.82±0.20
5	---------	---------	1.20±0.22
6	1.03±0.57	0.54±0.36	0.64±0.35
7	0.40±0.32	0.49±0.21	0.36±0.22
8	0.34±0.28	0.28±0.24	0.43±0.25
9	0.28±0.31	0.26±0.35	0.29±0.38
10	0.45±0.21	0.35±0.17	0.30±0.27
11	0.51±0.31	0.63±0.26	0.53±0.25
12	0.32±0.19	0.46±0.21	0.55±0.16
13	0.49±0.22	0.43±0.31	0.44±0.28
14	0.35±0.11	0.56±0.20	0.43±0.18
15	0.82±0.80	0.74±0.60	0.52±0.70

1 - Heritability estimates obtained from intra-sire regression of offspring body weight on dam body weight, expressed as a decimal fraction.

2 - Regression coefficient for male offspring was corrected for inequality of variance observed for each sex (see text).

3 - Data not available for within-sex intra-sire regression estimates.

for the realized heritability estimates in the high line. The values reported in Table XII were considerably more consistent than those shown in Table VIII. This would tend to indicate that the true heritability, based on the additive genetic variance, remained fairly constant during this study and was not fully reflected in the realized heritability obtained in the individual generations.

The heritability estimates calculated for twelve-week body weight in each generation for the high line males ranged from 28 percent to 103 percent. When the estimates which exceeded one hundred percent were omitted, the average estimate was 44 percent. The estimates calculated from data collected from the female progeny of the high line ranged from 26 percent to 74 percent and averaged 47.4 percent. Estimates obtained from the low line males averaged 39.8 percent and when estimates above one hundred were not utilized, the females averaged 28.1 percent. The heritability estimates shown in Table XIII for the low line seemed to be lower than those shown for the high line in Table XII. This would tend to indicate that the additive genetic variance was lower in the low line than in the high line.

A regression analysis of the standard deviation for twelve-week body weight, given in Table XIV, indicated that this parameter remained almost unchanged during this study in both of the selected lines. The coefficients of variation in the high line were relatively consistent between the sexes. This was also noted in the low line. The coefficient of variation for each sex in each generation and line are also shown in Table XIV. The regression analysis of the coefficients of variation indicated that this parameter was decreased at the rate of -0.419±0.18 percent per generation in the high line males and -0.030±0.134 percent

TABLE XIII

HERITABILITY ESTIMATES (h^2) OF TWELVE-WEEK BODY WEIGHT RESPONSE TO SELECTION IN THE LOW LINE FOR EACH SEX BY GENERATION

	h^2 ± Standard Error(1)		
Gen.	Male(2)	Female	Combined
2	---------(3)	---------	0.10±0.20
3	---------	---------	0.26±0.26
4	---------	---------	0.78±0.22
5	---------	---------	0.04±0.36
6	0.23±0.37	0.20±0.50	0.15±0.34
7	0.25±0.21	0.26±0.34	0.48±0.78
8	0.61±0.24	0.27±0.23	0.26±0.36
9	0.38±0.66	0.38±0.47	0.52±0.72
10	0.39±0.78	1.54±0.64	0.74±0.68
11	0.82±0.79	1.68±1.15	0.93±0.68
12	0.36±0.58	0.32±0.51	0.30±0.42
13	0.33±0.28	0.26±0.37	0.38±0.51
14	0.42±0.19	0.37±0.28	0.31±0.46
15	0.19±0.33	0.19±0.47	0.26±0.28

1 - Heritability estimates obtained from intra-sire regression of offspring body weight on dam body weight, expressed as a decimal fraction.

2 - Regression coefficient for male offspring was corrected for inequality of variance observed for each sex (see text).

3 - Data not available for within-sex intra-sire regression estimates.

TABLE XIV

VARIATION OBSERVED IN THE PROGENY OF THE TWO SELECTED LINES BY SEX BY GENERATION FOR TWELVE-WEEK BODY WEIGHT

	High Line				Low Line			
	Male		Female		Male		Female	
Gen.	σ(1)	C.V.(2)	σ	C.V.	σ	C.V.	σ	C.V.
0	0.46	16.7	0.33	13.9	----	----	----	----
1	0.50	17.9	0.34	14.4	0.46	18.5	0.33	16.0
2	0.44	15.8	0.30	12.6	0.42	18.9	0.26	14.3
3	0.39	12.4	0.26	10.4	0.50	22.0	0.33	17.4
4	0.40	11.0	0.27	9.4	0.51	19.7	0.39	18.9
5	0.49	12.7	0.33	11.0	0.43	18.1	0.27	14.6
6	0.39	9.2	0.29	8.8	0.46	17.3	0.38	17.5
7	0.42	10.0	0.23	6.9	0.35	13.3	0.28	13.9
8	0.41	10.0	0.39	12.5	0.27	11.3	0.25	13.8
9	0.76	17.0	0.33	9.5	0.28	11.3	0.25	12.5
10	0.51	11.8	0.22	6.5	0.31	14.6	0.26	15.6
11	0.47	9.4	0.38	9.9	0.22	11.7	0.28	18.9
12	0.54	10.1	0.40	9.6	0.42	22.8	0.34	23.1
13	0.30	5.3	0.50	11.4	0.39	18.6	0.42	25.7
14	0.96	16.6	0.31	6.8	0.63	32.5	0.63	43.7
15	0.43	7.4	0.43	9.2	0.51	25.7	0.38	24.5
Regression Analysis(3)								
σ	0.010±0.008		0.007±0.003*		-0.002±0.025		0.008±0.004	
C.V.	-0.419±0.179*		-0.030±0.134		0.033±0.030		1.008±0.338**	

1 - Standard deviation of twelve-week body weight.
2 - Coefficient of variation, in percent.
3 - Regression coefficient and standard error, given as unit change per generation.
* - Statistically significant at the 5 percent level of probability.
** - Statistically significant at the 1 percent level of probability.

in the females. The coefficients of variation in the high line for twelve-week body weight reflected the expected decline in variation which should occur as selection proceeds towards its limits. This decline should be accompanied by a decrease in heritability as well as a decrease in the rate of response. These decreases, as noted earlier, did not occur. A reduction in heritability probably would not occur if the reduction observed in the coefficients of variation was due to a decrease in both the additive genetic variance and the environmental variance.

The phenotypic variance of twelve-week body weight as measured by the coefficients of variation in the low line given in Table XIV did not exhibit the decline noted in the high line. The regression analysis indicated that the coefficients of variation exhibited a slight increase in the low line males during this study. The rate of increase was 0.03±0.03 percent per generation. The variance in the low line females seemed to indicate a definite trend to increase with each generation. The associated regression coefficient was 1.01±0.34 percent per generation. Since the growth selected lines did not indicate a decline in genetic variation, it may be possible that the trend indicated by the coefficients of variation reflects the effects of improved management during this experiment.

The failure of the low line to exhibit a decrease in phenotypic variation was also observed in studies reported by MacArthur (1949), Falconer (1953) and Robertson (1955). These authors thought that since the low line was being selected toward a physiological limit the interactions between genotype and environment may have caused the increase in variation.

The greater susceptibility of inbred lines to environmental sources of variation as compared to hybrid lines has been observed in a wide variety of characters and organisms. Consideration should therefore be given to the effects of inbreeding as a possible cause of the variation noted in the low line.

The amount of inbreeding was calculated by using Wright's formula [$(1/8\ M + 1/8\ F)$ = Inbreeding coefficient] when M is the number of males used each generation and F is the number of females used. The total inbreeding was found to be 24 percent in the high line and .29 percent in the low line after fifteen generations of selection.

The cause of the greater environmental variance of inbreds is not fully understood. It has been suggested (Mather, 1953) that the reduced homeostatic power of inbreds may be regarded as a manifestation of inbreeding depression. Homeostatic power was likely to be an important aspect of fitness, and would therefore be expected, like other aspects of fitness, to decline on inbreeding. The underlying mechanism would be directional dominance, genes that increase homeostatic power tending on the average to be dominant over their alleles that decrease it. Lerner (1954) suggested that a causal connection exists between variability and fitness. He believes greater stability to be a general property of heterozygotes and regards it as the cause of their greater fitness. Although the increase in environmental variance due to inbreeding is of theoretical interest and of some practical importance, too little is known about it to justify a more detailed discussion of its causes. More comprehensive discussions have been reported by Lerner (1954) and Waddington (1957).

The results of the effect of continuous selection for twelve-week body weight on six-week body weight is shown in Figure 3 for the male offspring and in Figure 4 for the females. Although the response noted in the high line males exhibited a large amount of fluctuation from generation to generation, the regression analysis indicated that the slope was significantly different than zero. The rate of increase was 0.102±0.015 pound per generation. The low line males decreased at the rate of 0.01±0.01 pound per generation. A slight difference was observed between the rate of response noted in the male and female offspring of the high line. The regression coefficient calculated for the high line females was 0.08±0.01 pound per generation. The rate of decrease noted in the low line females was identical to that calculated for the low line males.

An analysis of the actual selection differentials for six-week body weight obtained from selecting for twelve-week body weight indicated that the intensity of selection was about one-third of that applied for twelve-week body weight in the high line. The intensity of selection in the low line was less than one-fifth of that applied in the selection for twelve-week body weight.

The realized heritability for six-week body weight determined by the regression of the cumulated response on the cumulated selection differential was 78.5±8.9 percent for the high line males, 62.6±7.5 percent for the high line females, 14.3±11.3 percent for the low line males and 7.1±9.0 percent for the low line females. The realized heritability observed for the high line males and females indicate that some factor other than selection may have been responsible for the increase exhibited by these offspring. This conclusion is based primarily on the fact that these estimates are extremely high for

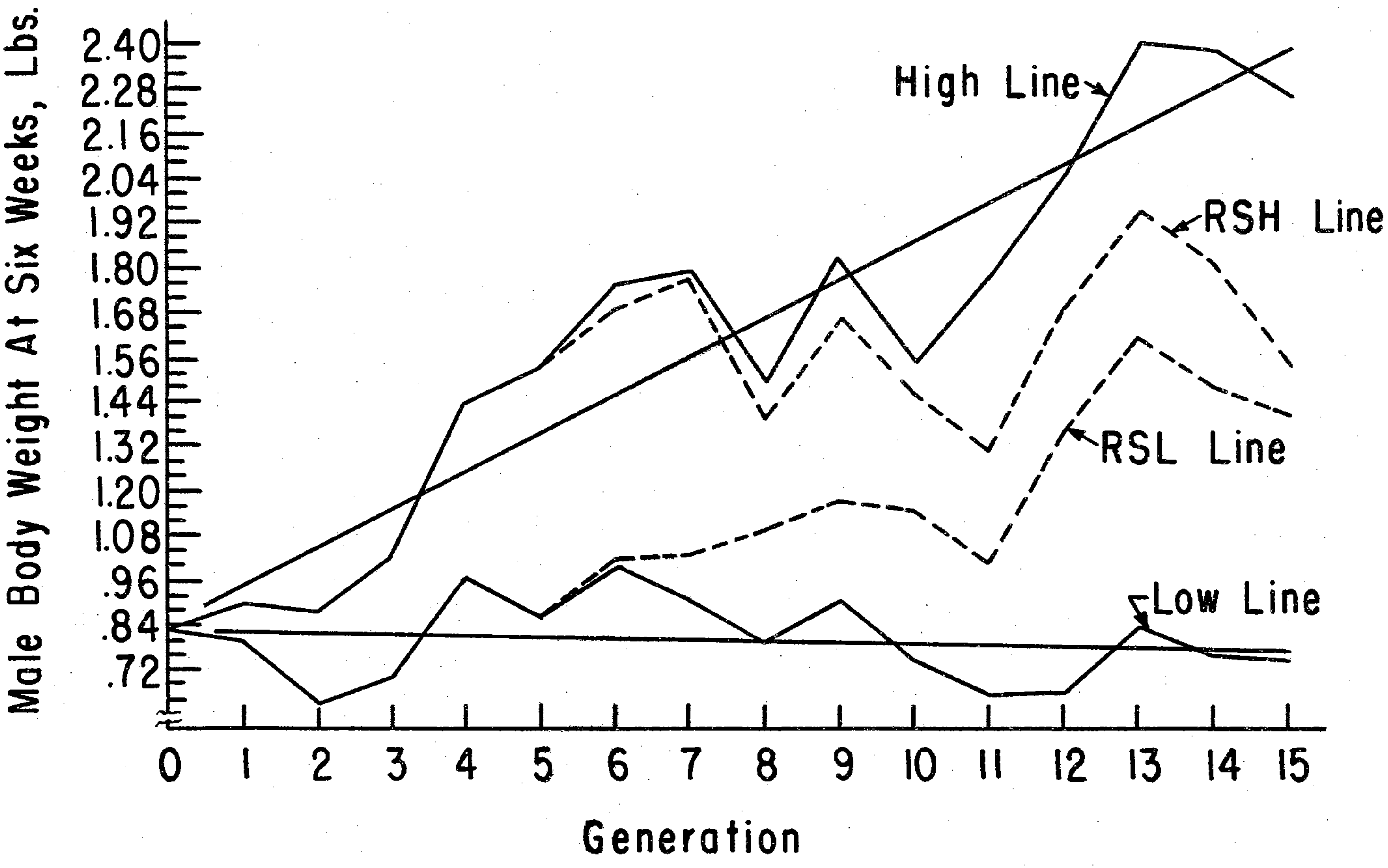

Figure 3. Male Offspring Six-week Body Weight Means by Generation. (Solid Lines Represent the Divergent Selected Lines and the Broken Lines Represent the Relaxed-Selected Lines.)

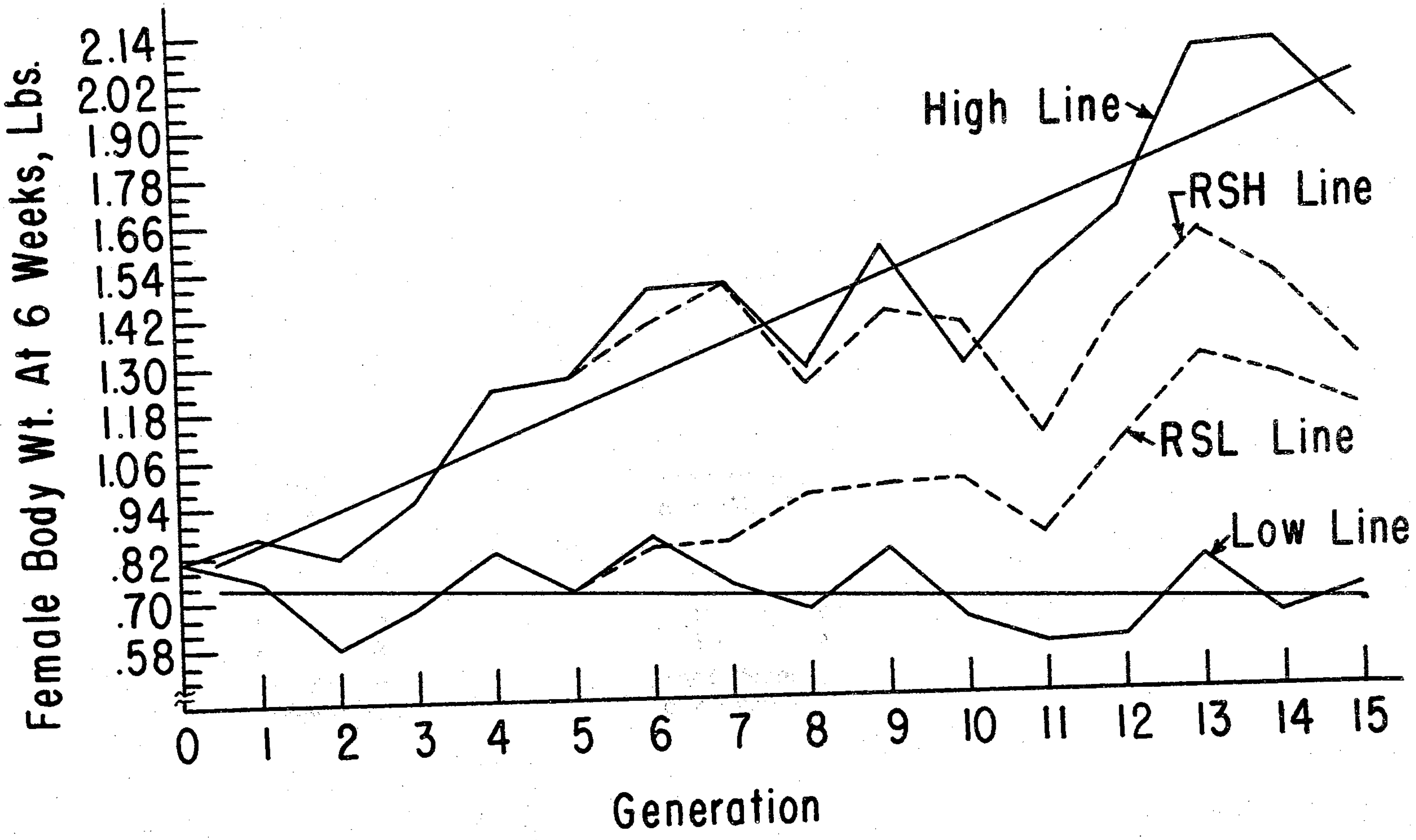

Figure 4. Female Offspring Six-week Body Weight Means by Generation. (Solid Lines Represent the Divergent Selected Lines and the Broken Lines Represent the Relaxed-Selected Lines.)

juvenile body weight in poultry.

Table XV and Table XVI give the estimates of the heritability of six-week body weight calculated for each generation by the intra-sire regression method for the two selected lines. The average heritability estimate in the high line was 58.9 percent for the males and 57.1 percent for the females. The range of the estimates calculated for the males ranged from 24.0 percent to 1.35 percent. The range of the estimates for the females was 26.0 percent to 88.0 percent. This would indicate that the realized heritability estimates for six-week body weight are well within the range of estimates. Realized heritability estimates reported by Falconer (1953) and Falconer (1960) and those estimated for twelve-week body weight in this thesis are consistently lower than the estimates of heritability by other methods.

Since the relationship between traits may increase due to selection, it is thought by some workers that correlation coefficients estimated from data obtained in a selection experiment are biased values. Both the estimates for regression coefficients and correlation coefficients are given in Table XVII. The regression of six-week body weight on twelve-week body weight in the high line males did not exhibit a tendency to change with generation. A regression analysis of the estimates indicated only a slight rate of increase per generation.

The phenotypic correlation estimated in each generation for the offspring did not indicate an associated change with time. The regression coefficients estimated for the high line females in each generation exhibited a tendency to increase, particularly between generations nine and generation thirteen. This may be associated with

TABLE XV

HERITABILITY ESTIMATES (h^2) OF SIX-WEEK BODY WEIGHT RESPONSE TO SELECTION FOR TWELVE-WEEK BODY WEIGHT IN THE HIGH LINE FOR EACH SEX BY GENERATION

	h^2 ± Standard Error(1)		
Gen.	Male(2)	Female	Combined
2	---------(3)	---------	0.62±0.20
3	---------	---------	0.18±0.18
4	---------	---------	0.74±0.20
5	---------	---------	0.80±0.16
6	1.35±0.36	0.67±0.29	0.70±0.15
7	0.77±0.21	0.49±0.20	0.67±0.18
8	0.54±0.31	0.46±0.28	0.66±0.29
9	0.45±0.22	0.69±0.19	0.49±0.20
10	0.50±0.19	0.50±0.22	0.47±0.17
11	0.56±0.21	0.88±0.18	0.74±0.19
12	0.78±0.32	0.51±0.19	0.66±0.21
13	0.24±0.30	0.43±0.22	0.50±0.27
14	0.45±0.22	0.82±0.23	0.49±0.19
15	0.25±0.27	0.26±0.20	0.15±0.15

1 - Heritability estimates obtained from intra-sire regression of offspring body weight on dam body weight, expressed as a decimal fraction.

2 - Regression coefficient for male offspring was corrected for inequality of variance observed for each sex (see text).

3 - Data not available for within-sex intra-sire regression estimates.

TABLE XVI

HERITABILITY ESTIMATES (h^2) OF SIX-WEEK BODY WEIGHT RESPONSE TO SELECTION FOR TWELVE-WEEK BODY WEIGHT IN THE LOW LINE FOR EACH SEX BY GENERATION

	h^2 ± Standard Error(1)		
Gen.	Male(2)	Female	Combined
2	---------(3)	---------	0.10±0.20
3	---------	---------	0.26±0.16
4	---------	---------	0.52±0.18
5	---------	---------	0.96±0.20
6	0.32±0.14	0.50±0.13	0.58±0.28
7	0.18±0.12	0.12±0.12	0.18±0.16
8	0.64±0.30	0.94±0.25	0.50±0.17
9	0.52±0.28	0.61±0.24	0.34±0.14
10	0.47±0.27	0.41±0.35	0.26±0.26
11	0.45±0.10	0.34±0.14	0.59±0.16
12	0.33±0.28	0.30±0.26	0.57±0.14
13	0.22±0.28	0.10±0.23	0.18±0.15
14	0.58±0.26	1.86±0.28	1.01±0.34
15	0.50±0.26	0.61±0.24	0.59±0.30

1 - Heritability estimates obtained from intra-sire regression of offspring body weight on dam body weight, expressed as a decimal fraction.

2 - Regression coefficient for male offspring was corrected for inequality of variance observed for each sex (see text).

3 - Data not available for within-sex intra-sire regression estimates.

TABLE XVII

ESTIMATES OF THE RELATIONSHIP BETWEEN BODY WEIGHT AT TWELVE AND SIX WEEKS OF AGE BY SEX IN THE TWO SELECTED LINES BY GENERATION

	High Line				Low Line			
	Male		Female		Male		Female	
Gen.	b$^{(1)}$	r$^{(2)}$	b	r	b	r	b	r
6	0.239	0.413$^{(3)}$	0.328	0.550	0.548	0.604	0.219	0.412
7	0.261	0.433	0.360	0.588	0.431	0.449	0.225	0.328
8	0.232	0.740	0.356	0.612	0.526	0.531	0.350	0.440
9	0.219	0.667	0.237	0.621	0.333	0.634	0.305	0.529
10	0.283	0.721	0.291	0.562	0.289	0.796	0.300	0.661
11	0.279	0.739	0.315	0.525	0.450	0.891	0.289	0.545
12	0.250	0.525	0.355	0.572	0.425	0.830	0.152*	0.341*
13	0.310	0.419	0.375	0.466	0.480	0.775	0.320	0.519
14	0.219	0.517	0.298	0.475	0.456	0.720	0.396	0.689
15	0.222	0.519	0.325	0.480	0.410	0.730	0.432	0.692

1 = The regression coefficient estimated from the regression of six-week weight on twelve-week weight,
2 = Simple correlation between twelve- and six-week weight.
3 = All estimates were significant at the 1 percent level of probability except where noted otherwise.
* = Significant at the 5 percent level of probability.

the increase in the rate of response noted in female six-week body weight during the same period. The estimates calculated for the low line did not indicate any significant change with time.

A similar correlated response was also noted in March egg weight. The mean egg weight, in grams, for each line by generation is shown in Figure 5. The response noted must be evaluated on the basis that it represents only the performance of the selected female parents in each generation. Conclusions probably cannot be applied directly to the female offspring population as a group. Since these means represent the selected female parents, their performance might be highly correlated with the expected performance of the subsequent generation.

Following the first generation, egg weight in the high line seems to have stabilized at about 58.0 grams which is 3.1 grams above the original population mean. A regression analysis indicated that the rate of increase, considering all generations, was 0.063±0.138 grams per generation. The low line exhibited an obvious decrease in egg weight. The associated rate of decrease was 0.47±0.08 grams per generation. This regression coefficient was highly significant. This resulted in a decrease of almost 7.0 grams below the original population mean by the end of the experiment. If one considers the effect of inbreeding on egg weight, then according to Blow and Glazener (1953) a decrease of about 0.5 gram in the high line and 0.6 gram in the low line would be expected. Inbreeding alone probably would not account for the decrease noted in the low line. The decrease noted in the low line selected females is very similar to that reported by Siegel (1963); Ideta and Siegel (1966b). Singh *et al.* (1960) and Siegel (1963) reported that selection for increased body size at broiler age resulted in an increase

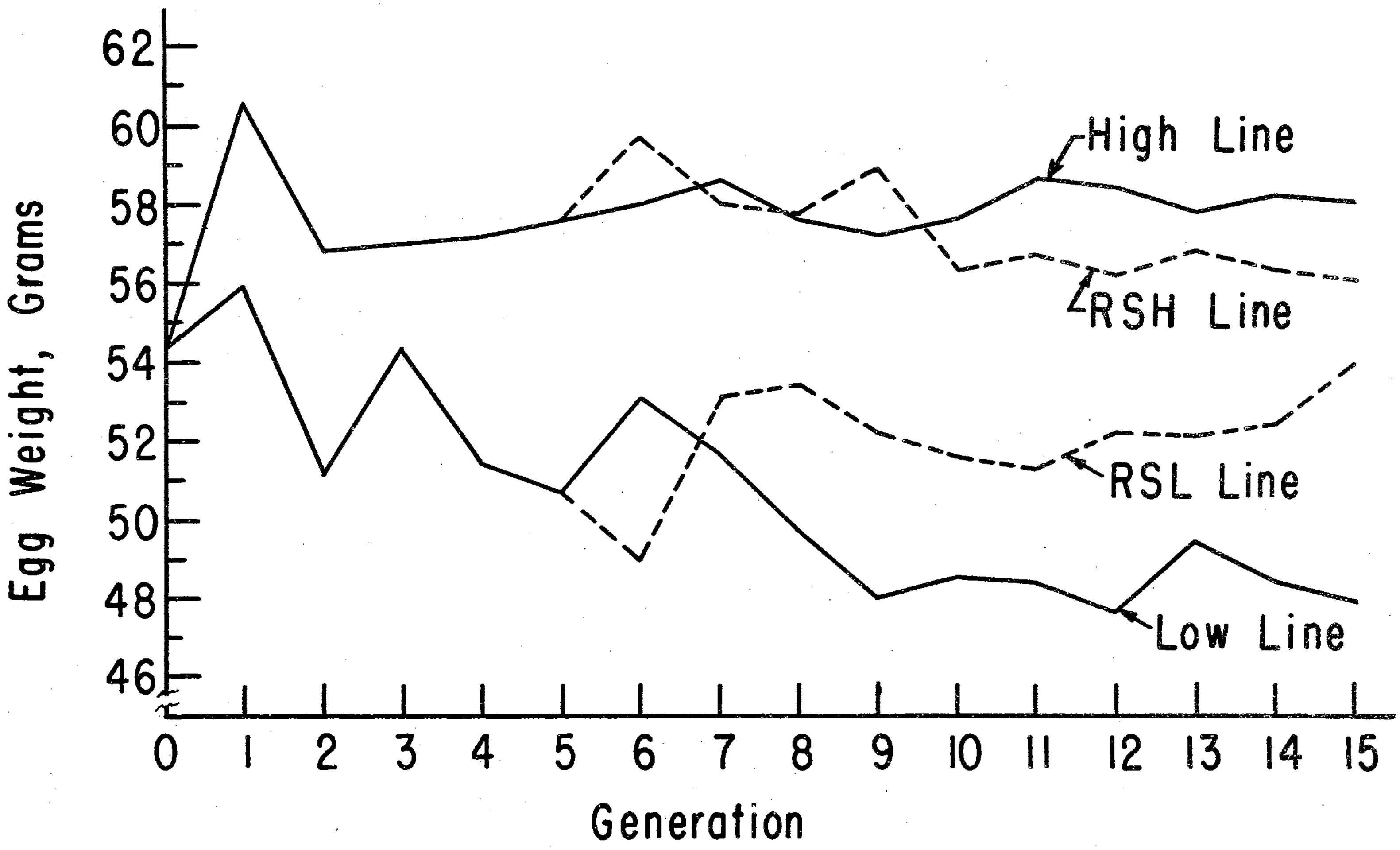

Figure 5. Average March Egg Weight by Generation. (Solid Line Represents the Divergent Selected Lines and the Broken Lines Represent the Relaxed-Selected Lines.)

in egg weight. This response was not exhibited in the selected high line female parents.

Percentage egg production was utilized as a measurement of egg production in order to correct for any effects due to sexual maturity. This correction was necessary since egg production was measured to a fixed end point, age at death or 500 days of age. The mean percentage egg production for each line by generation is shown in Figure 6. A regression analysis of the response observed in the selected female's performance indicated that percentage egg production was reduced at the rate of 0.73±0.31 percent per generation in the high line and 1.98±0.38 percent per generation in the low line. Both of these coefficients were statistically significant. It was noted that neither line indicated a decrease until the eighth generation of selection. A similar correlated response was observed by Siegel (1963) and Ideta and Siegel (1966b).

The decline associated with inbreeding would be expected to be about four percent in the high line and five percent in the low line. This would account for about 33 percent of the decrease observed in the high line and about 21 percent of the decrease observed in the low line. It may be concluded that selection for twelve-week body weight had an effect on percentage egg production.

The greatest decrease in percentage egg production was noted during the last seven generations of selection in the low line females. During this same period an extremely large amount of variation was observed within each generation. The average coefficient of variation during the last five generations was 86.0 percent. The high degree of variation observed in the low line females may account for the difference

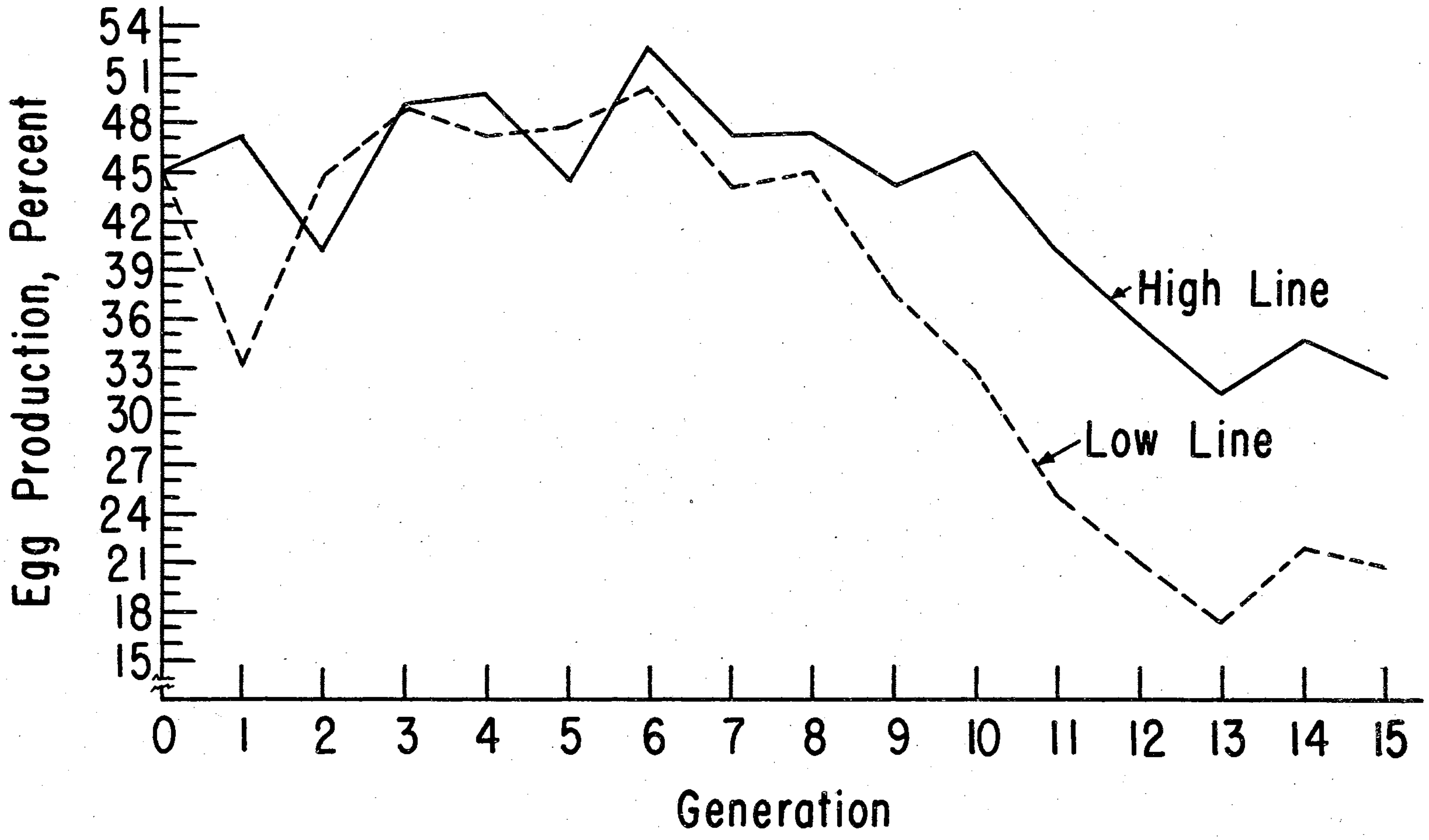

Figure 6. Average Percentage Egg Production for each of the Divergent Selected Lines by Generation.

noted earlier between the expected selection differential and the actual weighted selection differential for twelve-week body weight. The individual low line females which had higher twelve-week body weight tended to have a higher egg production rate during the hatching season and produced a relatively larger number of offspring than females of lower body weight. The relationship between body size and percentage egg production was not significant in any generation.

Data on the reproductive performance of the selected female parents is summarized in Figure 7 for percentage fertility and in Table XVIII for percentage hatch of fertile eggs. The regression analysis of percentage fertility indicated that fertility was decreased at the rate of -1.18±0.30 percent per generation. The slope of the regression line was significantly different than zero. The decrease noted in the low line was 0.84±0.35 percent per generation. This regression coefficient was significant at the five percent level of probability. The decrease expected due to inbreeding would be 8.9 percent in the high line and 10.7 percent in the low line. Inbreeding would account for about 40.0 percent of the decline noted in the high line and over 50.0 percent in the low line. The observed mean performance of the selected female parents for percentage hatch of fertile eggs over generations exhibited a similar response to that noted for percentage fertility. The resulting regression coefficients were -1.11±0.38 percent per generation in the high line and -0.70±0.54 percent in the low line. The observed decreases noted in the reproductive performance of the selected female parents correspond to the findings of Shoffner (1948), Glazener et al. (1951) and Schierman et al. (1959).

The average age at sexual maturity for the selected female parents

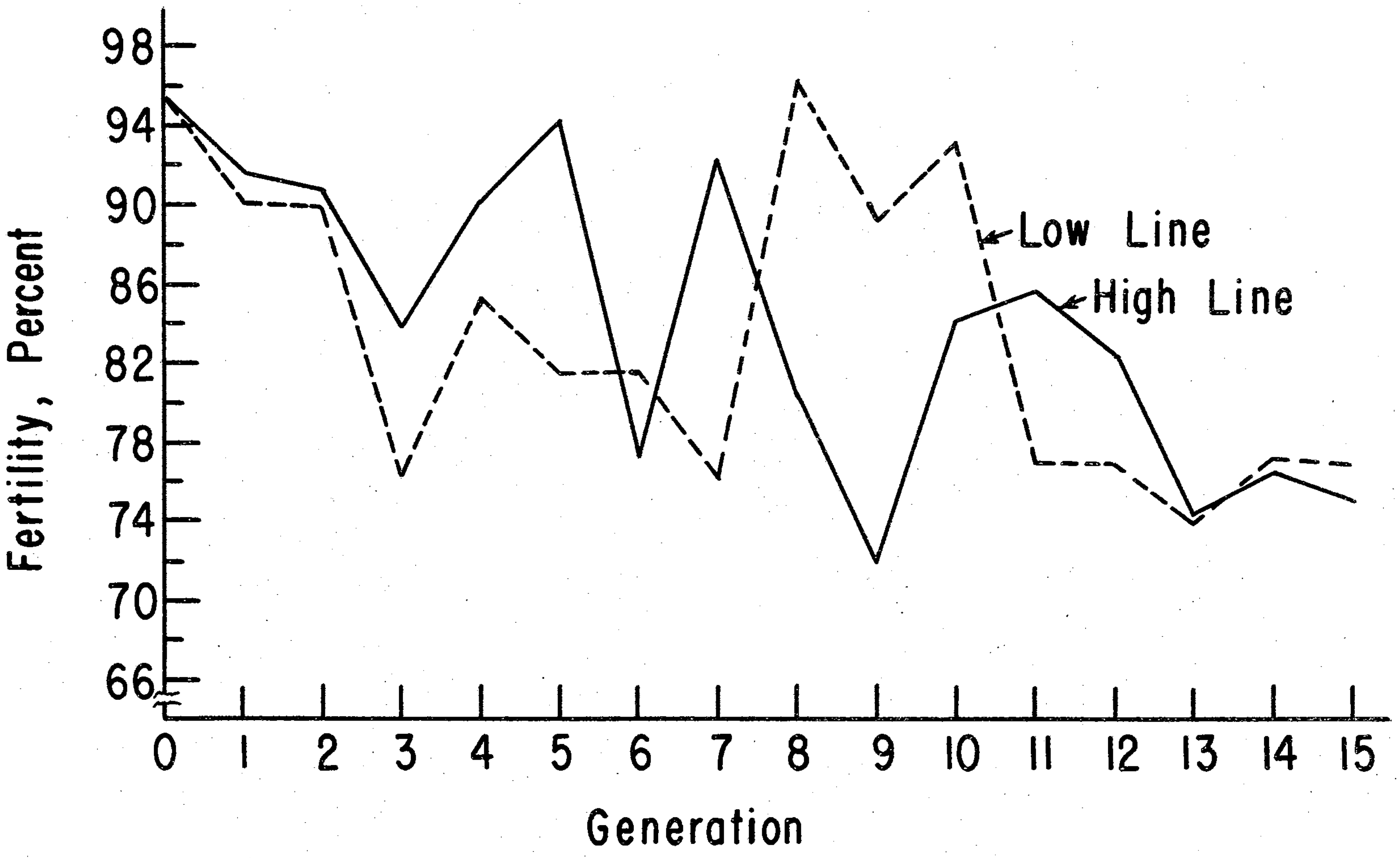

Figure 7. Average Percentage Fertility for each of the Divergent Selected Lines by Generation.

TABLE XVIII

AVERAGE PERCENTAGE HATCH OF FERTILE EGGS FOR THE SELECTED FEMALE PARENTS IN EACH SELECTED LINE BY GENERATION

Gen.	High Line	Low Line	Difference
0	94.0(1)	----	----
1	76.6	71.8	4.8
2	91.2	87.6	3.6
3	88.5	75.0	13.5*
4	92.4	89.0	3.4
5	82.2	82.0	0.2
6	74.2	70.1	4.1
7	79.3	75.6	3.7
8	70.2	78.5	8.3
9	77.6	86.2	8.6
10	77.5	76.7	0.8
11	72.9	76.2	3.3
12	77.1	85.6	8.5
13	61.4	49.5	11.9*
14	80.8	80.0	0.8
15	79.2	81.0	1.8
Regression(2)	-1.113±0.381*	-0.702±0.541	

1 - Measured as the number of days from hatch to first egg.
2 - Regression coefficient in days response per generation with its standard error.
* - Significant at the 5 percent level of probability.

in each selected line by generation is given in Table XIX. Although the generation means fluctuated to a great degree, the low line was consistently higher than the high line. A regression analysis indicated that the high line decreased at the rate of 0.33±1.15 day per generation. The low line analysis indicated an increase of 8.0±1.52 days per generation, which was significant. The increase observed in the low line far exceeds the expected increase due to inbreeding. The observed increase was 105 days compared to about 10 days expected from inbreeding. This increase also was greater than that reported by Siegel (1963) and Ideta and Siegel (1966b). The increase of the low line and the decrease in the high line generally correspond to the expected response based on the phenotypic and genetic correlations reported by Hazel and Lamoreaux (1947), Peeler et al. (1955), Jerome et al. (1956) and Ideta and Siegel (1966b).

It has been indicated by several investigators that selection may have an effect on percentage mortality. Duzgunes (1950) indicated that inbreeding may result in a reduced number of offspring surviving until breeding age. Table XX gives the percentage mortality of offspring to twelve weeks of age for the two selected lines. If one does not include the unusually high mortality observed in the original population, then the high and low lines did not indicate any specific response to selection for twelve-week body weight and further indications are that little, if any, increase was found to be related to inbreeding.

During the thirteenth generation a study was made to determine if any differences in feed conversion existed between the two selected lines. The data for this study are summarized in Table XXI. During

TABLE XIX

AVERAGE AGE AT SEXUAL MATURITY FOR THE SELECTED FEMALE PARENTS IN EACH SELECTED LINE BY GENERATION

Gen.	High Line	Low Line	Difference
0	182.5(1)	-----	----
1	178.1	190.3	12.2
2	170.3	172.9	2.6
3	200.4	212.2	11.8
4	214.0	217.0	3.0
5	229.0	267.0	38.0**
6	230.1	263.1	33.0**
7	208.1	250.1	42.0**
8	165.7	196.2	30.5**
9	188.6	218.1	29.5**
10	198.1	252.8	54.7**
11	154.3	218.6	64.3**
12	184.2	307.1	122.9**
13	192.9	328.1	135.2**
14	188.6	296.1	107.5**
15	189.2	288.4	99.2**
Regression(2)	-0.331±1.157	7.989±1.519**	

1 - Measured as the number of days from hatch to first egg.
2 - Regression coefficient in days response per generation with its standard error.
** - Significant at the 1 percent level of probability.

TABLE XX

PERCENTAGE MORTALITY TO TWELVE WEEKS OF AGE FOR THE HIGH AND LOW LINE BY GENERATION

Gen.	High Line (1)	Low Line (1)
0	30.9	----
1	12.0	6.5
2	2.0	7.0
3	5.1	18.6
4	6.7	13.0
5	7.2	7.6
6	5.2	5.7
7	9.5	5.9
8	4.6	6.9
9	10.8	9.4
10	7.5	13.2
11	5.2	9.2
12	11.2	6.9
13	10.2	11.3
14	8.2	6.8
15	7.2	6.9

1 = Percentages are corrected for mortality due to accidental death or loss.

TABLE XXI

COMPARATIVE FEED CONVERSION FOR THE HIGH AND LOW LINE DURING THE THIRTEENTH GENERATION, SEXES COMBINED

	High Line			Low Line		
Hatch No.	Mean wt.(2)	T.F.C.(3)	C.R.(4)	Mean wt.	T.F.C.	C.R.
Period No. 1(1)						
1	2.33	0.127	2.27	0.81	0.091	4.80
2	2.32	0.126	2.28	0.73	0.082	4.30
3	2.31	0.135	2.46	0.75	0.072	3.74
4	2.16	0.115	2.24	0.68	0.094	5.31
5	2.34	0.123	2.21	0.78	0.101	5.56
Average	2.29	0.125	2.29	0.75	0.088	4.74
Period No. 2(5)						
1	5.35	0.261	3.76	2.03	0.112	3.85
2	5.30	0.282	4.23	1.83	0.143	5.62
3	5.27	0.231	3.28	1.91	0.150	5.43
4	5.13	0.284	4.02	1.83	0.137	5.00
5	5.19	0.217	3.20	1.84	0.134	5.31
Average	5.25	0.255	3.70	1.89	0.135	5.04

1 = Zero to 6 weeks of age.
2 = Mean body weight, in pounds.
3 = Total feed consumed per bird per day.
4 = Conversion ratio, expressed as pounds of feed per pound of gain.
5 = Six to twelve weeks of age.

the period of growth between the time the birds were hatched and six weeks of age, the low line feed conversion was significantly different than that obtained in the high line. The average feed conversion was 2.29 pounds in the high line and 4.74 pounds in the low line for this period of growth. Between the sixth and twelfth weeks of growth, a significant feed conversion difference was also obtained. The average conversion was 3.7 pounds in the high line and 5.0 pounds in the low line.

Summary

In an original population of 715 Silver Oklabar chickens, a divergent selection program was initiated for high and low twelve-week body weight. Data were collected from 340 sires, 2140 dams and 20,980 offspring over a period of fifteen generations.

The results of the two-way selection study indicated that the response to selection was greater in the high line than in the low line. A difference in the rate of response per generation was also noted between the male and female offspring in the high line. These responses were 0.22 pound per generation in the male and 0.16 pound per generation in the females. Although a significant difference in response was noted, an analysis of the intensity of selection indicated that the selection pressure was not significantly different for the two sexes. The intensity of selection was measured by dividing the actual weighted selection differentials obtained in each generation by the phenotypic standard deviation of that generation. The rate of response observed in the low line male offspring was 0.045 pound per generation. The response noted in the low line female progeny was

0.047 pound per generation. The rate of response per generation for the two-way selection program was 0.27 pound in the male progeny and 0.21 pound in the female progeny.

The realized heritability was estimated to be 47.2 percent for the high line males, 35.1 percent for the high line females, 12.3 percent in the low line males and 12.7 percent in the low line females. The realized heritability for the difference obtained between the high and low line males was 35.6 percent. The realized heritability for the divergence between the high and low line females was 27.8 percent. The intra-sire regression heritability estimates ranged from 28.0 to 103.0 percent during the last ten generations in the high line males. The range in the high line females was 28.0 to 74.0 percent. Estimates obtained from the low line males ranged from 23.0 to 61.0 percent and from 19.0 to 168.0 percent for the low line females.

Six-week body weight was found to increase at the rate of 0.10 pound per generation in the high line males and 0.08 pound in the high line females. This response observed in the low line was -0.01 pound per generation for both sexes. The estimated realized heritability for the high line males, the high line females, the low line males and the low line females was 78.5 percent, 62.6 percent, 14.3 percent and 7.1 percent, respectively. Using the intra-sire regression analysis, the average estimates of the heritability were 58.9 percent in the high line males, 57.1 percent in the high line females, 42.1 percent in the low line males and 57.9 percent in the low line females. Regression coefficients estimated between six-week body weight and twelve-week body weight did not exhibit any tendency to change with generations.

Data collected on the performance of the selected low line female parents indicated that March egg weight was decreased at the rate of 0.47 gram per generation. March egg weight, as observed in the high line selected females, seemed to have stabilized after the second generation of selection. The selected female parents of both lines exhibited a decrease in percentage egg production, percentage fertility and percentage hatch of fertile eggs. The rate of reduction for these traits was significantly different than zero, except for the rate noted for percentage hatch of fertile eggs in the low line. Age at sexual maturity was reduced in the high line female parents. This trait was increased in the low line at the rate of eight days per generation.

Phase II. The Effects of Relaxed Selection in Divergent Lines Previously Selected for Twelve-week Body Weight

The technique of relaxing selection by random mating in a population or sample of the population after selection for particular traits has a number of useful purposes. The most significant of these is in answering the question: how permanent are the genetic gains in the selected trait? From a commercial point of view, if such gains are permanent, a purchaser of chicks could reproduce them for a considerable time without loss of performance. This technique has been used by geneticists in selection experiments to help shed light on a number of factors which affect selection. A principal consideration is the estimation of the effect of natural selection which opposes artificial selection, under the condition where negative correlation exists between the selected trait and fitness components.

Although the use of unselected control strains in laboratory selection experiments with *Drosophila* and other laboratory animals is a well established practice, only in recent years have workers with poultry and large animals given serious attention to the need for such adequate controls. The failure to use a control has made it difficult to interpret reports on the effects of selection programs. Two-way selection programs have been reported to improve the measurement of the response since both lines act as a control for each other. This improved measurement depends on the assumption of symmetrical response in the two divergent lines.

Since an asymmetrical response was observed in the two-way selection experiment presented in Phase I, the utilization of a control population may have improved the measurement of the actual response obtained. A control population must exhibit genetic stability with minimal inbreeding effect and minor interaction between environment and genotype. This population must also serve two functions; to smooth out short-term fluctuations due to the environment, and to provide a means of estimating long-term trends in the environment.

The objective of this study was to determine the effects of relaxed selection in the two divergent lines of chickens developed through five generations of selection for high and low twelve-week body weight. Another objective was to determine the genetic stability resulting from random breeding as measured by the response per generation and the genetic and environmental relationship among the various traits measured.

Review of Literature

Relaxed selection has been used by geneticists in selection experiments to help explain a number of factors functioning during selection. The use of relaxed selection as an experimental check on genetic selection achieved in *Drosophila melanogaster* was demonstrated by Reeve and Robertson (1953). In this study selection for long and short wing length was conducted for a period of 70 generation. Selection was relaxed during the 27th, 37th, and the 66th generations of selection. The authors stated that early in the experiment wing length returned to the original unselected length; however, this response was not noted after the 40th generation of selection.

Robertson (1955) selected for change in body size in *Drosophila melanogaster* during a period of 25 generations. This study included three different stocks selected for both large and small body size. Selection was relaxed after 15 generations of selection in all strains.

The author stated that in the three lines selected for large body size a moderate reduction occurred in two of the lines, while very little or no change occurred in the third line. The lines selected for small body size remained essentially the same following cessation of selection. The author concluded that correlated changes for fitness were not particularly important in the highly heritable trait, body size, in *Drosophila*.

Relaxed selection was also used by Clayton *et al.* (1957) in studying the effect of long term selection for bristle number in *Drosophila melanogaster*. The authors stated that relaxed selection initiated after eleven generations produced only a very slight tendency to return to the original mean value. The authors concluded that bristle number was not directly associated with fitness. The gene frequency, however, may have changed from that of the original population, and subsequently may have had some indirect correlation with fitness.

Various workers have utilized relaxed selection in poultry breeding experiments. Moultrie *et al.* (1956) studied the effects of relaxed selection on the performance of a strain of disease-resistant White Leghorns. In this study, selection was relaxed after eleven generations of selection. The authors stated that a small but consistent difference existed between the randomly reproduced unselected stock and the selected parental stock. The author concluded that a portion of this difference may have come from improvement in the selected stock. In addition, the fact that the two strains were separately housed might easily have accounted for the difference in mortality.

Shoffner and Grant (1960) reported the results of relaxed selection in a strain of White Leghorns previously selected for egg production. The genetic stock used in this experiment had been selected for this trait over a period of 25 generations. Both individual and family performance in egg production were used as the basis for selection. The relaxed selection study was conducted over a period of three generations. The author found no changes in body weight at eight weeks of age during the period of relaxed selection. Egg production measurements based on percentage production and on hen housed production showed little difference between the third generation and the first generation of relaxed selection. The authors further stated that the comparison made during the three generations of relaxed selection showed little or no decrease in performance for viability and hatchability based on the number of hens housed.

In poultry populations which have undergone artificial selection for egg production over many generations, a decline might be expected when selection is relaxed. Nordskog (1961) concluded that the cause of this decline may be due to the concentrated selection for a single fitness trait. Such selection may lead to a negative genetic correlation with other fitness components. In this study the author observed that the net decline in egg production rate due to relaxed selection was 1.69 percent and 1.16 percent per generation in two of the lines studied. A third line exhibited a decline of 0.97 percent per generation.

An additional application of relaxed selection may be the development of control populations. Lerner (1950) has briefly discussed the value of control strains. The author used a line selected for egg production as a control for "specialty lines" selected for such traits as shank length. The author assumed that these traits were uncorrelated and that the two lines were maintained under the same environment. Lerner (1950) suggested that the reverse was not true, and that the "specialty lines" did not act as a reasonable control for the strain selected for egg production. With a population that had "plateaued" or ceased to respond to selection, such a comparison could be misleading if there were marked environmental trends. Dickerson (1955) also recognized the need for genetically constant control populations to measure the actual trends due to environment over time.

It has been suggested that one might possibly control the environment over long periods of time, but this is impractical except for very small populations being maintained under elaborate laboratory conditions. Standardizing the more obvious and easily controlled factors of the environment, such as day length, feed hopper and floor space, diet and general management, did not reduce the environmental fluctuation from farm to farm or year to year in the data reported on by Gowe and Wakely (1954).

Skaller (1956) reported the use of a random-bred control strain in a selection study. Unfortunately, the author used such a small control population that inbreeding depression and random drift made it less useful than it might have been. Gowe et al. (1959) reported a detailed study of a control population which consisted of an average mating population of 47 males and 182 females in each of six generations. This study indicated that there was no evidence of any significant change in the genetic value of the strain during the period in which this study was conducted. The authors reported a positive and significant increase in March egg weight as well as a significant negative regression for sexual maturity. They suggested that these changes can probably be related to environmental trends.

Experimental Procedure

The study reported in this phase of the thesis involves ten generations of relaxed selection initiated during the fifth generation of selection for divergent body weight. All management practices were maintained the same from generation to generation insofar as possible.

The initiation of the relaxed selection program was accomplished by allowing the growth selected lines to produce the sixth generation progeny and then the parental stock within each line was randomly mated. From these random matings the relaxed-selected lines were produced. The two random-bred lines were designated as the relaxed-selected high line and the relaxed-selected low line. Each of these lines was propagated by random mating without any type of artificial selection.

A flock mating system was used to propagate the relaxed-selected lines. Approximately five males, 50 females within each line were randomly assigned to each mating pen. The number of pens used in each generation varied depending upon the number of females available in each line. The random selection of the progeny produced in each generation was accomplished after twelve-week body weight was measured. The relaxed-selected lines were hatched, brooded and reared in the same manner as the growth-selected lines.

The analysis of variance used in this study to determine the heritability and correlation coefficients of the various traits measured was presented in a report by Faiars _et al._ (1962). In order to facilitate the estimations of the covariances between different traits, a method indicated by Kempthorne (1957) was used. By taking advantage of the fact that the variance of the sum of two traits is equal to the variance of each trait plus twice the covariance between these traits, an IBM computer program could be utilized to obtain the estimates of the components of variance. These components were used to calculate the heritability and correlation coefficients reported. A more detailed discussion of these methods is presented in Appendix B of the thesis.

Results and Discussion

The average twelve-week body weights of the randomly selected parents for the relaxed-selected lines are summarized in Table XXII for each generation. The initial or intended means and the actual weighted means obtained for each of the lines indicated a non-significant difference. As pointed out by Falconer (1953) the difference between the intended mean weight and the actual weighted means may be due to natural selection operating in the population. The analysis of the means presented in Table XXII may indicate that this type of selection did not occur to any great extent in this study for twelve-week body weight. When a comparison of the intensity of natural selection is calculated for each sex and each line, the average intensity in the high line was 0.41 for the males and -0.11 for the females. The average intensity in the low line was 0.75 for the males and -0.04 for the females. The observed differences were not significant. This selection may be due to sampling variation, but the difference between the males and females could be associated with an interrelationship between fitness as measured by reproduction and body weight at twelve weeks of age.

The response as exhibited by the mean twelve-week body weight in

TABLE XXII

THE AVERAGE TWELVE-WEEK WEIGHT OF SELECTED PARENTS FOR THE RELAXED-SELECTED LINES GIVEN IN POUNDS BY GENERATION

	Males			Females		
Gen.	Initial	Actual	Act. wt.(1)	Initial	Actual	Act. wt.
			RSH(2)			
0	3.84	3.89	3.87	3.00	3.02	3.03
1	3.91	3.82	3.74	3.01	3.06	2.99
2	3.67	3.69	3.68	2.84	2.81	2.81
3	3.65	3.67	3.71	3.00	3.03	3.17
4	4.14	4.11	4.09	3.27	3.19	3.13
5	3.75	3.75	3.72	3.00	2.90	2.81
6	3.71	3.89	3.84	3.00	2.98	3.11
7	3.95	4.02	4.17	3.17	3.11	3.26
8	4.39	4.39	4.30	3.39	3.29	3.20
9	4.20	4.20	4.19	3.14	3.15	3.08
			RSL(3)			
0	2.38	2.42	2.41	1.87	1.96	1.98
1	2.63	2.63	2.65	1.97	1.93	1.81
2	2.58	2.57	2.59	1.98	2.01	2.04
3	2.90	2.94	2.98	2.33	2.24	2.27
4	3.20	3.09	2.90	2.32	2.20	2.17
5	2.81	2.82	2.79	2.18	2.14	2.20
6	2.82	3.22	3.14	2.15	2.18	2.15
7	3.07	3.98	3.91	2.48	2.46	2.48
8	3.59	3.36	3.21	2.54	2.57	2.62
9	3.58	3.59	3.64	2.69	2.67	2.65

1 - Actual weighted mean.
2 - Relaxed-selected high line.
3 - Relaxed-selected low line.

the relaxed-selected lines for each generation is shown as the broken line in Figure 1 for the male progeny and Figure 2 for the female progeny. The linear regression analysis of the response noted in these lines is given in Table XXIII. The response noted in the relaxed-selected high line males was 0.03±0.02 pound per generation and 0.01±0.02 pound per generation in the females. The response for twelve-week weight in the relaxed-selected low line males was observed to increase significantly during this study. The regression coefficient was 0.11±0.06 pound per generation. A coefficient of 0.08±0.01 pound per generation obtained for the relaxed-selected low line females was significantly different than zero.

Since the relaxed-selected low line exhibited a definite tendency to return to the original population mean weight when selection was relaxed, it may be concluded that very little permanent change in twelve-week body weight occurred during the first five generations of selection for low body weight. The increase noted in both sexes of the relaxed-selected high line may be indicative of natural selection or environmental improvements. The environmental improvement would also explain the reason for the relaxed-selected low line to continue to increase above the level of the original population mean. A further conclusion may be made that the selection for high twelve-week body weight caused some permanent change in the genetic control of this trait.

If one considers the selection differentials which occurred in this study as being real, an estimate of realized heritability can be made. The estimates calculated are shown in Table XXIII. All of these estimates exceeded one hundred percent, which indicated that some force other than the observable natural selection caused the response.

TABLE XXIII

LINEAR REGRESSION ANALYSIS OF TWELVE-WEEK BODY WEIGHT FOR THE RELAXED-SELECTED LINES BY SEX OVER ALL GENERATIONS

	RSH (1)		RSL(2)	
	Male	Female	Male	Female
Rate of Change (b)(3)	0.030	0.014	0.111*	0.077**
Variance of (b)	0.0006	0.0003	0.0036	0.0001
Standard Error of (b)	0.024	0.018	0.060	0.012
Realized Heritability(4)	217.4±36.6	189.5±12.6	130.5±19.1	103.5±08.7

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Slope of the fitted regression line expressed in pounds.
4 - Heritability expressed as percent, with its standard error.
* - Significant at the 10 percent level of probability.
** - Significant at the 1 percent level of probability.

The intended and actual mean six-week body weights for the selected parental stock of the relaxed-selected lines by sex and generation are given in Table XXIV. Very little difference was observed in the means obtained for each generation in each of the lines. The resulting response exhibited in these lines is shown graphically in Figures 3 and 4. After the initiation of relaxed selection, six-week body weights increased above the fifth generation mean of the respective growth-selected lines. The regression analysis of these responses is given in Table XXV. This analysis indicated that the six-week body weight response observed for both sexes in the relaxed-selected high line was about the same, 0.01±0.02 pound per generation. These coefficients were not significantly different than zero.

The six-week body weight regression coefficients calculated for the relaxed-selected low line male and relaxed-selected low line female offspring were both significant at the one percent level of probability. These regression coefficients were 0.06±0.01 pound per generation and 0.05±0.01 pound per generation, respectively. Since the effect of natural selection on the selected parents was indicated to be negligible, one would suspect that some other force must have caused the response noted, particularly in the relaxed-selected low line. The response, however, was not as great as that observed for twelve-week body weight. A greater amount of variation from generation to generation was also observed in six-week weight than that noted for twelve-week weight in the relaxed-selected high line. This would tend to suggest that six-week body weight was more responsive to environmental changes than body weight at twelve weeks of age.

The response observed in percentage fertility and percentage

TABLE XXIV

THE AVERAGE SIX-WEEK WEIGHT OF SELECTED PARENTS FOR THE RELAXED-SELECTED LINES GIVEN IN POUNDS BY GENERATION

	Males			Females		
Gen.	Initial	Actual	Act. wt.(1)	Initial	Actual	Act. wt.
			RSH(2)			
0	1.54	1.55	1.54	1.27	1.27	1.28
1	1.70	1.72	1.76	1.39	1.46	1.46
2	1.79	1.63	1.65	1.44	1.42	1.37
3	1.39	1.42	1.40	1.22	1.22	1.24
4	1.69	1.70	1.70	1.48	1.50	1.42
5	1.47	1.46	1.40	1.39	1.39	1.40
6	1.30	1.34	1.34	1.16	1.25	1.30
7	1.70	1.87	1.92	1.49	1.52	1.58
8	2.01	1.85	1.85	1.60	1.39	1.45
9	1.86	1.86	1.86	1.51	1.50	1.47
			RSL(3)			
0	0.87	0.90	0.87	0.79	0.75	0.76
1	1.03	1.10	1.09	0.83	0.83	0.85
2	1.11	1.11	1.10	0.85	0.88	0.89
3	1.10	1.10	1.10	0.96	0.99	0.98
4	1.16	1.18	1.17	0.97	0.98	0.99
5	1.16	1.14	1.14	0.99	1.00	1.01
6	1.10	1.10	1.10	0.85	0.86	0.91
7	1.34	1.35	1.34	1.09	1.11	1.28
8	1.56	1.55	1.50	1.30	1.32	1.22
9	1.52	1.52	1.54	1.22	1.24	1.16

1 - Actual weighted mean.
2 - Relaxed-selected high line.
3 - Relaxed-selected low line.

TABLE XXV

LINEAR REGRESSION ANALYSIS OF SIX-WEEK BODY WEIGHT FOR THE RELAXED-SELECTED LINES BY SEX OVER ALL GENERATIONS

	RSH(1)		RSL(2)	
	Male	Female	Male	Female
Rate of Change (b)(3)	0.011	0.008	0.060**	0.048**
Variance of (b)	0.00036	0.00019	0.00014	0.00008
Standard Error of (b)	0.019	0.014	0.012	0.009

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Slope of the fitted regression line expressed in pounds.
** - Significant at the 1 percent level of probability.

hatch of fertile eggs is given in Table XXVI. The fluctuation noted may have been due to extreme environmental conditions exerted against the reproductive performance of the relaxed-selected lines. Although the variation was not as great in the relaxed-selected low line, the difference between the two relaxed-selected lines was not significant except in the ninth generation. The linear regression analysis indicated that the mean percentage of fertile eggs increased at a non-significant rate of 0.11 percent per generation in the relaxed-selected high line. The rate of increase observed in the relaxed-selected low line was 0.87±0.66 percent per generation. By using the formula developed by Wright (1921), the inbreeding accumulated over the ten generations was about seven percent for each of these lines. This would indicate that percentage fertility should have decreased by 2.5 percent during this study due to inbreeding. This conclusion is based on the work reported by Blow and Glazener (1953). The response in the percentage hatch of fertile eggs was -0.84±0.48 percent per generation for the relaxed-selected high line. This response was noted to be 0.17±0.49 percent per generation in the relaxed-selected low line. The overall comparison of these lines to the original mean indicates that neither line exhibited a definite tendency to return toward the original population mean. It may be concluded that both of the relaxed lines remained at about the same level as that of the fifth generation of the divergent selected lines.

The great amount of variation observed in the relaxed-selected lines for percentage egg production (Table XXVII) seems to indicate that non-genetic factors may have had a greater influence on this trait and may overshadow any effects due to genetic sources. The rate

TABLE XXVI

THE AVERAGE PERCENTAGE FERTILITY AND PERCENTAGE HATCH OF FERTILE EGGS BY GENERATION FOR EACH OF THE RELAXED-SELECTED LINES FEMALE OFFSPRING

	Percentage Fertility				Percentage Hatch of Fertile Eggs			
	RSH(1)		RSL(2)		RSH		RSL	
Gen.	Mean	s	Mean	s	Mean	s	Mean	s
0	77.1	14.5	88.9	11.1	88.2	12.2	83.9	15.4
1	90.0	21.9	82.3	31.7	90.0	24.7	82.3	23.9
2	61.9	31.6	66.3	45.7	75.0	32.4	68.7	44.3
3	83.5	28.5	84.8	52.4	77.3	30.8	81.2	11.9
4	68.9	22.6	85.2	20.6	78.4	26.9	86.6	25.2
5	78.8	28.6	83.2	22.2	79.2	29.2	85.0	26.1
6	72.0	25.2	89.7	12.6	72.0	29.0	78.1	24.1
7	72.9	23.3	88.4	18.9	74.6	25.4	86.2	20.4
8	73.9	28.2	81.9	23.1	77.7	23.6	80.3	26.6
9	79.9	18.9	88.4	18.2	76.8	19.9	81.7	16.7
10	84.1	26.3	91.4	15.2	81.0	33.3	80.9	21.1
Regression(3)	0.11±0.79		0.87±0.66		-0.84±0.48		0.17±0.49	

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Regression of mean on generation.

TABLE XXVII

THE AVERAGE PERCENTAGE EGG PRODUCTION, EGG WEIGHT AND SEXUAL MATURITY BY GENERATION FOR THE RELAXED-SELECTED LINES' FEMALE OFFSPRING

	Percentage Egg Prod.				Egg Weight(1)				Sexual Mat.(2)			
	RSH(3)		RSL(4)		RSH		RSL		RSH		RSL	
Gen.	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s
0	44.7	26.7	47.9	19.6	57.6	4.7	50.7	4.3	217	51.8	229	53.9
1	50.7	12.8	50.6	18.7	59.7	4.3	48.9	3.1	229	39.4	267	71.4
2	47.6	11.1	47.8	14.9	58.0	4.8	53.1	3.5	233	27.7	264	32.1
3	42.2	13.7	52.4	10.0	57.7	3.5	53.4	3.9	190	24.9	186	13.3
4	41.6	14.4	44.1	15.6	58.9	9.9	52.2	3.4	204	26.0	215	42.8
5	44.9	15.3	45.5	16.8	56.3	3.2	51.6	3.1	205	53.7	230	26.2
6	39.2	17.4	42.3	13.4	56.7	4.2	51.3	4.9	194	29.8	226	34.6
7	51.3	13.3	50.7	14.3	56.2	4.1	52.1	9.4	228	62.1	263	49.0
8	42.6	10.4	43.4	10.7	56.8	4.1	52.1	4.2	186	36.9	224	56.4
9	44.7	19.9	42.8	19.2	56.3	3.0	52.4	3.6	268	68.0	259	75.2
10	48.7	15.9	46.0	17.9	56.0	3.9	53.9	7.3	251	66.0	255	57.6
Regression(5)	-0.03±0.40		-0.54±0.30		-0.28±0.08**		0.20±0.14		2.92±3.00		1.10±3.12	

1 - Egg weight in grams.
2 - Sexual maturity in days.
3 - Relaxed-selected high line.
4 - Relaxed-selected low line.
5 - Regression of the observed mean on generation.
** - Significant at the 1 percent level of probability.

of change exhibited by the relaxed-selected high line was -0.03±0.40 percent per generation and -0.54±0.30 in the relaxed-selected low line. The decline due to inbreeding would be expected to be about 0.0002 percent per generation in these lines. Thus, the change that was observed, although small, may have been due to sampling error rather than changes in the genetic makeup of the population.

During the first six generations of relaxed-selection in the high line, March egg weight was noticeably decreased but did not return to the mean egg weight of the original population. The mean for each line by generation is given in Table XXVII. In the last six generations, this trait remained fairly stable. The average change per generation, estimated from the regression analysis, was -0.28±0.08 gram. This slope was considered to be significantly different than zero. The response observed in the relaxed-selected low line indicated that egg weight was increased at a non-significant rate of 0.20±0.14 gram per generation. The final mean weight after ten generations was 53.9 grams and may not be significantly different than that of the original population mean of 54.3 grams. This would tend to indicate that although selection for low twelve-week body weight was effective in reducing egg weight, this reduction may not have resulted from permanent changes in the genetic composition of the population associated with egg weight. This does not mean, however, that continued selection for periods greater than five generations may not cause permanent changes in egg weight.

The relaxed-selected lines exhibited an almost immediate return toward the original population mean of 183 days for sexual maturity. As indicated by the means given in Table XXVII for age at sexual maturity, this decline was not sustained during the latter part of this study.

The average change when all generations are considered was 2.92±3.00 days per generation in the relaxed-selected high line and 1.00±3.12 days in the relaxed-selected low line. The overall fluctuation of these lines indicate that age at sexual maturity may have been influenced to a great degree by non-genetic variation in this experiment.

Heritability estimates for six and twelve-week body weight in the relaxed-selected high line are given in Table XXVIII. These estimates were derived from the dam component of variance and from the intra-sire regression method. Estimates were omitted if a negative estimate of a variance component was calculated. The results indicated a large amount of variation in the estimates from generation to generation. The overall mean of 63.9 percent for the male offspring compared very well with the average heritability discussed in the general literature review for dam component estimates. The overall mean for the female offspring indicates that a definite difference may exist in the heritability between the two sexes, although the difference observed was not significant. The average heritability of 32.3 percent for the males and 23.9 percent for the females, estimated from the regression technique, were lower than those generally reported in the literature. The average estimate for the dam component of 45.9 percent for six-week male body weight was considerably higher than that calculated for female six-week body weight (20.9). The mean estimates from the regression method were 24.9 percent for the males and 27.2 percent for the females.

The estimates of heritability derived from the dam components, estimated from mass mating, may contain less dominance variance than under a hierarchical mating system. However, a large portion of the maternal

TABLE XXVIII

ESTIMATES OF HERITABILITY FOR SIX AND 12-WEEK BODY WEIGHT IN THE RELAXED-SELECTED HIGH LINE BY GENERATION, IN PERCENT

	12-week wt.				6-week wt.			
	h^2_d (1)		h^2_r (2)		h^2_d		h^2_r	
Gen.	Male	Female	Male	Female	Male	Female	Male	Female
0	18.4	16.8	28.8	22.7	13.5	25.0	18.6	17.2
1	62.1	75.9	35.6	21.9	26.2	13.1	16.5	19.1
2	+	40.8	30.8	26.2	68.7	11.3	11.0	21.1
3	35.7	11.0	29.6	23.6	48.5	34.4	26.5	20.1
4	101.9	68.9	26.6	20.7	30.1	19.8	22.9	16.8
5	59.6	+	28.9	19.9	38.5	127.1	21.1	23.2
6	97.9	159.4	33.0	21.6	12.9	10.6	14.8	28.4
7	84.0	38.8	22.4	22.0	107.7	29.3	26.9	17.2
8	62.7	11.3	60.8	33.4	60.6	14.4	33.6	40.4
9	56.0	65.2	26.3	22.6	64.9	15.6	46.5	51.5
10	60.8	51.5	32.9	28.8	32.9	17.9	35.1	44.4
Mean	63.9	53.9	32.3	23.9	45.9	20.9	24.9	27.2

1 - Heritability estimated from dam component of variance.
2 - Heritability estimated from regression of offspring on dam.
+ - Negative estimate of variance component interfered with estimation.

effects will still be included in the variance component for dams. This would tend to increase this type of estimate in juvenile body weight as compared to estimates from the intra-sire regression method. This tendency is presented further in Table XXIX. This table shows the heritability estimates for body weight obtained from the relaxed-selected low line by generation and by sex. In this line the mean estimates for both six and twelve-week body weight were reasonably close together for the dam component of estimation. These estimates were consistently higher than those obtained by the intra-sire regression method.

Table XXX and Table XXXI give the estimates of heritability for the various traits related to the production performance of the female progeny of each generation in each of the relaxed-selected lines. In these traits the estimates obtained from the dam component of variation were higher than those obtained from the intra-sire regression analysis. It was also noted that the average of the estimates was very similar in the two lines. The average estimates for percentage fertility and percentage hatch of fertile eggs in the relaxed-selected high line were 16.1 percent, 29.1 percent when estimated from the dam component of variance. The estimates were 16.6 percent for fertility and 20.5 percent for hatch of fertile eggs in the relaxed-selected low line. These estimates are above the estimates generally reported for these traits. The intra-sire regression estimates average 5.9 percent for percentage fertility and 8.0 percent for percentage hatch of fertile eggs in the relaxed-selected high line. The average heritability estimates in the relaxed-selected low line were 5.1 percent for percentage fertility and 10.8 percent for percentage hatch of fertile eggs. These

TABLE XXIX

ESTIMATES OF HERITABILITY FOR SIX AND 12-WEEK BODY WEIGHT IN THE RELAXED-SELECTED LOW LINE BY GENERATION, IN PERCENT

	12-week wt.				6-week wt.			
	h^2_d (1)		h^2_r (2)		h^2_d		h^2_r	
Gen.	Male	Female	Male	Female	Male	Female	Male	Female
0	+	16.8	22.8	20.9	36.0	38.2	20.1	9.1
1	29.9	44.9	25.7	12.7	28.7	+	23.6	17.7
2	38.0	40.4	33.8	30.1	47.6	47.1	24.6	18.9
3	55.5	+	19.6	22.6	41.8	49.4	19.6	21.1
4	75.9	54.8	36.7	26.7	132.1	28.6	26.6	24.7
5	47.6	46.1	41.1	26.8	41.8	34.7	28.1	26.8
6	112.0	169.2	16.9	24.0	+	123.7	27.2	22.3
7	60.5	37.9	44.9	25.9	50.6	+	26.1	27.6
8	38.1	70.7	40.4	25.8	72.1	39.3	38.2	31.8
9	138.9	56.1	61.6	54.2	88.9	60.8	40.6	36.0
10	72.2	41.4	58.2	38.0	66.7	49.2	29.6	26.9
Mean	66.9	57.8	36.5	27.9	60.6	52.3	27.7	23.9

1 = Heritability estimated from dam component of variance.
2 = Heritability estimated from regression of offspring on dam.
+ = Negative estimate of variance component interfered with estimation.

TABLE XXX

ESTIMATES OF HERITABILITY FOR TRAITS RELATED TO FITNESS IN THE RELAXED-SELECTED HIGH LINE BY GENERATION, IN PERCENT

	% Fert.*		% H. of F.*		% Eg. Pd.*		Egg Wt.*		S. M.*	
Gen.	h^2_d(1)	h^2_r(2)	h^2_d	h^2_r	h^2_d	h^2_r	h^2_d	h^2_r	h^2_d	h^2_r
0	9.6	2.9	+	4.8	21.6	14.7	29.6	20.6	36.9	10.9
1	9.7	4.0	26.7	10.1	41.6	18.6	40.6	36.0	28.6	18.6
2	+	15.8	20.0	9.8	38.4	15.5	38.2	31.8	45.7	22.9
3	11.1	5.9	31.6	12.9	16.4	13.3	28.1	20.3	+	11.8
4	15.0	7.8	18.8	10.0	22.2	10.9	26.6	18.9	19.9	31.2
5	27.0	6.2	12.3	9.9	70.8	17.3	50.6	28.9	140.1	15.0
6	14.7	5.9	12.7	6.3	39.6	20.5	33.1	18.5	23.9	8.4
7	10.9	3.6	11.1	3.9	41.2	30.0	72.6	26.2	+	23.9
8	29.6	0.5	63.9	5.0	20.0	21.2	95.6	51.9	39.2	18.4
9	17.5	7.5	64.5	8.2	37.8	22.8	119.4	56.3	112.5	14.2
10	15.9	5.1	+	6.8	24.1	22.5	+	35.5	57.6	22.6
Mean	16.1	5.9	29.1	8.0	34.0	18.8	53.4	31.4	56.0	18.0

1 - Heritability estimated from dam component of variance.
2 - Heritability estimated from regression of offspring on dam.
+ - Negative estimate of variance component interfered with estimation.
* - Fitness traits are, respectively; percentage fertility, percentage hatch of fertile eggs, percentage egg production, egg weight, and age at sexual maturity.

TABLE XXXI

ESTIMATES OF HERITABILITY FOR TRAITS RELATED TO FITNESS IN THE RELAXED-SELECTED LOW LINE BY GENERATION, IN PERCENT

	% Fert.*		% H. of F.*		% Eg. Pd.*		Egg Wt.*		S. M.*	
Gen.	$h^{2(1)}_d$	$h^{2(2)}_r$	h^2_d	h^2_r	h^2_d	h^2_r	h^2_d	h^2_r	h^2_d	h^2_r
0	11.6	9.9	18.6	11.0	41.2	22.2	60.7	26.1	33.3	12.6
1	15.9	10.0	20.7	12.0	38.7	25.0	34.7	19.9	37.8	22.8
2	19.6	8.7	15.6	13.1	29.1	29.6	27.4	22.1	21.9	8.4
3	16.9	4.0	12.2	9.2	40.0	18.1	47.6	20.0	18.6	16.7
4	22.8	5.7	21.6	7.0	19.6	10.6	32.1	25.0	22.7	15.4
5	23.4	4.3	19.6	8.2	18.7	14.2	25.0	15.6	26.9	20.0
6	12.0	1.1	33.8	15.0	20.0	18.3	39.5	19.5	21.9	18.4
7	20.5	5.9	3.9	7.5	28.3	15.8	40.0	16.7	105.4	26.7
8	15.9	0.8	37.5	9.1	55.9	22.6	51.9	11.9	12.5	18.6
9	10.1	0.9	21.1	11.1	41.7	17.7	33.3	15.5	57.6	27.7
10	13.6	4.7	+	14.2	62.4	28.9	48.0	26.8	38.6	22.9
Mean	16.6	5.1	20.5	10.8	35.9	20.3	40.0	19.9	36.1	19.1

1 - Heritability estimated from dam component of variance.
2 - Heritability estimated from regression of offspring on dam.
+ - Negative estimate of variance component interfered with estimation.
* - Fitness traits are, respectively; percentage fertility, percentage hatch of fertile eggs, percentage egg production, egg weight, and age at sexual maturity.

estimates are more in line with the estimates reported in the literature. The average estimate obtained for the heritability of percentage egg production reported in the literature is about 18 percent. This corresponds reasonably well with that obtained in the relaxed-selected lines from the intra-sire regression method. These estimates were 18.8 percent in the relaxed-selected high line and 20.3 percent in the relaxed-selected low line.

The average of the heritability for March egg weight in the review of literature was 47.0 percent for the dam component and 42.0 percent for the intra-sire regression. The average of the estimates obtained in this study were 53.4 percent and 40.0 percent from the dam component in the relaxed-selected high and low lines, respectively. The intra-sire regression estimates were 31.4 percent in the relaxed-selected high line and 19.1 percent in the relaxed-selected low line for March egg weight.

The heritability estimates for age at sexual maturity showed the same degree of variation from generation to generation as the other estimates obtained from the analysis of variance. The estimates obtained from the intra-sire regression analysis did not exhibit the same degree of fluctuation. The average estimates were 56.0 percent in the relaxed-selected high line and 36.1 percent in the relaxed-selected low line from the dam component. The estimates obtained from the intra-sire regression method was 18.0 percent in the relaxed-selected high line and 19.1 percent in the relaxed-selected low line.

Estimates of genetic, environmental and phenotypic correlations were obtained from the analysis of variance estimates of the dam component of variation and covariance.

The correlation coefficients between six-week body weight and twelve-week body weight are given in Table XXXII. These estimates indicate that the genetic correlation between these traits was consistently higher in the male offspring than in the female offspring. These estimates further indicate that environmental effects may have caused a large degree of relationship between the traits. The large genetic correlation would suggest that there should be a great similarity in the response exhibited by six-week body weight and twelve-week body weight to selection.

The correlations estimated for twelve-week body weight and six-week body weight with percentage egg production, egg weight and sexual maturity are given in Tables XXXIII through XXXVIII. Although these estimates vary considerably, the overall means are well within the range of those reported in the literature. In general, it is considered that a negative relationship exists between body weight and percentage egg production, while a positive relationship is indicated between body size and egg weight. These estimates also indicate that body weight was positively correlated, genetically, with age at sexual maturity to a low degree.

The correlation coefficients estimated between egg production and egg weight in this study are given in Table XXXIX. The average estimates for the genetic correlation were 0.115 in the relaxed-selected high line and 0.048 in the relaxed-selected low line. The average estimates of the environmental correlation between egg production and egg weight were -0.014 and 0.123 for the relaxed-selected high line and relaxed-selected low line, respectively. The phenotypic correlations between these two traits were found to be 0.058 in the

TABLE XXXII

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN SIX AND TWELVE WEEK BODY WEIGHT BY GENERATION FOR THE RELAXED-SELECTED PROGENY

	RSH[1]						RSL[2]					
	Male			Female			Male			Female		
Gen.	r_g[3]	r_e	r_p	r_g	r_e	r_p	r_g	r_e	r_p	r_g	r_e	r_p
0	0.692	0.362	0.472	1.010	-0.292	0.212	*	0.629	0.159	-.738	*	0.496
1	-.072	0.491	0.671	0.521	0.362	0.421	0.821	0.721	0.147	*	0.961	0.672
2	*	0.671	0.881	-0.420	0.515	0.133	0.743	0.914	0.219	0.921	0.811	0.414
3	0.947	-0.380	0.492	0.718	0.258	0.572	0.697	0.222	0.436	*	0.421	0.129
4	0.738	0.301	0.397	0.442	0.367	0.228	0.888	0.371	0.392	0.724	0.372	0.491
5	1.711	0.222	0.370	*	0.408	0.927	0.739	0.362	0.673	-1.196	0.480	0.140
6	1.041	0.091	0.546	1.626	0.421	0.470	*	0.620	0.261	0.180	0.442	0.390
7	1.070	0.470	0.552	0.962	0.339	0.612	0.762	0.471	0.523	*	0.372	0.671
8	-0.578	*	0.386	0.298	0.677	0.684	0.912	0.361	0.718	0.848	0.758	0.752
9	0.783	0.665	0.626	0.399	0.463	-0.008	0.890	0.525	0.601	1.726	0.306	0.512
10	0.781	0.147	0.592	0.721	0.606	0.399	0.925	0.412	0.421	1.112	0.252	0.425
Mean	0.711	0.304	0.544	0.628	0.375	0.423	0.820	0.510	0.414	0.447	0.518	0.463

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dams component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXIII

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN TWELVE-WEEK BODY WEIGHT AND PERCENTAGE EGG PRODUCTION BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	-0.392	0.091	-0.217	0.279	-0.111	-0.004
1	0.208	-0.062	-0.022	-0.784	0.182	-0.434
2	0.211	-0.248	0.008	-0.742	0.009	-0.060
3	-1.033	0.040	0.417	*	-0.134	-0.055
4	0.042	-0.027	-0.098	-0.082	-0.273	-0.075
5	*	0.149	0.144	-0.156	0.080	0.110
6	0.089	-0.194	-0.027	0.230	-0.020	0.001
7	-0.923	0.122	-0.094	-0.670	0.055	-0.022
8	-0.371	0.101	-0.165	-0.175	0.049	-0.150
9	0.542	-0.180	-0.091	-0.559	-0.166	0.095
10	0.039	-0.111	-0.008	-0.412	-0.127	-0.013
Mean	-0.167	-0.029	-0.014	-0.307	-0.041	-0.055

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXIV

ESTIMATION OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN TWELVE-WEEK BODY WEIGHT AND EGG WEIGHT BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

		RSH$^{(1)}$			RSL$^{(2)}$	
Gen.	$r_g^{(3)}$	r_e	r_p	r_g	r_e	r_p
0	0.125	-0.048	0.107	-0.510	0.314	0.365
1	0.100	0.080	0.128	0.325	0.111	0.095
2	0.455	0.359	0.145	0.011	0.360	0.114
3	-0.208	*	0.094	*	0.300	0.189
4	0.595	-0.133	0.425	-0.225	0.240	0.045
5	*	0.058	0.270	0.115	0.315	0.160
6	-0.115	0.013	-0.003	-0.443	-0.243	-0.300
7	0.897	0.125	0.111	0.400	0.360	0.228
8	-0.540	0.488	0.150	0.190	0.191	0.148
9	0.137	-0.022	0.083	0.010	-0.085	0.111
10	*	-0.226	-0.022	0.333	0.192	0.241
Mean	0.161	0.057	0.137	0.021	0.187	0.127

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXV

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN TWELVE-WEEK BODY WEIGHT AND SEXUAL MATURITY BY GENERATION IN THE RELAXED-SELECTED FEMALE PROGENY

		RSH(1)			RSL(2)	
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	0.125	-0.100	0.078	-0.172	-0.095	-0.200
1	-0.228	-0.051	-0.220	0.333	0.005	0.314
2	-0.142	0.010	-0.128	0.111	-0.010	0.089
3	*	0.166	0.088	*	-0.139	-0.225
4	0.577	-0.341	0.139	-0.147	-0.009	-0.250
5	*	-0.157	-0.222	-0.088	-0.090	-0.127
6	0.452	-0.297	0.051	-0.329	-0.045	-0.132
7	*	-0.344	-0.186	-0.169	-0.007	-0.181
8	0.312	-0.162	0.246	0.117	*	0.101
9	-0.136	-0.015	-0.185	-0.238	-0.112	-0.246
10	0.197	0.006	0.177	-0.146	-0.099	-0.138
Mean	0.145	-0.117	-0.015	-0.073	-0.060	-0.090

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXVI

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN SIX-WEEK BODY WEIGHT AND PERCENTAGE EGG PRODUCTION BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	-0.180	0.047	-0.191	0.140	*	-0.019
1	0.104	-0.020	-0.004	*	0.061	-0.087
2	0.035	-0.082	0.018	-0.444	0.218	-0.311
3	-0.210	0.008	0.081	0.089	-0.134	-0.092
4	0.089	-0.194	-0.027	-1.171	-0.199	0.015
5	-0.392	0.091	-0.277	0.047	0.150	0.144
6	-1.314	-0.111	-0.003	-6.209	0.244	-2.507
7	-0.281	-0.001	-0.197	*	0.808	-0.063
8	0.612	-0.212	0.398	2.211	-0.175	0.018
9	-0.395	-0.134	-0.055	0.542	-0.180	-0.099
10	0.251	0.108	0.188	-0.250	-0.011	-0.208
Mean	-0.198	-0.046	-0.006	-0.783	0.0782	-0.292

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXVII

ESTIMATION OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN SIX-WEEK BODY WEIGHT AND EGG WEIGHT BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	0.031	-0.012	0.032	-0.170	*	0.121
1	0.050	0.040	0.064	*	0.040	0.031
2	0.111	0.090	0.031	0.015	0.191	0.125
3	-0.080	*	0.131	-0.079	-0.243	-0.150
4	0.104	0.100	0.115	0.040	0.175	0.099
5	-0.018	0.021	-0.442	0.200	0.050	0.122
6	0.575	-0.069	0.223	-0.359	0.533	0.186
7	0.300	0.041	0.141	*	0.120	0.114
8	-0.125	0.271	0.089	0.072	0.101	0.050
9	0.132	-0.044	0.038	0.137	-0.022	0.083
10	*	0.114	0.089	0.215	0.124	0.310
Mean	0.108	0.055	0.046	0.008	0.107	0.099

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXVIII

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN SIX-WEEK BODY WEIGHT AND SEXUAL MATURITY BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	$r_g^{(3)}$	r_e	r_p	r_g	r_e	r_p
0	0.250	-0.198	0.125	-0.197	*	-0.012
1	-0.114	-0.077	-0.118	*	0.096	0.164
2	-0.226	0.060	-0.233	0.211	-0.101	0.175
3	*	0.041	0.111	0.146	-0.109	0.089
4	0.362	-0.123	0.202	-0.021	-0.019	-0.071
5	0.576	0.069	0.386	-0.181	-0.010	-0.200
6	0.299	-0.110	0.251	-0.149	0.245	0.014
7	*	-0.349	-0.201	*	-0.111	-0.100
8	0.106	0.103	0.191	0.121	*	0.156
9	-0.159	0.012	-0.045	-0.331	0.128	-0.167
10	0.013	-0.109	-0.076	-0.166	-0.100	-0.201
Mean	0.123	-0.062	0.054	-0.063	0.002	0.014

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XXXIX

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN PERCENTAGE EGG PRODUCTION AND EGG WEIGHT BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	0.209	-0.144	0.141	0.137	0.170	0.148
1	0.178	-0.115	0.019	-0.139	0.224	0.090
2	-0.300	-0.085	0.189	0.230	0.099	0.170
3	0.102	*	0.040	-0.035	0.101	0.075
4	0.156	-0.175	0.009	-0.073	0.151	-0.019
5	0.258	0.223	0.217	-0.025	0.098	0.060
6	0.387	-0.016	-0.075	-0.142	0.260	0.190
7	-0.091	-0.033	-0.080	0.142	0.100	0.109
8	0.111	-0.001	0.048	0.115	0.225	0.188
9	0.142	-0.033	-0.039	0.079	0.099	0.102
10	*	0.233	0.166	0.243	-0.172	0.147
Mean	0.115	-0.014	0.058	0.048	0.123	0.105

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

relaxed-selected high line and 0.105 in the relaxed-selected low line. Most investigators report that a low positive phenotypic correlation may exist between these traits and that the genetic correlation was usually slightly negative, with some estimates being as high as 0.310 (Quinn, 1963).

Table XL and Table XLI give the correlation estimates between age at sexual maturity and egg production and between sexual maturity and egg weight. These estimates indicate that age at sexual maturity had a negative genetic correlation with egg production, and the phenotypic correlation between these traits was indicated to be near zero in both of the relaxed-selected lines. A negative genetic correlation was obtained between sexual maturity and egg weight in the relaxed-selected high line. This compared to a near-zero estimate in the relaxed-selected low line. The average phenotypic correlation between sexual maturity and egg weight was -0.036 and 0.069 in the relaxed-selected high and low lines, respectively.

Although several estimates have been reported for the correlation among various traits measured in the domestic fowl, very few investigators have reported estimates between juvenile body weight and traits related to hatchability.

The correlation coefficients estimated between body weight, at twelve and at six weeks of age, and percentage fertility are given in Table XLII and Table XLIII. The relaxed-selected low line exhibited a high positive genetic correlation between twelve-week weight and percentage fertility. The genetic relationship between these traits was indicated to be very low in the relaxed-selected high line. These conclusions were based on the overall average correlation obtained in

TABLE XL

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN EGG PRODUCTION AND SEXUAL MATURITY BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	0.111	-0.204	0.025	0.110	-0.126	-0.009
1	0.236	-0.112	0.008	0.156	0.080	0.106
2	-0.100	-0.063	-0.071	-0.082	0.151	0.075
3	*	0.005	-0.056	-0.031	-0.273	-0.147
4	-0.251	0.183	-0.088	0.102	-0.120	-0.010
5	-0.098	-0.031	-0.054	0.101	-0.124	0.008
6	-0.060	0.035	-0.031	-0.443	0.176	0.052
7	*	-0.083	0.081	0.029	0.126	0.090
8	-0.148	0.118	0.060	0.111	*	-0.016
9	-0.229	0.042	-0.172	-0.225	0.121	-0.022
10	-0.203	0.107	-0.094	-0.027	0.049	0.015
Mean	-0.082	-0.001	-0.036	-0.018	0.006	0.013

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XLI

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN EGG WEIGHT AND SEXUAL MATURITY BY GENERATION FOR THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g (3)	r_e	r_p	r_g	r_e	r_p
0	0.114	-0.030	0.101	0.111	0.100	0.195
1	-0.300	-0.030	-0.222	0.098	0.140	0.100
2	0.114	-0.070	0.150	0.110	0.100	0.176
3	*	*	-0.085	-0.090	-0.150	-0.144
4	-0.368	0.415	0.050	-0.100	0.220	0.133
5	-0.467	0.178	-0.240	0.204	-0.095	0.116
6	0.117	-0.103	0.026	0.176	-0.009	0.015
7	*	-0.030	0.084	0.295	-0.125	0.225
8	-0.144	0.100	-0.059	-0.188	*	-0.104
9	-0.018	-0.120	-0.101	0.005	-0.007	0.008
10	*	-0.170	-0.095	0.067	-0.010	0.041
Mean	-0.119	0.014	-0.036	0.063	0.016	0.069

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XLII

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN TWELVE-WEEK WEIGHT AND PERCENTAGE FERTILITY BY GENERATION IN THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	0.467	-0.212	0.009	0.673	*	0.011
1	0.101	0.067	-0.017	0.291	-0.125	0.047
2	*	0.612	0.291	0.412	-0.621	0.197
3	-1.732	0.421	0.007	*	-0.314	0.742
4	-0.019	0.031	-0.119	1.111	0.217	0.148
5	*	0.049	-0.222	0.348	-0.020	0.035
6	-1.145	0.130	-0.003	-0.443	-0.243	-0.300
7	0.371	-0.126	0.044	0.341	*	-0.198
8	0.671	*	0.099	1.332	0.097	0.125
9	1.366	-0.215	0.824	0.782	0.167	0.052
10	-0.540	0.217	0.155	-0.629	0.299	0.020
Mean	-0.051	0.097	0.115	0.422	-0.060	0.080

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XLIII

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN SIX-WEEK BODY WEIGHT AND PERCENTAGE FERTILITY BY GENERATION IN THE RELAXED-SELECTED FEMALE PROGENY

		RSH(1)			RSL(2)	
Gen.	r_g (3)	r_e	r_p	r_g	r_e	r_p
0	0.012	-0.015	0.008	0.191	*	0.022
1	-0.265	0.112	0.109	*	-0.191	0.078
2	*	-0.111	0.091	-1.421	0.127	0.063
3	0.195	-0.073	0.009	0.207	-0.017	0.089
4	0.185	-0.050	0.072	0.184	-0.127	0.007
5	0.638	-0.089	-0.367	0.017	0.617	0.092
6	0.395	0.021	0.056	-0.161	-0.045	0.002
7	0.084	-0.271	-0.074	*	*	0.067
8	0.333	*	-0.734	0.735	0.263	-0.172
9	-0.985	-0.033	-0.084	0.278	-0.167	0.099
10	-0.097	0.250	-0.171	-0.208	0.044	-0.086
Mean	0.129	-0.030	-0.044	-0.020	0.050	0.022

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

each line. Both lines indicate a low positive phenotypic correlation between twelve-week body weight and percentage fertility. The relationship between six-week body weight and fertility indicated a negative relationship. Both lines indicated an extremely low phenotypic correlation.

The estimates of the genetic, environmental, and phenotypic correlations between body weight at the two different ages and percentage hatch of fertile eggs are given in Table XLIV and Table XLV. All of these estimates were relatively consistent from generation to generation, and the overall mean indicates very little relationship between these traits in this study.

During this study mortality records were also maintained during the growth period from hatch to twelve weeks of age. The percentage mortality for each line is given in Table XLVI. Although a slight increase was observed in the relaxed-selected high line during the first three generations, the mortality in the two lines remained almost unchanged during this study.

From the response exhibited by most of the traits studied, it may be concluded that the relaxed-selected high line remained almost unchanged during this study. If the intra-sire regression analysis is considered as the best estimate of the additive genetic variance, it may be concluded that the genetic variation remained relatively constant for most of these traits. Therefore, it may be concluded that the response observed, especially in six and twelve-week body weight, was primarily due to environmental influences during this study. When the relaxed-selected high line was used as a control population for the high line described in Phase I of this thesis,

TABLE XLIV

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN TWELVE-WEEK WEIGHT AND PERCENTAGE HATCH OF FERTILE EGGS BY GENERATION IN THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	r_g(3)	r_e	r_p	r_g	r_e	r_p
0	*	-0.011	0.003	-0.341	-0.005	-0.018
1	-0.012	0.075	0.022	0.100	-0.041	0.012
2	-0.221	0.106	0.073	0.103	-0.106	0.041
3	-0.380	*	0.001	*	-0.111	0.211
4	-0.002	0.050	-0.012	0.124	*	0.030
5	*	0.009	-0.004	0.070	-0.004	0.007
6	0.035	-0.001	0.004	0.239	-0.031	0.074
7	0.078	0.085	0.004	0.040	-0.030	-0.025
8	0.037	-0.013	0.012	0.070	0.010	0.013
9	-0.273	0.042	0.007	-0.341	0.082	-0.021
10	*	0.109	0.018	*	*	0.011
Mean	-0.092	0.045	0.012	0.007	-0.026	0.031

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XLV

ESTIMATES OF GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS BETWEEN SIX-WEEK BODY WEIGHT AND PERCENTAGE HATCH OF FERTILE EGGS BY GENERATION IN THE RELAXED-SELECTED FEMALE PROGENY

	RSH(1)			RSL(2)		
Gen.	$r_g^{(3)}$	r_e	r_p	r_g	r_e	r_p
0	*	-0.009	0.010	0.100	*	0.012
1	-0.132	0.060	0.052	*	-0.021	0.008
2	0.013	-0.066	0.033	-0.203	0.018	0.009
3	0.032	*	0.001	0.034	-0.003	0.013
4	0.044	-0.010	0.032	0.111	*	0.132
5	-0.016	0.001	-0.037	0.117	0.302	0.100
6	0.035	-0.002	0.001	-0.016	0.001	0.015
7	0.090	0.108	-0.006	*	0.211	-0.114
8	-0.267	0.211	0.004	0.411	0.147	0.049
9	-0.011	0.030	-0.013	0.107	-0.006	0.003
10	*	0.125	-0.036	*	*	0.039
Mean	-0.024	0.045	0.004	0.083	0.081	0.024

1 - Relaxed-selected high line.
2 - Relaxed-selected low line.
3 - Genetic correlation estimated from dam component of variance.
* - Negative estimate of variance component interfered with estimation.

TABLE XLVI

PERCENTAGE MORTALITY TO TWELVE-WEEKS OF AGE FOR THE RELAXED-SELECTED HIGH AND RELAXED-SELECTED LOW LINES BY GENERATION

Gen.	RSH(1)	RSL(1)
0	7.2	7.6
1	9.3	8.3
2	10.0	7.9
3	11.6	6.7
4	8.0	4.7
5	5.7	5.3
6	5.2	7.1
7	4.5	4.9
8	6.9	8.3
9	8.5	7.7
10	6.9	7.2

1 - Percentages are corrected for mortality due to accidental death or loss.

some changes were noted in the response to selection. The regression analysis of the mean twelve-week body weight during the last ten generations of the divergent selection experiment was 0.215±0.0224 pound per generation in the high line. The regression analysis of the difference obtained between the relaxed-selected high line and the high line twelve-week body weight means was 0.187±0.020 pound per generation. The difference between these regression coefficients was not significant. The realized heritability during the latter ten generations of high line selection was 43.7±4.2 percent. This compares to 37.3±8.5 percent for the adjusted response. The twelve-week body weight response was 0.175±0.017 pound per generation during this period of high line selection for the female progeny. The adjusted response was 0.156±0.020 pound per generation. The difference between the two estimates was not significant. The realized heritability for the unadjusted means was 36.3±3.3 percent, which compares to the adjusted estimate of 31.2±4.6 percent.

The only trait which indicated a significant difference between the adjusted and unadjusted response was March egg weight. The unadjusted response was 0.022±0.035 gram per generation, whereas the adjusted response was 0.293±0.078 gram per generation. These coefficients were significantly different at the one percent level of probability. The response noted for March egg weight in the relaxed-selected high line exhibited a fluctuating decrease during the first four generations, and then stabilized during the last six generations. From this it may be concluded that the genetic stability is questionable during the period when the decline was noted and the adjustment of the high line mean may not be justified.

Summary

A relaxed-selection breeding program was initiated in each of the two groups of parents which had previously been selected for divergent body weight at twelve weeks of age for five generations. Each of the subsequent generations consisted of offspring produced by mass mating of the randomly selected parents within each of these lines. The line derived from the population being selected for high twelve-week body weight was called the relaxed-selected high line, and the line derived from the population being selected for low twelve-week body weight was called the relaxed-selected low line.

The data presented in this study were obtained over a period of ten generations and from a total of 420 sires, 3250 dams and 10,000 offspring. From these data estimates were obtained for the heritability of each trait and estimates of the genetic, environmental and phenotypic correlations among these traits were also calculated. Two methods were used to estimate heritability, a modified analysis of variance procedure outlined by Fairars et al. (1962) and the intra-sire regression method suggested by Falconer (1960).

Apparently little natural selection occurred in six and twelve-week body weight in this study, when this type of selection was measured as the difference obtained between the intended selection and the actual weighted selection attained for these traits.

The response noted in these lines indicated that the relaxed-selected low line returned toward the unselected original population mean for twelve-week body weight. The response also suggested that improvement in environmental conditions may have been a factor in

this study. Similar results were also obtained in six-week body weight. The rate of change in the relaxed-selected high line was 0.03±0.02 pound per generation for the male offspring twelve-week body weight and 0.01±0.02 pound per generation for six-week body weight. The response observed for the female offspring in this line was slightly lower than the response noted in the male offspring. The responses were 0.11±0.6 pound and 0.06±0.01 pound per generation in relaxed-selected low line males for twelve and six-week body weight, respectively. The respective responses exhibited by the females in the relaxed-selected low line were 0.08±0.01 pound per generation and 0.05±0.01 pound per generation.

The response observed in percentage fertility and age at sexual maturity indicated an increase over generations in both of the lines. A negative response was exhibited in both of the lines for percentage egg production. The relaxed-selected high line decreased in average egg weight at the rate of 0.28±0.08 gram per generation and 0.84±0.5 percent per generation in percentage hatch of fertile eggs. These traits were observed to increase in the relaxed-selected low line.

The estimates of heritability of twelve-week weight ranged from 19.6 to 139.0 percent in the two lines when estimated by the analysis of variance method. The average estimate for male offspring was 65.0 percent and 56.0 percent in the female offspring. The average estimate for six-week body weight using this method was 53.0 percent in the males and 37.0 percent in the females. The intra-sire regression heritability estimates were all lower than the estimates obtained by the analysis of variance method. The average heritability estimate for twelve-week body weight was 34.0 percent in the males and 26.0 percent in the females in the two lines. The average estimate for six-week body weight was 26.5

percent and 24.0 percent for the male and female offspring, respectively.

In this study the analysis of variance method which was utilized overestimated the heritability for percentage fertility, percentage hatch of fertile eggs, percentage egg production, March egg weight and age at sexual maturity as compared to estimates by the intra-sire regression method. The average intra-sire regression estimate in the two lines was 5.5 percent for percentage fertility, 9.4 percent for percentage hatch of fertile eggs, 19.0 percent for percentage egg production, 25.0 percent for March egg weight, and 18.5 percent for age at sexual maturity.

Based on the dam components of variance and covariance, the genetic correlation between six-week body weight and twelve-week body weight ranged from -0.580 to 1.711 in the male progeny and from 1.200 to 1.730 in the female progeny. The mean genetic correlation was 0.615 in the males and 0.547 in the females. The average environmental correlation was about 0.450 for both sexes and 0.460 in the two sexes for the phenotypic correlation.

The average estimates of the genetic, environmental and phenotypic correlations between juvenile body weight and percentage egg production were -0.364, -0.010 and -0.092, respectively. The average estimates of genetic, environmental and phenotypic correlation between juvenile body weight and egg weight in the two lines were 0.075, 0.100 and 0.101, respectively. The mean values of the estimates obtained from the two relaxed-selected lines for the genetic, environmental and phenotypic correlation between juvenile body weight and age at sexual maturity were 0.033, -0.059 and -0.009, respectively. The relaxed-selected low line indicated a high positive genetic correlation of 0.422 between twelve-week body weight and percentage fertility in this study. All other correlation coefficients calculated between juvenile body weight and hatchability were near zero.

A positive genetic correlation between egg production and egg weight was found in both the relaxed-selected high line and the relaxed-selected low line. The average phenotypic correlation between these traits for the two lines was 0.080. A small negative genetic relationship between egg production and age at sexual maturity was indicated in both of the lines studied. This was also observed in the estimates obtained between egg weight and sexual maturity.

The utilization of the relaxed-selected high line as a control for the divergent selected high line resulted in a decrease in the estimated rate of response during the last ten generations of selection for high twelve-week body weight. This reduction was considered as non-significant. The realized heritability was also reduced non-significantly. The adjusted response was 0.187±0.02 pound per generation in the high line males and 0.156±0.02 pound per generation in the high line females.

Phase III. The Effects of Reciprocal Crosses Between Two Lines Selected for High and Low Body Weight on Several Traits

Since the number of individuals utilized as parent stock is relatively small in many selection experiments, the consequence of inbreeding must be considered. The most striking consequence of inbreeding is the reduction of the mean phenotypic value shown by characteristics related to reproductive capacity or physiological efficiency. Some examples of depression due to inbreeding have been presented in the literature review for Phase I. From the results of these studies the generalization can be made that inbreeding tends to reduce fitness when selection is directed toward some trait other than those closely related to fitness.

Contrary to the phenomenon of inbreeding depression is its opposite, "hybrid vigor" or heterosis. When inbred lines are crossed, the progeny often show an increase in those characters that previously suffered a reduction from inbreeding. This was demonstrated by Roberts, 1960. The progeny produced from a reciprocal cross mating system with parents from two divergent lines, such as those developed in Phase I of this study, may exhibit a heterotic effect in some of the traits related to fitness. This mating system would also permit the estimation of the effects due to sex linkage and maternal influences.

The objective of this study was to determine if heterosis would be observable in the progeny produced from reciprocal crosses between two divergent lines. Further objectives were to estimate the heritability, sex-linkage effects and maternal effects associated with juvenile body weight and other traits of economic importance.

Review of Literature

Recent investigations by a number of geneticists are reviving the early theory of heterosis expounded in principle by Shull (1908, 1911) and East (1908). They explained heterosis largely on the basis of heterozygosity *per se* in contrast to the more widely accepted hypothesis of linked dominant factors initiated by Jones (1917). On the basis of regression analysis of yield data in corn, Hull (1946) concluded that overdominance, (the heterozygote, *Aa* being superior to either homozygote, *AA* or *aa*) must play a role in heterosis. Analysis of corn data by Robinson *et al*. (1948) tend to support this conclusion. From theoretical calculations, Crow (1948) concluded that a heterosis value higher than five percent above the random bred population cannot be explained on the basis of dominant factors alone. The author suggested that heterosis of this nature was due to epistasis or overdominance.

A number of examples of overdominance have been reported. Almost seventy five years ago, Cushman (1892) reported that first-generation hybrids of two different breeds of chickens were hardy and easy to raise. Another early study by Pearl and Surface (1910) showed improved hatchability of hybrid eggs. Although the term "hybrid" today is usually used to indicate a cross between inbred lines, it is also used to designate a cross between breeds or species.

The more modern work dealing with the subject of crossbreeding in poultry dates back to Warren (1927, 1930). The author found that crosses between Single Comb White Leghorns and Jersey Black Giants were superior in performance when compared with the purebred parental breeds. A number of experiments in poultry comparing crossbreds and purebreds have been reported in the literature. This literature has been reviewed in detail by King and Bruckner (1952) and by Glazener *et al.* (1952). There is general agreement that crossbreeding results in improved growth rate. The reported studies on the effects of crossbreeding did not consistently improve hatchability and chick viability. The evidence to date is less convincing that crossbreeding improves egg production and adult viability, although the recent reports cited above indicated that egg production was favorably influenced by crossbreeding.

King and Bruckner (1952) found a highly significant increase in egg production from a cross between Rhode Island Reds and Barred Plymouth Rocks when compared with the parental strains. The crossbreds reached sexual maturity earlier and effects of sex-linkage were noted in egg production. Glazener *et al.* (1952) compared several crosses involving White Leghorns, Barred Plymouth Rocks, Rhode Island Reds and New Hampshires over a period of two years. Three-fourths of these crosses were equal to or superior to their respective purebreds in age at sexual maturity and in egg production.

Dickerson *et al.* (1950) compared intra-strain matings with inter-flock matings of the same breed. The inter-flock matings produced progeny with consistently better adult viability and egg production. The authors suggested that a considerable part of the superiority of the inter-flock mating might be due to the recovery of the initial loss due to inbreeding. A comparison of an inter-strain cross of Leghorns with two slightly inbred parental strains was reported by Hutt and Cole (1952). The strain cross was superior in hatchability, sexual maturity, rate of lay and body weight, but not in viability. These results led the authors to conclude "that enough heterosis may be obtainable by crossing strains, not much inbred, to make unnecessary the development of highly inbred strains for crossing, with all the attendant risks and losses".

Moultrie et al. (1952) compared an inter-strain cross of Leghorns with the parental strains with respect to viability. The two strains used differed in adult mortality. The authors reported that strain crosses showed consistent heterosis for adult viability in three successive years when the female parent was the high-viability strain.

Hybrid vigor was consistently observed in growth of chickens to eight weeks of age in a study conducted by Nordskog and Ghostley (1954). It was further noted in the experiment that heterosis for livability occurs early in the life of the chick but tends to disappear as the chick approaches maturity. The authors also reported that the results favored the strain crosses over the pure strains for total egg production. According to Yao (1958) single incrossbreds were found to be superior to four-way incrossbreds and the randombreds in egg production and rate of egg production. The four-way incrossbreds had larger egg size and higher fertility and hatchability than single incrossbreds in this study. The author also reported that the single incrossbreds had the largest genetic variabilities in all of the traits measured. Similar results were found in a study reported by Kan et al. (1959). In this study a diallel analysis was used which indicated that non-additive gene effects contributed to the variation in shank length, keel length, body depth and possibly gain in weight but were found to have little or no effect on body weight at nine weeks of age.

Goto and Nordskog (1959) investigated the effects due to general combining ability, specific combining ability, maternal effects and reciprocal effects for inbred line crosses. In this study most of the sire-lines and dam-lines showed statistically significant differences. Important maternal effects and reciprocal cross mating effects were estimated for percentage hatch of all eggs set. Reciprocal cross effects were found to be important for percentage laying house mortality.

Most of the information obtained from crossing two divergent selected lines has been reported in experiments using laboratory animals. In most of these studies heterosis was observed in the F_1 generation but tended to decline in the F_2 generation (Falconer, 1955) and(Robertson, 1955). Robertson and Reeve (1952) and Reeve and Robertson (1953) suggested that this type of result may be due to the greater resistance to environmental variation in the more heterozygous types. Improvement in most of the traits related to fitness was reported by Falconer (1955) when reciprocal crosses were made between the lines of mice derived from a two-way selection experiment.

Experimental Procedure

During the tenth generation of the divergent selection experiment reported in Phase I, reciprocal cross matings were made between the two divergent lines. One line, the high line, had been selected for high body weight at twelve weeks of age and the other line, the low line, was developed by selection for low twelve-week body weight. The reciprocal crosses were made from the tenth generation selected parents after the eleventh generation of high and low line offspring were produced.

The reciprocal mating system consisted of two matings. The L x H mating was accomplished by mating the selected low line male parent with the selected high line female parent. The second mating, H x L, was initiated by mating the selected high line males with the selected low line females. The assignment of the various males to the opposite line females was done randomly, and individual male mating pens were utilized. Each male was mated to ten females. A two-week interval was allowed to elapse after the matings were assigned in order to insure proper parentage of the offspring. Two hatches were produced from eggs pedigreed by pen and dam. The eggs were gathered twice daily, stored at 55 degrees Fahrenheit and set at two-week intervals. The progeny from each of the crosses were brooded together within hatches. The two hatches were brooded in adjacent pens in the same house.

The traits recorded in this study were measured in the manner outlined in the general experimental procedure section of this thesis. In order to check fertility, hatch of fertile eggs and rate of egg production, the progeny of each cross were randomly selected at twelve weeks of age. The selected male and female offspring were randomly assigned to breeding pens after they reached sexual maturity. The integrity of the crosses was thus maintained.

Estimates of maternal effects, effects due to sex-linkage and heritability were calculated by an analysis of variance as outlined in Appendix C of this thesis. A "t" test analysis was used to test the effects due to the reciprocal crossing of the two lines. In addition, an intra-sire regression analysis was used to estimate the heritability of March egg weight and age at sexual maturity.

Results and Discussion

The data presented in this section were obtained from 18 sires, 86 dams and 312 progeny. Insufficient fertility was obtained from the

H x L mating and only 90 progeny were produced. The low fertility may have been due to the difference in body size between the high line males and the low line females. Due to low numbers of individuals, the results presented may not represent the true genetic responses which might have been obtained if the number of offspring had been adequate.

The results of the reciprocal cross mating are given in Table XLVII for each type of mating and for each sex with respect to six and twelve-week body weight. The unweighted mean for the parents used in the H x L mating was 1.45 pounds for six-week body weight and 3.37 pounds at twelve weeks of age. These values compared to the offspring body weight mean of 1.58 pounds at six weeks of age and 3.29 pounds at twelve weeks of age. The mean, when both sexes were considered as one group, was superior to the expected intermediate weight of the parents for six-week body weight. The unweighted mean for the parents used in the L x H mating was 1.37 pounds and 3.35 pounds for six and twelve-week weights, respectively. This compares to the combined mean of 1.53 pounds for six-week weight and 3.37 pounds for twelve-week weight observed in the offspring produced. These data indicated that the six-week body weight mean, when the sexes were combined, was greater than the combined mean of the parents. In a comparison of the offspring from the two matings, it was noted that the male six-week body weight of the progeny produced from the H x L mating was significantly higher than that observed in the male progeny produced from the L x H mating. The differences observed in the female progeny of the matings were not significant either in six-week body weight or in twelve-week body weight. The mean twelve-week weight exhibited by the L x H male progeny was significantly different

TABLE XLVII

AVERAGE SIX- AND TWELVE-WEEK BODY WEIGHT FOR THE SELECTED PARENTS AND THE PROGENY PRODUCED FROM RECIPROCAL MATINGS BETWEEN THE HIGH AND LOW LINES

	Six-week weight		Twelve-week weight	
	Male	Female	Male	Female
Mating (H x L)(1)				
Parents	2.23	0.67	5.24	1.50
Progeny	1.85	1.31	3.76	2.82
Mating (L x H)(2)				
Parents	0.88	1.85	2.04	4.65
Progeny	1.68	1.38	3.89	2.84

1 - High line males mated to low line females.
2 - Low line males mated to high line females.

than the mean weight of the H x L male offspring.

These results compare favorably with those reported by Brunson (1955) in making reciprocal crosses between New Hampshire and Silver Oklabar chickens. Brunson (1955), however, reported that the female offspring as well as the male offspring were superior when the smaller Silver Oklabar male was mated to the New Hampshire female.

In considering the response noted for percentage fertility (Table XLVIII), both sets of progeny indicated mean values greater than either of the female parents. Although the percentage fertility measured in the offspring from the L x H mating was higher than that measured in the offspring produced from the H x L matings, this difference was not significant. The mean percentage hatch of fertile eggs for each group of progeny was not significantly different. The average percentage egg production for both groups of progeny was below the mid-point average of 36.0 percent for the two female lines. Similar results were obtained in March egg weight and in age at sexual maturity.

The heritability estimates for the various traits measured are given in Table XLIX. Estimates of heritability for six-week body weight ranged from 0.04 to 1.23. It is impossible to have a true estimate that exceeds unity, and it is unlikely that estimates as low as 0.04 are correct. The necessary use of small samples would lead to sampling errors that might explain this wide range. Since the sire and dam components of variance have to be multiplied by four to calculate heritability estimates, it can readily be seen that any error, whether sampling or otherwise, will also be multiplied by four. The range of heritability estimates for twelve-week body weight was from 0.28 to 0.78. The overall average estimate for six-week body weight was 53.0 percent in the males

TABLE XLVIII

ESTIMATED MEANS OF TRAITS MEASURING THE LAYING HOUSE PERFORMANCE OF THE RECIPROCAL CROSS FEMALE PARENTS AND PROGENY

	Traits				
	% F.(1)	% H of F(2)	% Egg Pd.(3)	Egg wt.(4)	S.M.(5)
Mating (H x L)(6)					
Parents	79.6	77.0	31.8	48.4	218.6
Progeny	83.7	75.1	33.0	50.3	180.7
Mating (L x H)					
Parents	81.4	76.2	40.2	58.6	154.6
Progeny	85.7	76.7	32.8	50.1	188.1

1 - Percentage fertility.
2 - Percentage hatch of fertile eggs.
3 - Percentage egg production.
4 - Egg weight in grams.
5 - Sexual maturity in days.
6 - Means given for female parents only.

TABLE XLIX

GENETIC PARAMETERS ESTIMATED FOR THE TRAITS OBSERVED IN THE PROGENY PRODUCED FROM THE RECIPROCAL CROSSES BETWEEN THE HIGH AND LOW LINES

	Traits								
	6-week wt.		12-week wt.						
Parameter(1)	Male	Female	Male	Female	% F(2)	% H of F(3)	% Eg.Pd.(4)	Eg.Wt.(5)	S.M.(6)
				H x L Progeny					
Heritability									
(Sire)	0.78	0.65	0.42	0.33	0.070	0.110	0.08	0.950	0.021
(Dam)	0.30	0.42	0.43	0.50	0.04	0.120	0.13	0.800	0
(Comb)	0.54	0.53	0.42	0.41	0.05	0.114	0.08	0.936	0
Sex-linkage	0.119	0.057	0.209	0	0.008	0	0	0.038	0
Maternal	0	0	0	0.042	0	0.005	0.013	0	0
				L x H Progeny					
Heritability									
(Sire)	1.00	1.23	0.23	0.29	0.051	0.09	0.25	0.47	1.13
(Dam)	0.04	0.29	0.78	0.28	0.019	0.07	0.09	0.03	1.78
(Comb)	0.52	0.76	0.51	0.29	0.037	0.07	0.13	0.25	1.46
Sex-linkage	0.241	0.235	0	0.002	0.008	0.005	0.04	0.11	0
Maternal	0	0	0.139	0	0	0	0	0	0.160

1 - If estimate resulted in a negative value, then it was considered as zero.
2 - Percentage fertility.
3 - Percentage hatch of fertile eggs.
4 - Percentage egg production.
5 - Egg weight in grams.
6 - Sexual maturity in days.

and 64.6 percent in the females. The overall average estimate for twelve-week body weight was 46.5 percent and 35.0 percent for the males and females, respectively.

Sex-linked gene effects on body weight, estimated by subtracting the dam component of variance from the sire component of variance, ranged from 0.0 to 0.24. These estimates are given in Table XLIX. The mean sex-linked gene effect in six-week body weight was 0.16. It was noted that the estimates for sex-linkage were consistently higher in body weight at six weeks of age than at twelve weeks of age. For six-week body weight, the estimate calculated for the sire component of variance was higher in most cases than that calculated for the dam component, which would account for the higher estimate of sex-linkage effects in this trait. Estimates of maternal effects on body weight were near zero in all cases except in the analysis of the twelve-week body weight in the male progeny produced from the L x H mating. The analysis of these data seems to indicate that sex-linkage effects may have had an important influence on body weight at six weeks of age. The observed means of the reciprocal crosses, however, did not indicate this (Table XLVII).

The heritability estimates obtained from the two cross mating types for percentage fertility ranged from 0.02 to 0.07, with a mean of 0.05. The heritability estimated from the two different sets of progeny was similar. These values are given in Table XLIX. Only a slight sex-linkage effect was estimated for this trait. The average heritability estimate for percentage hatch of fertile eggs was about 11.0 percent in the offspring produced from the H x L mating. This value was 4.0 percent higher than the average of 7.0 percent obtained from the L x H progeny.

While the estimates for heritability of percentage fertility were well within the range of the reported estimates for this trait, the estimates obtained for percentage egg production were comparatively low. The estimates obtained in this study for percentage egg production ranged from 0.08 t0 0.25 (Table XLIX). The overall average was about 11.0 percent. The average estimate of those reported in the literature was about 27.0 percent.

The heritability estimates obtained for percentage egg production in the H x L progeny were 0.08 for the sire component, 0.13 for the dam component and 0.08 for the combined components. The estimates calculated from the L x H progeny were consistently higher than those obtained from the H x L progeny. These estimates were 0.25, 0.09, and 0.13 for the sire, dam and combined components, respectively. The overall estimate of percentage egg production was 13.0 percent. Most of these estimates are below the average estimate reported in the literature review.

The estimates of the heritability of egg weight were noticeably different in comparing the two offspring groups. The combined estimate in the H x L progeny was 0.94 as compared to 0.25 in the L x H progeny. The highest reported estimate in the review of literature was 1.15, calculated from the sire component in a study conducted by Hogsett and Nordskog (1958), while the average reported estimate was about 0.58. By using an intra-sire regression analysis, the heritability of this trait was estimated to be 0.413±0.036 when all progeny were combined.

Since negative estimates of variance were noted in the analysis of sexual maturity data collected from the H x L progeny, and noticeably high and unrealistic values were obtained in the L x H progeny, a combined heritability estimate was made. The heritability estimates were

0.72 for the sire component, 0.65 for the dam component and 0.68 for the combined estimate from the sire and dam. The intra-sire regression estimates were 0.08±0.163 in the H x L progeny, 0.13±0.274 in the L x H progeny and 0.08±0.062 when all progeny were combined.

Summary

The data obtained from reciprocal crosses of two lines of Silver Oklabar chickens of divergent body weight were used to determine if heterosis was expressed in some of the traits measured in the progeny produced. Heritability estimates were obtained by using an analysis of variance and an intra-sire regression method. The data represented 18 sires, 86 dams and 312 offspring.

A slight heterotic effect was observed in the offspring mean body weight at six weeks of age in both sexes, since these values were above the intermediate value calculated from the parental means. The male progeny exhibited a heterotic effect in the mean twelve-week body weight. The mean twelve-week body weight in the female progeny was similar to the expected intermediate value of the parents.

The average heritability obtained as an unweighted mean of all estimates calculated for twelve-week body weight was 46.5 percent in the male offspring and 35.0 percent in the female offspring. The overall unweighted mean heritability estimated for six-week body weight was 53.0 percent and 64.6 percent in the male and female progeny, respectively.

Percentage fertility was the only other trait in this study to exhibit heterosis. The overall mean percentage fertility in the progeny was 84.7 percent, which compared to the parental mean of 80.5 percent. The overall unweighted average estimate of the heritability for

percentage fertility was 5.0 percent, and for percentage hatch of fertile eggs the estimate was 11.0 percent. The overall mean heritability estimate for percentage egg production was 13.0 percent. The estimates of the heritability of March egg weight and age at sexual maturity exhibited a high degree of variation when estimated by the analysis of variance method. The heritability estimated from the intra-sire regression method was 41.3 percent for egg weight and 7.6 percent for age at sexual maturity.

Phase IV. The Effects of Incomplete Negative Assortive Mating on Juvenile Body Weight and Traits Related to Fitness

In breeding programs where selection is directed toward a single trait or toward several traits which are not directly related to reproductive fitness, the selection may result in a decrease in performance for the traits related to fitness. This type of phenomenon has been observed in several selection experiments reported in the literature. If this decrease occurs in a commercial breeding program, the breeder often introduces new stock into the population. This usually results in a decrease in the performance for the trait originally selected for; however, the reproductivity of the population may be increased.

Several types of theoretical breeding systems have been derived to enable the breeder to overcome this phenomenon to some degree. One of these systems is the utilization of a negative assortive mating system where the extreme phenotypes for the traits are mated together. This should bring about the production of intermediate individuals and would tend to hold the population at the intermediate level. This type of system would be beneficial only if a sufficient amount of variation for the trait exists in the population.

During the twelfth generation of selection for divergent body weight, presented in Phase I of this thesis, a reverse selection procedure was initiated. In comparing the reverse-selected high line parents with the divergent-selected high line parents, it was noted that these groups differed significantly in percentage egg production, but not in body weight at twelve weeks of age. Based on these observations, a breeding program was initiated to determine the effects of negative assortive mating on juvenile body weight, March egg weight, age at sexual maturity, percentage egg production and the reproductive performance in the resulting progeny.

Review of Literature

The mating of unlike individuals (negative assortive mating on the basis of phenotypic resemblance) is most commonly practiced either to hold the population at a particular level of performance or in a situation where the "ideal individual" is an intermediate. As pointed out by Lush (1945), this system can also be used to correct defects by mating each animal to one which is equally extreme but in the opposite direction.

The theoretical consequences of negative assortive mating were first described by Wright (1921). The author suggested that very little increase in heterozygosity would result if the entire population was utilized. The author stated that if only one pair of genes were involved, the maximum increase in heterozygosis would be one-third. If two pairs of genes were considered, then the increase would be only one-eleventh. The author based these calculations on the assumption that the correlation between full sibs was equal to minus one.

The mating of "unlikes" may also reduce the correlation between parent and offspring, since the two parents are quite different from each other. As pointed out by Wright (1921, 1931), this would also be due to the effects of the genes which an offspring inherits from one parent tending to be canceled by the effect of the gene inherited from the other parent.

The references cited above and the work reported by Li (1955) indicate that this mating system will result in a more uniform population than that resulting from random mating. This would be essentially accomplished in the first generation. Very little further reduction in the variation would be observed in succeeding generations. Li (1955) also suggested that the reduction in the variation would not be fixed, since the population would return to the original variability as soon as this mating system was abandoned.

All of these references deal with the population as an entire group. It would seem that if only the extreme individuals were utilized in the mating system, then a greater amount of uniformity should result. Further, if traits not being considered for mating are controlled by a large number of genes, then the distribution of these genes may be changed with respect to individuals being produced from such matings. This would occur only if the genes for the trait being used as the basis of negative assortive mating are not linked with the other traits.

Experimental Procedure

The data presented in this experiment were collected from individuals produced from an incomplete negative assortive mating system. This system was initiated in the twelfth generation of the experiment conducted to study the effects of divergent selection for body weight at twelve weeks of age, reported in Phase I.

From the twelfth generation high line progeny, two groups were selected. One group consisted of the individual birds having body weights at twelve weeks of age in the upper seventeen percent of the population. These were the regular selected high line parents for the thirteenth generation high line progeny. The other group consisted of the individuals in the lower seventeen percent of the high line offspring population with respect to twelve-week weight.

After the selected birds reached maturity, reciprocal crosses were made between these two groups. The selected high line males were mated to the reverse selected high line females and the reverse selected high line males were mated to the selected high line females. Individual mating pens were utilized and the breeders were assigned randomly to these pens insofar as possible. All other management practices were followed as outlined in the section entitled, General Experimental Procedures. From the progeny produced from these matings, all of the females and a random sample of the males were selected as breeders.

The first generation progeny were separated at maturity into four groups of individuals on the basis of sex and parental mating type. These four groups were divided in half and randomly assigned to individual male mating pens. The assignment of the parental stock resulted in each mating pen having one male and ten females. The progeny designated as the second generation were derived from four different mating combinations based on the parental cross and sex of the first generation offspring. The individuals used as parents for the next generation were randomly selected at twelve weeks of age. A completely random mating system was used to produce the third generation offspring. A schematic representation of the mating regime used to produce each generation is given in Appendix D.

Records were kept on body weight at six and twelve weeks of age, percentage egg production, percentage fertility, percentage hatch of fertile eggs, March egg weight, and age at sexual maturity on all parents and offspring. These traits were measured in the same manner as previously described in the general experimental procedures section of this thesis.

The estimated heritability for the various traits measured in this experiment were obtained from two different methods. A hierarchical analysis with unequal numbers in the sub-class, as outlined by Snedecor (1959), was used to determine the heritability component for the sire and dam contribution to the variation measured. A detailed description of this analysis is given in Appendix C. An intra-sire regression analysis was also used. This procedure is outlined in Appendix A.

Results and Discussion

The average body weight at six and twelve weeks of age for the selected parents is given in Table L. Tha analysis of the body weights obtained were not significantly different when the two groups of parents were compared within each sex. The twelfth generation high line progeny from which these individuals were selected had an average body weight at six weeks of age of 2.05 pounds for the males and 1.66 pounds for the females. The coefficient of variation for six-week body weight was 11.2 percent and 9.6 percent for the males and females, respectively. The average twelve-week body weight was 5.35 pounds in the males and 4.13 pounds in the females. The related coefficients of variation for these two means were 10.1 percent and 9.6 percent for the males and females, respectively.

The results obtained in each of the offspring generations are also given in Table L. These values indicate that six-week body weight was increased above the value observed for either parent in both sexes in the first generation. The data indicated that a decrease in variation occurred during the three generations of this study. The theoretical

TABLE L

MEAN BODY WEIGHTS OF SELECTED PARENTS IN THE INCOMPLETE NEGATIVE ASSORTIVE MATING SYSTEM AND SUBSEQUENT RESPONSE OF PROGENY BY SEX BY GENERATION

	6-week wt.				12-week wt.			
	Male		Female		Male		Female	
Selected Parents								
SH(1)	2.00		1.68		5.41		4.19	
NSH(2)	1.89		1.61		5.32		4.09	
Average	1.95		1.65		5.37		4.14	
INAM Progeny(3)								
Gen.	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s
1	2.12	0.26	1.81	0.28	5.36	0.35	4.20	0.30
2	2.17	0.25	1.84	0.26	5.37	0.38	4.30	0.39
3	2.16	0.21	1.81	0.19	5.49	0.28	4.19	0.37

1 - Parents selected from the upper 17 percent of the 12th generation high line progeny at 12 weeks of age.
2 - Parents selected from the lower 17 percent of the 12th generation high line progeny at 12 weeks of age.
3 - Progeny produced from the incomplete negative assortive mating system.

response calculated by both Wright (1921) and Li (1955) indicated that the variation should increase as the pressure of negative assortive selection was reduced. These authors further suggested that the overall mean would remain at about the same level as that of the original population. The results obtained in this study with respect to six-week body weight may be due to a very low degree of segregation for these genes in the offspring. In addition, this type of mating may have increased the epistatic or interaction effect between genes that control six and twelve-week body weight.

The male offspring produced in the first and second generations were not significantly different from the intermediate value for twelve-week body weight estimated from the parents. The third generation twelve-week body weight mean was significantly higher than the second generation mean in the male offspring. The female offspring remained at about the same level as that of the high line female parental weight at twelve weeks of age in the first generation. The mean twelve-week body weight observed in the second generation females was significantly higher than that of the twelfth generation high line female progeny.

The coefficient of variation for twelve-week body weight observed in the first generation male progeny, produced from the incomplete negative assortive mating, increased above the value obtained for the twelfth generation high line males. The coefficients in the second and third generations decreased at the rate of about 1.5 percent per generation. The variation was greatly increased in the first generation female progeny. The coefficient of variation for the first generation of progeny was 15.4 percent compared to the twelfth generation high line female coefficient of 9.6 percent. The variation observed in the female offspring produced from the incomplete negative assortive mating system increased from 7.0 percent in the first generation to 9.0 percent in the third generation. The coefficient of variation calculated for the male offspring for this mating system remained at about the same level during the three generation reported.

The heritabilities estimated for six and twelve-week body weight from the two methods used in this study are presented in Table LI for each generation and for each sex. The heritability of six-week body weight was increased in both sexes during this study. These estimates were calculated from the sire and from the dam component of the analysis of variance. The heritabilities estimated from the intra-sire regression method for this trait did not indicate this increase. The increase noted in the estimates calculated from the components analysis may have been due to an increase in the covariance between half-sibs. This increase might be expected as the pressure of negative assortive mating is decreased. The estimated heritability for twelve-week body weight did not exhibit the same trend as observed for heritability of six-week body weight. The heritabilities estimated from the sire and from the dam component indicated a decrease for the male offspring but no decrease for the female offspring. The estimates from the intra-sire regression method exhibited an increase in heritability of six-week body weight in the female progeny. The overall average heritability for body weight at six weeks of age was 39.0 percent and 42.0 percent at twelve weeks of age, when estimated from the intra-sire regression method in the female progeny. These estimates were 38.0 percent for six-week body weight and 42.0 percent for twelve-week body weight in the male progeny.

TABLE LI

HERITABILITY ESTIMATES FOR SIX-WEEK AND TWELVE-WEEK BODY WEIGHTS IN THE INAM PROGENY FOR EACH SEX BY GENERATION

Gen.	Sex	h^2_s (1)	h^2_d (2)	b_{OD}±St.Er. (3)
		6-week wt.		
1	Male	13.3	38.8	0.34±0.32
	Female	18.8	34.6	0.40±0.22
2	Male	27.9	46.0	0.45±0.28
	Female	34.3	57.5	0.41±0.23
3	Male	41.4	58.2	0.35±0.27
	Female	49.2	52.6	0.36±0.20
		12-week wt.		
1	Male	46.2	60.0	0.41±0.28
	Female	36.8	59.6	0.39±0.26
2	Male	13.7	17.1	0.38±0.11
	Female	19.9	25.1	0.42±0.20
3	Male	38.1	36.1	0.41±0.80
	Female	35.0	39.3	0.46±0.60

1 - Estimated from sire component of the analysis of variance.

2 - Estimated from dam component of the analysis of variance.

3 - Estimated from intra-sire regression of progeny body weight on dam body weight. Regression coefficient for male offspring corrected for inequality of variance observed between the sexes.

The response noted in percentage fertility for the female offspring in each generation is given in Table LII. The first generation mean for this trait was significantly lower than that of either of the parental female groups. The average percentage fertility exhibited an increase in the second generation and a decrease in the third generation. Percentage hatch of fertile eggs exhibited a tendency to increase during the three generations of this study. The mean value for this trait in each generation are shown in Table LII.

An analysis of variance indicated that the difference in percentage egg production between the two groups of females initially selected as parents was significant at the five percent level of probability. The expected intermediate value derived from the parental means was 42.7 percent, (Table LII). This value compares to 40.7 percent observed in the first generation female progeny. The decline noted in percentage egg production in the second and third generation progeny was not significant. The average percentage egg production in the third generation progeny was 3.6 percent higher than that of the selected high line parents.

The mean egg weight in grams observed in each generation is given in Table LII. The difference in egg weight observed between the two groups selected as female parents was not significant. The resulting response observed in the female progeny indicated a definite tendency to remain at about the same level as the reverse-selected female parents. The difference observed between the three generation means was not significant.

The mid-point value between the original female parents for age at sexual maturity was 176.4 days. The mean age at sexual maturity in the first generation progeny was 180.6 days. The mean value for this trait

TABLE LII

THE AVERAGE LAYING HOUSE PERFORMANCE OF THE INAM SELECTED PARENTS AND PROGENY BY GENERATION

	% F.(1)		% H of F.(2)		% Egg Pd.(3)		Egg Wt.(4)		S.M.(5)	
Selected Parents										
SH(6)	82.3		77.1		35.6		58.4		184.2	
NSH(7)	79.9		75.8		49.8		56.9		168.5	
Average	81.1		76.5		42.7		57.7		176.4	
INAM Progeny										
Gen.	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s
1	74.8	23.1	71.5	20.9	40.7	10.4	57.6	4.0	180.6	27.0
2	76.4	29.2	75.9	31.6	39.8	17.4	56.5	4.2	190.6	29.8
3	72.6	25.0	74.6	23.1	39.2	13.7	56.8	4.0	189.0	24.9

1 - Percentage fertility.
2 - Percentage hatch of fertile eggs.
3 - Percentage egg production.
4 - Egg weight in grams.
5 - Age at sexual maturity in days.
6 - Parents selected from the upper 17 percent of the 12th generation high line progeny at 12-weeks of age.
7 - Parents selected from the lower 17 percent of the 12th generation high line progeny at 12-weeks of age.
8 - Progeny produced from the incomplete negative assortive mating system.

increased above the average value of both of the parental groups in the second and third generations. The mean age at sexual maturity was 190.6 days in the second generation. The difference between the first and second generation means for this trait was significant at the five percent level of probability.

The heritability estimates for the traits measuring the female's reproductive performance during the 500-day test period is given in Table LIII. The heritability as estimated from the analysis of variance and from the intra-sire regression method was very similar in all generations for percentage fertility and percentage hatch of fertile eggs. These estimates remained at about the same level and did not exhibit a tendency to change with generations. The overall average estimate obtained for the three generations from the sire component was 6.6 percent for percentage fertility. The overall average estimate for this trait obtained from the dam component was 5.7 percent, and 5.3 percent was estimated by the intra-sire regression method. The overall average estimates obtained for percentage hatch of fertile eggs were 12.0 percent from the sire component, 10.3 percent from the dam component and 8.0 percent from the regression method.

The estimates obtained from the sire component of variance for the heritability of percentage egg production indicated that heritability was increased in the second and third generations as compared to the first generation (Table LIII). The heritability estimated in the first generation was 8.0 percent and the estimates in the second and third generations were 24.0 percent and 22.0 percent, respectively. This would tend to indicate that the additive genetic variance was increased. This may have been due to an increase in the covariance of

TABLE LIII

HERITABILITY ESTIMATES FOR HEN HOUSE PERFORMANCE MEASURED IN THE INAM PROGENY BY GENERATION

	% Fertile(1)	% H of F(2)	% E.P.(3)	Egg Wt.	S.M.(4)
			Generation one		
h^2_s(5)	.05	.17	.08	.28	.09
h^2_d(6)	.06	.13	.13	.14	.12
Reg.(7)	.04±.13	.08±.16	.09±.17	.31±.21	.09±.12
			Generation two		
h^2_s	.08	.08	.24	.34	.08
h^2_d	.05	.07	.15	.17	.09
Reg.	.07±.21	.06±.11	.18±.12	.27±.11	.06±.11
			Generation three		
h^2_s	.07	.11	.22	.35	.15
h^2_d	.06	.11	.13	.32	.22
Reg.	.05±.14	.09±.16	.14±.09	.30±.09	.10±.13

1 = Percentage fertility.
2 = Percentage hatch of fertile eggs.
3 = Percentage egg production.
4 = Age at sexual maturity.
5 = Estimated from sire component of the analysis of variance.
6 = Estimated from dam component of the analysis of variance.
7 = Estimated from intra-sire regression method.

half-sibs. This increase was not noted in the estimates calculated from the dam component. These estimates averaged about 13.7 percent. The increase observed in the estimates obtained from the intra-sire regression method for percentage egg production was similar to that exhibited in the estimates obtained from the sire component of the analysis of variance. The intra-sire regression estimates were 9.0 percent, 18.0 percent and 14.0 percent in the first, second and third generations, respectively. The estimate obtained from the regression analysis is generally considered as the best unbiased estimate of heritability in a selection experiment (Falconer, 1960). The increase in heritability noted in the second generation seems to give additional evidence of an increase in the additive genetic variance.

Similar increases in heritability were also noted in the estimates calculated for egg weight. The estimate obtained from the sire component increased from 28.0 percent in the first generation to 34.0 percent in the second generation. The greatest increase in heritability was noted in the third generation, when the estimates were obtained from the dam component of variation. Since the phenotypic variation, as given in Table LII, did not change, the increase in heritability could thus be due to an increase in the additive genetic variance with a reduction in the non-genetic variation. This was not supported by the estimates obtained from the intra-sire regression analysis. This latter method indicated that heritability remained almost unchanged during this study. The estimates for the first, second and third generations were 31.0 percent, 27.0 percent and 30.0 percent, respectively.

The heritabilities estimated for age at sexual maturity from the analysis of variance were very similar in the first and second generations. The average estimate calculated from the sire component of variance was 8.5 percent and the average estimate from the dam component was 10.5 percent. The estimates obtained in the third generation were higher. The sire and dam component estimates were 15.0 percent and 22.0 percent, respectively. This increase was not indicated in the coefficient of variation noted in the third generation as compared to the second generation. The intra-sire regression estimate of heritability increased from 6.0 percent in the second generation to 10.0 percent in the third generation. This may tend to indicate that the additive genetic variance was increased in the third generation without an increase in the total phenotypic variance.

In order to determine the effect of this type of breeding system on the reproductive fitness of the offspring, the traits used measuring fitness should be considered as a group. The traits measured in this study which are most closely related to fitness were percentage fertility, percentage hatch of fertile eggs and percentage egg production. The only trait which indicated an increase over the twelfth generation selected high line parents was percentage egg production. It would seem, however, that any increase in reproductive fitness obtained in percentage egg production was lost with the decrease observed in percentage fertility and percentage hatch of fertile eggs. Since a relatively large decrease was observed in percentage fertility, it may be concluded that the reproductive fitness as a whole decreased as compared to either of the originally selected parental groups.

Summary

From a population of chickens previously selected for high body

weight at twelve weeks of age over a period of twelve generations, two groups of individuals were selected. These two groups consisted of the individuals with twelve-week body weights in the upper and lower seventeenth percentiles of the population. The first generation offspring were produced from reciprocal crosses between these two groups of parents. The second generation was produced by making all possible mating combinations with respect to sex and type of mating. The third generation resulted from a completely randomized (pooled) mating system.

The progeny six-week body weight mean was increased above the value of the original parental means in both sexes in the first generation. Body weight at twelve weeks of age and egg weight remained almost unaltered during this study. Age at sexual maturity exhibited an increase during the second and third generations. This resulted in a significant difference between the first and second generation means.

The traits measured in this study which were related to reproductive fitness seemed to indicate that the fitness of the offspring was reduced as compared to the original parental groups. This reduction was primarily due to a decrease in percentage fertility and percentage hatch of fertile eggs. Percentage egg production, however, increased above the level of the parental group selected from the upper seventeen percent of the original population.

Heritability of six-week body weight increased in both sexes when estimated from the sire component of variance. The estimates obtained from an intra-sire regression analysis did not exhibit this increase but remained relatively constant during the study. The unweighted average for the heritability of six-week body weight estimated from the regression method was 39.0 percent in the female progeny and 38.0

percent in the male progeny. The heritability estimates for twelve-week body weight seemed to indicate a decrease for the male and female offspring during the second generation. The increase noted for heritability of twelve-week body weight in the third generation was not as high as that estimated during the first generation. The intra-sire regression estimates for body weight at twelve weeks of age were very similar to those obtained for six-week body weight. The unweighted average was about 42.0 percent in both sexes.

Increases in heritability were also noted for percentage egg production, egg weight and age at sexual maturity during the three generations reported. The estimates of heritability calculated for percentage fertility and percentage hatch of fertile eggs remained relatively constant during this study.

CHAPTER V

GENERAL SUMMARY AND CONCLUSIONS

Data were collected from four different breeding regimes to determine the effects of long term selection for body weight at twelve weeks of age on juvenile body weight and other traits of economic importance. The initial mating system consisted of a two-way selection experiment based upon the selection for high and low body weight at twelve-weeks of age. This divergent selection system was conducted over a period of fifteen generations. The second breeding regime was initiated during the fifth generation of the divergent selection study. This system consisted of relaxed-selected lines developed from each of the divergent body weight lines. Random breeding was used to propagate the lines over a period of ten generations. During the tenth generation of selection for high and low twelve-week body weight in the divergent selection study, reciprocal cross matings between the two divergent-selected lines were made. This mating system made up the third breeding regime studied. The fourth breeding regime consisted of an incomplete negative assortive mating system involving individuals produced from the high body weight line during the twelfth generation of selection. The data collected from these breeding regimes represented 850 sires, 6,290 dams and 39,980 offspring.

The results obtained in the two-way selection study indicated that an asymmetrical response in twelve-week body weight occurred. This was apparently due to a greater response to selection in the high line, as compared to the response attained from selection in the low line. A difference was also noted in the rate of response per generation between the two sexes in the high line. An analysis of the intensity of selection indicated that the selection pressure was not significantly different for the two sexes. The response to selection for low twelve-week body weight was very similar in the male and female offspring produced by the low line selected parents. Even though the low line seemed to indicate a decreased response to selection during the latter part of the two-way selection study, the high line was still responding to selection at the end of fifteen generations when this study was terminated.

The relaxed-selected lines initiated from each of the growth-selected lines indicated that permanent genetic changes may have occurred in six and twelve-week body weight in the high line. The relaxed-selected lines further indicated that some type of environmental improvement may have developed, since juvenile body weight was increased during the ten generations of relaxed selection.

The response noted in the offspring produced from the reciprocal cross matings of the two growth-selected lines for six-week body weight indicated a heterotic effect in both sexes. Heterosis was also observed in the male offspring for twelve-week body weight, but not in the female progeny.

Heterosis was also noted in the six-week body weight means in the first generation progeny produced from the incomplete negative assortive mating system. Although heterosis might be expected in the progeny produced from the reciprocal crosses, this would not usually be expected in progeny from an incomplete negative assortive mating system. The general supposition that heterosis may result from the cancellation of the inbreeding depression noted in the two inbred lines would not seem to apply to results obtained in the incomplete negative assortive mating study. The parental groups utilized in this latter study were selected from the same population and would probably have the same degree of inbreeding. The heterosis observed for six-week body weight in the incomplete negative assortive mating system may have resulted from an interaction between the genes affecting six-week body weight and twelve-week weight, since the selection of the parents was based on twelve-week body weight.

The realized heritability for the two-way selection experiment estimated from the cumulated difference attained between the high and low lines at twelve weeks of age was 35.6 percent in the male progeny and 27.8 percent in the female progeny. The overall unweighted average heritability for twelve-week body weight estimated from an intra-sire regression method was about 46.0 percent and 42.0 percent in the male and female progeny, respectively.

The heritability estimates obtained in the relaxed-selected line, calculated from the dam component of variance by a modified analysis of variance, were consistantly higher than the estimates obtained from an intra-sire regression method. The overall unweighted mean heritability for twelve-week body weight in the relaxed-selected high line was 32.3 percent in the male offspring and 23.9 percent in the female offspring. These estimates were obtained from the intra-sire regression method. The average estimates of heritability for twelve-week body weight in the relaxed-selected low line were 36.5 percent and 27.9 percent in the male and female offspring, respectively. The heritability estimates calculated for six-week body weight were about 10.0 percent lower than those obtained for twelve-week body weight in both of the relaxed-selected lines.

The overall average heritability estimated for twelve-week weight in the progeny produced from the reciprocal cross mating of the two growth-selected lines was 46.5 percent in the male progeny and 35.0 percent for the female progeny. The estimate for twelve-week body weight was 42.0 percent in both the male and female progeny produced from the incomplete negative assortive mating system.

In the two-way selection experiment, a correlated response between twelve-week body weight and six-week body weight was noted in the high line. Correlated responses were also noted between twelve-week body weight and traits related to the reproductive performance of the selected female parents. March egg weight was decreased in the low line female parents. Both the high and the low lines exhibited a decrease in percentage egg production, percentage fertility and percentage hatch of fertile eggs. Age at sexual maturity was reduced in the high line female parents and increased in the low line female parents. These responses to twelve-week body weight selection seem to parallel the genetic, environmental and phenotypic correlations estimated in the relaxed-selection study. These correlations indicated that juvenile body weight was negatively related to percentage egg production and positively related to March egg weight. The correlations calculated for the relationship between juvenile body weight and age at sexual maturity were near zero.

The inbreeding which occurred during the two-way selection study probably accounted for a small part of the decline noted in the traits related to reproductive fitness. It was concluded that the decline in reproductive fitness was probably due to the selection pressure directed toward twelve-week body weights in the divergent-selected lines.

The overall reproductive fitness of the progeny produced from the relaxed-selected lines was probably reduced, since a decrease was noted in the average percentage egg production and in the percentage hatch of fertile eggs during this study. The mean percentage fertility, however, was increased during the ten generations of relaxed selection. The decrease in the reproductive fitness was not as great as that observed in the two-way selection experiment.

The data obtained from the progeny produced from reciprocal crosses between the high body weight line and the low body weight line seemed to indicate that the overall reproductive fitness of the offspring was improved. This conclusion was based on the heterotic effect exhibited in the mean percentage fertility of the offspring and the non-significant increase observed in the mean percentage hatch of fertile eggs. The average percentage egg production, however, was slightly lower than the expected intermediate value calculated from the parental means.

The traits measured in the incomplete negative assortive mating experiment which were related to the reproductive fitness of the progeny seemed to indicate that fitness of the progeny was reduced when compared to the original parental groups. This reduction was primarily due to a decrease in percentage fertility and in the percentage hatch of fertile eggs. Percentage egg production was increased above the level of the parental group which had been selected from the upper seventeen percent of the original population.

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APPENDIXES

Appendix A

Intra-sire Regression of Offspring on Dam

In order to simplify computations, full-sib family means were used as the observational unit for estimating heritability by this method. Each sex was analysed separately.

A full-sib family mean was represented by the following statistical model:

$$\bar{\bar{P}}_{ijk} = \mu + s_i + d_{ij} + \frac{1}{N_{ij}} \Sigma e_{ijk}$$

where:

$\bar{\bar{P}}_{ijk}$ = the mean phenotypic value of a trait for all individuals from the j^{th} dam and the i^{th} sire

μ = the population mean for the trait

s_i = an effect common to all offspring of the i^{th} sire

d_{ij} = an effect common to all offspring of the j^{th} dam mated to the i^{th} sire

e_{ijk} = a residual effect on phenotypes of the k^{th} offspring from the j^{th} dam and the i^{th} sire

N_{ij} = the number of offspring from the j^{th} dam and the i^{th} sire

The computational form of the dam offspring regression is as follows:

$$b_{OD} = \frac{\sum_i \sum_j D_{ij} \bar{\bar{P}}_{ij} - \sum_i \frac{1}{N_i} \sum_j D_{ij} \sum_j \bar{\bar{P}}_{ij}}{\sum_i \sum_j D_{ij}^2 - \sum_i \frac{1}{N_i} [\sum_j D_{ij}]^2}$$

where:

D_{ij} = measurement of the j^{th} dam mated to the i^{th} sire

$\bar{\bar{P}}_{ij}$ = mean of progeny from the j^{th}dam and i^{th} sire

N_i = the number of full-sib families from the i^{th} sire

Heritability of traits was estimated by doubling the parent-offspring regression values, i. e. $h^2 = 2 \cdot b_{OD}$

The standard error of a regression coefficient was estimated in the manner outlined by El-Issawi and Rempel (1961) for the intra-sire regression estimates.

The standard errors of regression estimates were calculated as:

$$SE\ b_{OD} = \frac{\Sigma y^2 - \frac{(\Sigma xy)}{\Sigma x^2}}{d.f.\ \Sigma x^2}$$

where:

b_{OD} = estimated parent offspring regression

y = average performance of progeny for each parent

x = performance of parent

d.f. = (d-s-1) where d = number of dam and s = number of sire

Appendix B

Analysis of Variance Used for the Computation of Dam and Progeny Variance Components Under a Mass Mating System

A mass mating system, where progeny are pedigreed to the female parent only, does not allow the separation of a sire effect as does a hierarchical mating system. Thus, an analysis reported by Kaiars, <u>et al</u> (1962) was used.

Allowing P to equal the probability that two progeny of the same dam are full-sibs, and P* to equal the probability that two progeny of different dams are half-sibs, assuming no non-additive genetic variance, the expectations of the dam and progeny mean squares are as shown in the following table.

Source	d.f.	Expected Mean Squares
Among sire groups	s-1	
Among dams within sire groups	d-s	$\sigma_e^2 + (1-P)\ \sigma_s^2 + R_1\ [(P-P^*)\ \sigma_s^2 + \sigma_D^2]$
Among progeny within dams within sire groups	N-d	$\sigma_e^2 + (1-P)\ \sigma_s^2$

where:

s = number of pens used (each having a ratio of 1 male to 10 females)

d = the total number of dams

N = the total number of offspring measured

R_1 = coefficient calculated in the same manner as in hierarchical analysis with unequal subclass numbers

The probability P* was assigned a value which represented the reciprocal of the average number of cockerels used in a pen. The probability

P was assigned a value based on the average number of progeny measured per dam. The computation of the value for P was as follows:

$$P = \frac{\frac{\eta!}{2!\,(\eta-2)!}}{\frac{N!}{2!\,(N-2)!}}$$

where:

η = the estimated average number of progeny produced by a dam from a specific sire

N = the average number of progeny produced by a dam

These two assigned values assumed that each dam mates with the different sires in a pen at equal frequency over the course of a hatching season and that each male has equal probability of mating with any female in a pen. These two assumptions may be somewhat violated in a mass mated population of chickens, but values based on these assumptions provide a reasonable guess of the values of P and P* which must be established for estimates of σ_S^2 and σ_D^2. Assuming further that $\sigma_S^2 = \sigma_D^2 = \sigma_g^2$, where σ_g^2 is the additive genetic variance, σ_e^2 and σ_D^2 can be estimated by equating the mean squares to their expectations.

The heritability was estimated from the formula:

$$h^2 = \frac{4\,\sigma_D^2}{2\,\sigma_D^2 + \sigma_e^2}$$

Estimates of Correlations:

The covariance components for dams ($ij\sigma_D$) and for error ($ij\sigma_e$) between traits i and j for all $i \neq j$ were estimated from covariance analyses similar in form to the variance analysis previously given. The expected mean products for any pair of traits were obtained by replacing the variance components in the expected mean squares by the corresponding covariance components.

After the genetic variance and covariance components were estimated, they were used to obtain estimates of genetic correlation (ijr_D) between traits i and j (for $i \neq j$) as follows:

$$ijr_D = \frac{ij\,\sigma_D}{\sqrt{(i\sigma_D^2)\,(j\sigma_D^2)}}$$

The error variance, σ_e^2 denoted in the analysis of variance, contains one-half of the genetic variance plus the environmental variance (σ_{en}^2). The value of σ_{en}^2 may be estimated by $\sigma_e^2 - 2\sigma^2$. Similarly, estimates of environmental covariance ($ij\sigma_{en}$) between pairs of traits may be obtained from: $ij\sigma_{en} = ij\sigma_e - 2\,(ij\sigma_D)$.

The estimates of environmental variances and covariances having been obtained, the estimate of the environmental correlation (ijr_e) were calculated from:

$$ijr_e = \frac{ij\,\sigma_{en}}{\sqrt{(i\sigma_{en}^2)\,(j\sigma_{en}^2)}}$$

where $i\sigma_{en}^2$ and $j\sigma_{en}^2$ are the estimates of environmental variance for traits i and j respectively.

The phenotypic variance (σ_{ph}^2) may be estimated by $\sigma_e^2 + 2\,\sigma_D^2$. From estimates of phenotypic covariance [$ij\sigma_{ph} = ij\sigma_e + 2\,(ij\sigma_D)$], estimates of phenotypic correlations (ijr_p) were obtained from:

$$ijr_p = \frac{ij\sigma_{ph}}{\sqrt{(i\sigma_{ph}^2)\,(j\sigma_{ph}^2)}}$$

Appendix C

Analysis of Data Collected From Reciprocal Cross Matings

Since the data were collected from two different matings with respect to parental classification (line and sex), each resulting set of progeny was analyzed separately using the following analysis of variance.

Source	d.f.	Composition of M. S.
Between sires	s-1	$\sigma_e^2 + K_2\,\sigma_D^2 + K_3\,\sigma_S^2$
Between dams with sires	d-s	$\sigma_e^2 + K_1\,\sigma_D^2$
Between progeny with dams within sires	N-d	σ_e^2

In this analysis (s) is the number of sires, (d) is the number of dams and N is the total number of offspring measured. The values for the K_1 coefficients were calculated in the usual manner for unequal subclass numbers in a hierarchical analysis of variance.

Heritability estimates were obtained from the components of variance. These estimates were calculated for the sire component, dam component and for the sire plus dam component.

Heritability from sire component:

$$h_s^2 = \frac{4\,\sigma_S^2}{\sigma_T^2} \qquad \text{where} \quad \sigma_T^2 = \sigma_e^2 + \sigma_D^2 + \sigma_S^2$$

Heritability from the dam component:

$$h_D^2 = \frac{4\,\sigma_s'^2}{\sigma_T^2}$$

Heritability from the combination of sire and dam:

$$h_{S+D}^2 = \frac{2\,(\sigma_S^2 + \sigma_D^2)}{\sigma_T^2}$$

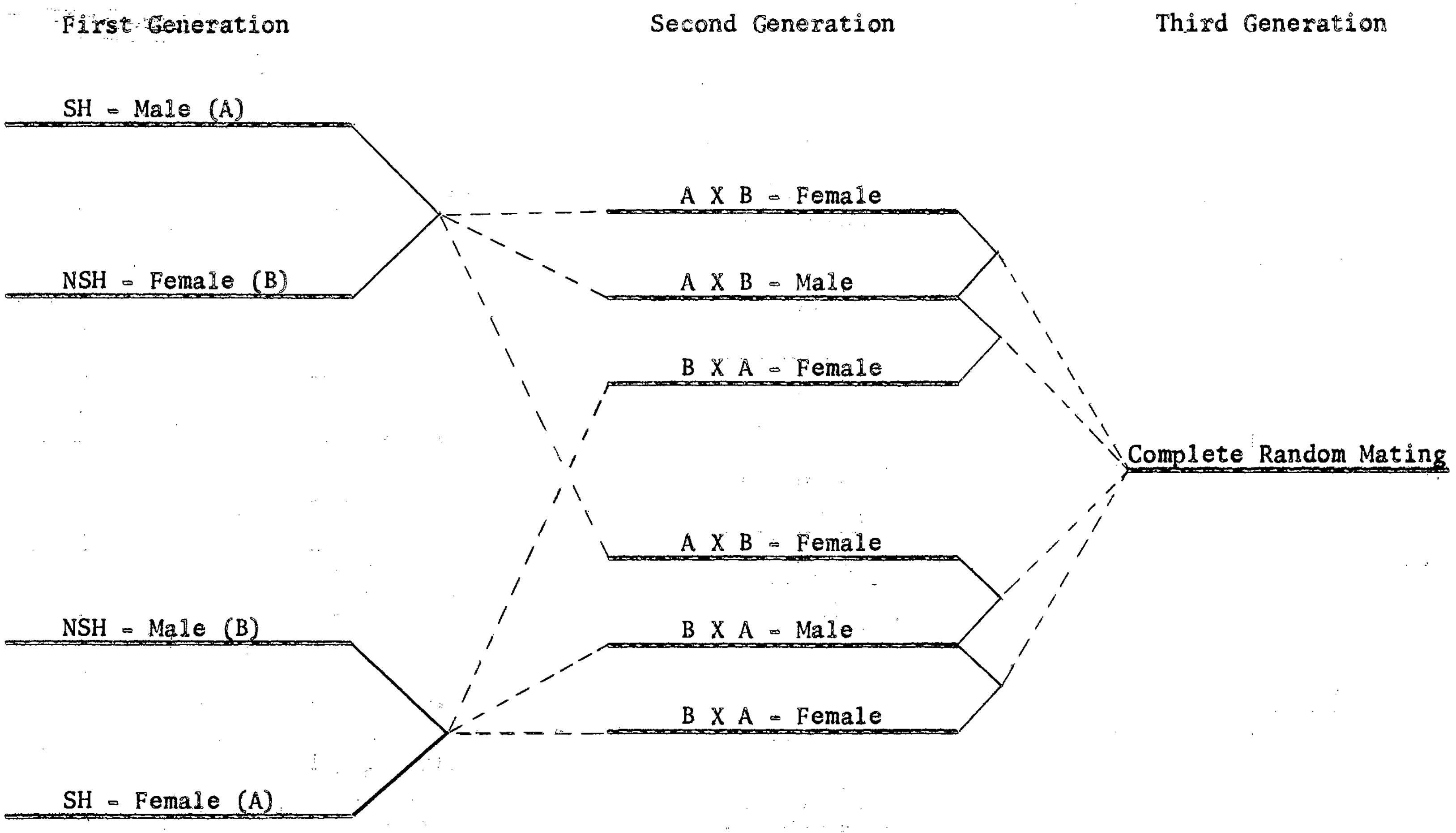
Since the sires and dams in the analysis are from different lines, then the difference between the estimates of sire and dam components of variance gives an estimate of sex-linkage component. This sex-linkage effects can thus be expressed as a fraction of the phenotypic variance or total variance by the following formula.

$$\text{Sex-linkage effects} = \frac{\sigma_S^2 - \sigma_D^2}{\sigma_T^2}$$

If maternal effects are indicated, then the estimate of sex-linkage effects would be negative and considered as zero. Thus, the maternal effects are estimated by $\dfrac{\sigma_D^2 - \sigma_S^2}{\sigma_T^2}$.

These estimates are based on the assumption that each of the parents contribute equally to their offspring and the difference that may exist between these two components is related either to the sex-linked genes or to maternal effects of the dam.

Appendix D



Schematic Representing the Incomplete Negative Assortive Mating System Utilized in Phase IV. (SH represents the parents selected from the upper seventeen percent of the twelfth generation high line progeny with respect to twelve-week body weight; NSH represents the parents selected from the low seventeen percent of the population.)

VITA

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Doctor of Philosophy

Thesis: THE EFFECTS OF SELECTION FOR TWELVE-WEEK BODY WEIGHT ON JUVENILE BODY WEIGHT AND OTHER TRAITS OF ECONOMIC IMPORTANCE IN THE DOMESTIC FOWL

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Biographical:

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Education: Attended grade school in Seminole, Oklahoma; graduated from Seminole High School in 1954; received the Bachelor of Science degree from the Oklahoma State University, with a major in Poultry Husbandry, in May, 1958; received the Master of Science degree from the Oklahoma State University, with a major in Poultry Breeding, in May, 1963; completed requirements for the Doctor of Philosophy degree in January, 1967.

Professional experience: Entered the United States Army in 1958, and is now a Captain in the Army reserve; Research Assistant and Instructor, Poultry Science Department, Oklahoma State University, September, 1960 to present.

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Date of Final Examination: January, 1967.