

SELECTION FOR HIGH AND LOW BODY
WEIGHT IN THE DOMESTIC FOWL

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INTRODUCTION

The broiler industry has become one of the most prominent segments of the poultry industry. Even with the genetic advances of the past two decades, however, the nation's broiler breeders are confronted with the constant challenge of future requirements. Since today's broiler breeds probably do not approach maximum potential performance, there is little doubt that improvement can be obtained.

The broiler breeder must maintain and utilize an efficient breeding system in order to meet the keen competition. Therefore, 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 between traits of economic importance, types 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 at broiler age. Even though body size is highly influenced by selection, there is very little information available to suggest the maximum body size which might be obtained through selection.

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

are as follows:

1. To determine the response to selection over a period of ten generations of selecting for high and low twelve-week body weight.
2. To determine the response to relaxed selection over a period of five generations of selecting for high and low twelve-week body weight.
3. To determine the effect of selection for high and low body weight on the phenotypic variance.
4. To calculate the phenotypic correlations between twelve-week body weight and other economic traits.
5. To determine the effect of selection for twelve-week body weight on other economic traits.

LITERATURE REVIEW

Because this investigation deals with several problems, the review of the literature will be divided into the following parts: measurement of response, asymmetry of response, effectiveness of selection for body size, effectiveness of relaxed selection, correlation between traits, reproductive performance, and egg production.

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, 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. The measurement of response can be improved in accuracy 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.

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 are not yet known, the possible causes 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 types of asymmetry in the genetic properties of the

initial population that could give rise to asymmetry of the response to selection, according to Falconer (1954). These concern the dominance and the gene frequencies of the loci concerned 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, according to Lerner (1954), the response would become slow as the gene frequencies approached their equilibrium values. However, the response in the other direction would be rapid until the favored alleles approached 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 way in the small line. This would tend to aid selection in both directions; however, it was also 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 which 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; however, during the last three generations the effectiveness of selection had decreased considerably. Falconer (1953) found similar response to selection for large and small body size in mice. 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 (1953) based his selection on within-litter variation for body weight at six-weeks of age. Falconer (1953) and MacArthur (1949) stated that the effectiveness of selection was greater in both lines during the first ten generations, and that it steadily decreased as the trait under selection approached its limit. Also, these experiments showed the same trend in the effect of selection on the variance, in that variance increased in the large line and decreased in the small line. The coefficient of variation was equal in both lines, however, until near the end of the period of selection.

In using Drosophila melanogaster, Robertson (1955) found a response to selection for large and small body size similar to that reported by MacArthur (1949) and Falconer (1953). There was an immediate and sustained response to selection in both directions. The actual units of

size at which 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. Selection for growth rate was found to be moderately effective between weight at birth and at 180 days of age. The most effective selection was at 180 days of age, since the weight at this age was dependent mostly upon the individual performance and 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 studies of selection of body weight in chickens using White Leghorns, Light Brahmas and their reciprocal crosses. This study extended over a period of ten years and included a total of 2966 birds. All chicks were weighed at weekly intervals during the first three months and then at monthly intervals until ten months of age. The F_1 reciprocal hybrids were intermediate in weight, at ten months of age, between the parental averages. Variability was no greater than that of either parent breed. The mean weight of the F_2 hybrids was also intermediate between the parental breeds, but their variability was significantly greater than that of the F_1 progeny. From the F_2 progeny, large, intermediate and small-sized birds were selected to be mated with their own size group. These three groups produced progenies with different means and variabilities. Waters (1931) stated that this was evidence for genetic as well as phenotypic differences, and that it was certain that segregation for large and small size took place

in the F_2 generation. Variability curves based on monthly weighings showed that the differences in variability between the original breeds and the F_1 and F_2 hybrids demonstrated no significant genetic differences until growth was nearly complete. The author made the assumption that differences in weight were dependent primarily upon two pairs of genes, each with equal and cumulative effects. Possibly many other genes of lesser influence were also active.

A study was made by Asmundson and Lerner (1933) of the genetic difference in growth rate of White Leghorns. They divided 340 chicks into four lots on the bases of sex and time of hatching. Growth from two weeks to four weeks was measured. Comparisons among the progenies of three males revealed no significant differences in growth rate. Six more or less closely-related families were divided into rapid, intermediate and slow-growing lines.

Some of the factors which may influence initial selection were studied by Gyles et al. (1955). This study involved a total of 1513 pullets from four different breeds of chickens. Over a period of eight generations, the size of the selected 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 authors 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 genetic difference in growth rate was evident, and that this difference was dependent upon multiple factors. The small number of sire families and progeny probably was responsible for the lack of a

significant difference in some cases. The sires could have possessed about the same genotypes.

It was demonstrated by Schnetzler (1936) that inherent differences in body weight are present at eight and nine weeks of age. From a group of 242 Barred Plymouth Rocks, this investigator selected the heaviest males and females and the lightest males and females on the basis of eight- and nine-week body weights. Keeping these lines separate and continuing this type of selection for several generations, the author was able to establish fast- and slow-growing lines.

Martin et al. (1953) studied the efficiency of selection for broiler growth at various ages in Rhode Island Red chickens. Live weights of 1238 pedigreed chicks from 71 dams and 24 sires were taken at three, six, nine and twelve weeks of age. These workers found that dominance effects did not show statistical significance in this study. The additive genetic influences were slightly more persistent during broiler growth than were the random environmental influences. The authors stated that the best index from this study was secured on the basis of the six- and twelve-week body weights, and estimated the index to be four percent more efficient as a criterion of genetic gain to twelve-weeks than any single weight. It was also stated that any weight taken after six-weeks would provide an efficient index for selection for genetic gain to twelve-weeks.

Effectiveness of Relaxed Selection

The technique of relaxed selection has a number of useful purposes. One of the most significant of these is in answering the question as to how permanent are the genetic gains achieved in selection. This technique

is generally accomplished by the random mating of a population or a sample of a population after selection has been practiced for a particular trait. From a commercial point of view, if such genetic gains are permanent, a purchaser of chicks could keep on reproducing the chicks for a considerable time without loss of performance.

Relaxed selection has been used by geneticists in selection experiments to help shed light on a number of factors which affect 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 generations. Selection was relaxed during the 27th, 37th and the 66th generation of selection. The authors stated that early in the experiment wing length returned to the original unselected length; however, this decline 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 caused 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 been 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 effect 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 authors 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 bases of selection. The selected parent population was considered to have reached a plateau, since comparative records of the past few years had indicated little or no change in egg production. Relaxed selection was conducted over a period of three generations. The authors found no change in body weight at eight weeks of age during the period of relaxed selection. Egg production measurements based on percentage production and on numbers of hens

housed showed little difference between the third generation and the first generation of relaxed selection. The authors further stated that the comparisons made during the three generations of relaxed selection showed little or no decrease in performance, based on hens housed, in terms of viability and hatchability.

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. A seven-year experiment involving two strains of White Leghorns and one strain of Rhode Island Reds was analyzed. The experiment included 4080 birds, which consisted of about eight sires and 80 dams in each breeding group per year. The author stated that the net decline in egg production rate due to relaxed selection was 1.69 percent and 1.16 percent per generation in the two White Leghorn strains. The decline per generation in the Rhode Island Red Strain was 0.97 percent.

Correlations Between 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. However, a negative correlation may exist in cases where improvement in one character brings about an opposite change in another character. A positive correlation may be advantageous in a selection program, since

improvement may be obtained in two or more traits of economic importance at the same time.

Correlation between traits may be due to genetic 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, so that if the gene is segregating it causes simultaneous variation in the characters which it affects. The environment may also be a cause of correlation insofar as two characters are similarly influenced by the same environmental conditions.

In some cases traits may be correlated because of their relationship to fitness. A mammal such as the mouse may be taken as an example. 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. Body size, for example, influences not only litter size but also lactation, longevity and probably many other characters. Therefore, the relationship between any particular character and fitness is important in any breeding program.

The amount and degree of correlation between traits may be measured by several different means. Phenotypic correlation is usually the simplest method to use to analyse the relationship between characters. Falconer (1960) defines the phenotypic correlation as being the association between two characters that can be directly observed. This is determined from measurements of the two characters taken from a number

of individuals of a population.

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 stated 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.

Callenbach (1934) studied the relationship of body weight, egg weight and age at sexual maturity in the chicken. Data from 803 White Leghorn pullets and 282 Barred Plymouth Rock pullets were analyzed in this study. Body weight was measured at hatching date, three weeks, eight weeks and sixteen weeks of age and at sexual maturity. Weight of first egg and age at sexual maturity were also measured. Coefficients of correlation were calculated to determine the degree of relationship between the characters measured. The author stated that chick weight at hatching time appeared to have little or no relationship to the subsequent weights measured in this study. The correlation between weights at three weeks and at eight weeks of age was large and highly significant. A highly significant correlation was also found to exist between weight at sixteen weeks of age and weight at sexual maturity. The author further stated that a significant positive correlation existed between weight of the first egg and age at sexual maturity in both White Leghorns and Barred Plymouth Rocks.

A high association between early sexual maturity and rapid early growth was reported by Hays (1951). This study consisted of 528 Rhode Island Red pullets selected for high body weight at twelve weeks of age. The author also stated that body weight at sexual maturity showed a

linear increase with age at sexual maturity.

The relative influences of egg size, age at sexual maturity and body weight at maturity upon growth to twelve-weeks of age was studied by Godfrey et al. (1953). Partial correlation coefficients were used to calculate the relationship value of 0.246 between age at sexual maturity and weight at twelve weeks of age. The correlation between weight at six weeks of age and age at sexual maturity was calculated to be 0.206. The authors concluded that age at sexual maturity began to affect body weight at age four to six-weeks, and that this relationship was more valuable than the expression of the influence of egg size on body weight during the same period.

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). This study involved 134 growth-selected pullets and 167 randomly-bred control pullets. The pullets were brooded, reared and housed intermingled, in order to measure the response correlated with a change in growth rate. Females of the growth-selected line reached sexual maturity earlier than the random-bred control pullets. The authors also stated that the selected females were larger in body weight at all ages than those of the unselected line. Also, 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.

Reproductive Performance

The reproductive performance of the fowl has been noted as being influenced by several factors. Many of these factors are known to be of

genetic origin. Reproduction may be divided into two categories, first those factors which influence fertility and secondly those factors which influence hatchability.

There are nineteen lethal genes which, if present in a population, reduce the hatch of fertile eggs (Landauer, 1948 and Jull, 1952). There is considerable evidence that a relationship exists between hatch of fertile eggs and such traits as egg size, egg shape and shell quality. Since these traits are known to be heritable, it is apparent that hatchability is inherited at least to the degree that it is influenced by such traits.

While differences in fertility between breeds and strains of chickens and between strains of turkeys have been suspected, it has been difficult to establish the significance of such differences. Under conditions of natural mating, social, mechanical and other environmental factors may mask the fertilizing ability of a male and/or the physiological receptivity of the female. It has been indicated that at least some of the variation of fertility may be due to genetic causes. Hays (1950) reported that fertility may be regulated by sex-linked genes. It was further noted by Gowe and Hutt (1949) that the control of fertility is at least to some degree of genetic origin. Other workers such as Williams and McGibbon (1954) found a significant difference in duration of fertility between the males of two inbred lines. This would tend to indicate that the genetic constitution of both male and female may influence fertility.

Egg Production

Numerous investigators have reported small linear correlations

between body weight and egg production. This may indicate that little if any relationship exists between these traits. Platt (1927) and others have shown that the relationship which does exist is non-linear. This author also stated that extremely small and extremely large hens were the poorest layers in his study. The hens which were between these extremes, however, did not exhibit any relationship between egg production and body weight. This was also evident in the study conducted by Taylor (1930). In a study conducted by Jerome et al. (1956) a negative correlation between these traits of 0.590 was determined to be significant. Singh et al. (1960) reported that in selecting for increased body weight at nine-weeks of age, percentage egg production was decreased.

The amount of variation in the results obtained from reported studies is due in part to differences in breed and strain of bird and in type of experiment. Various refinements in the handling of egg production data are discussed by Oliver et al. (1957) and Bray et al. (1960). In these studies some of the variation encountered was eliminated by removing the effects of age at sexual maturity and mortality during the laying period. Age at sexual maturity may affect early production when egg numbers from the date of first egg is the measurement. The effects may be removed by using percentage production. This was noted by Oliver et al. (1957). It should be pointed out, however, that the only time when transformation of egg numbers to percentages is advantageous is when different females have varying numbers of production days.

EXPERIMENTAL PROCEDURE

The study reported in this thesis involves ten generations of selection for high and low body weight at twelve weeks of age. A report on the effects of relaxed selection, conducted for the five generations following the first five generations of growth selection, is also included. Each generation consisted of a 500-day test period for the selected parental stock in each line.

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. George Jaap, who was poultry geneticist at the Oklahoma State University from 1935 to 1946. The Silver Oklabar is a columbian-patterned bird which was developed from a series of cross matings (Godfrey, 1953). 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 variety was "purified" for the silver gene, the resulting birds were named Silver Oklabars. The development was completed in 1940.

Since the development of the Silver Oklabar, a large population of these birds was randomly bred under a closed-flock system until the initiation of this study in January of 1950. Selection was based on individual body weight at twelve-weeks of age. From the original population two groups of birds were selected. One group consisted of all individual birds having body weights greater than one standard deviation above the population mean weight. This group was designated as the high line. All individual birds which had weights less than one standard deviation below the population mean were designated as the low line. Selection was not changed at any time during the experiment in the two selected lines. A more detailed discussion of the selection procedure used in this study was reported by Williams (1952).

A relaxed-selected line was initiated from each of the selected lines during the fifth generation. The growth-selected parents produced progeny for the next generation. This allowed the original lines to be continued under the regular selection pressure. After the progeny from the pedigreed matings were selected, the parental stock within each selected line was randomly mated. From these random matings the relaxed-selected lines were produced. The two randombred 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.

Individual-male mating pens were used in order to maintain pedigree records of all progeny produced within the selected lines. Approximately ten females were utilized in each mating pen; however, 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 in-breeding.

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.

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 between generations, depending upon the number of females available in each line.

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 eggs.

Eggs were trayed according to individual pedigree. On the 18th day of incubation, all eggs were candled and the infertiles 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 showing signs of development were recorded as fertile.

On the day of hatching, all chicks were wing-banded and pedigreed by sires and dams. They were vaccinated intranasally against Newcastle disease and infectious bronchitis with a live-virus vaccine. Each hatch of chicks was randomly distributed into brooder house pens. Both lines were brooded together in the same pen until the fourth generation. Due

to the difference in size, after the fourth generation, the lines could no longer be brooded together. In order to minimize environmental differences, each hatch of high- and low-line progeny was brooded in adjacent pens within the same house. Each brooding pen was 30 ft. x 15 ft. in dimensions to insure adequate floor space for maximum performance. Natural gas and electric brooders were used as the sources of heat for all groups of chicks.

During this study a standard starter and grower ration was fed as recommended by the Poultry Science Department. The ration was once during this study, changed at the beginning of the fourth generation growth period, in order to provide a more efficient grower ration.

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

At six and at twelve weeks of age all birds were weighed to the nearest tenth of a pound. During the first eight generations, sex was determined at six weeks of age in both lines. The ninth and tenth generations of low-line progeny were sexed at twelve-weeks of age, since the sex could not be determined accurately at six weeks of age because of their slow growth.

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. Also during this period 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 at

about October first, 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 females in each pen, in order to minimize inbreeding. The mating procedure was conducted within each generation in the same manner as previously described. All egg production records were maintained through 500 days of age on all females selected as parental stock.

The layer-breeder ration fed during the laying and breeding seasons was changed at the beginning of the sixth generation. 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 between generations.

Age at sexual maturity was recorded as the number of days from date of hatch to date of first egg laid. Two methods of calculating egg production were used. The first method was calculated on the basis of the performance of all birds housed. The second method utilized only the records of the individuals which completed the 500-day test period.

During the first ten days of March, all pedigreed eggs were weighed. From these weights, the individual female's average egg weight was calculated. To obtain the average egg weight for comparisons of lines, each hen's average was used as a single measurement.

The relaxed-selected lines were hatched, brooded, and reared in the same manner as the growth-selected lines. The management practices, other than the type of mating system, were the same for all lines. The

same methods were used for recording and calculating traits measured for the relaxed lines as for the growth-selected lines.

RESULTS AND DISCUSSION

Selection for Twelve-Week Body Weight

Selection Differential. The selection differential is the difference between the mean of the selected parents and the mean of the population from which they were selected. The progress made through selection depends upon the magnitude of the selection differential. The magnitude of the selection differential depends primarily on the fraction of the population which is saved for breeding. It also depends to a lesser extent on the size of the population from which the selection is made, (Lerner, 1958). In planning a selection program to give the maximum rate of progress, the expected differential is the first matter of consideration. However, in the assessment of the results of selection, the actual differential obtained must be calculated.

The theoretical value of the expected selection differential, common to mass selection in situations where the upper percentage or the lower percentage of the population is chosen, can be calculated. However, the distribution of the phenotypic values in the population should be known. On the basis of a normal distribution, the expected selection differential may be determined by the formula, $D = K \sigma_p$, where (D) is the expected selection differential, (K) is a constant, and (σ_p) is the standard deviation of the population. The values of the constant (K) are given by Lush (1945).

Table I contains the expected and actual selection differentials

obtained in this study for both the high and low lines over the ten generations of selection. Even though there is some variation between the expected and the actual selection differentials, the overall means are not significantly different. To test for significant differences between the means of the expected and the actual differentials, an analysis of variance was used. This type of analysis is outlined by Snedecor (1959). It was further noted from this analysis (Table II) that the difference which existed between the differential means of the high line and those of the low line was not significant. On the basis of this analysis it may be concluded that, even though there was a slight difference between the expected and actual selection differential, it was not significant. This means that the distribution of the weights within each generation conformed closely enough to the properties of a normal distribution to allow fairly accurate differentials.

The total selection differentials are also shown in Table I. The high line was consistently higher than the low line with respect to the total selection differentials. The difference observed may have been due to the measurement in pounds and might not exist if it was measured in standard deviations, since the fraction of the population saved for breeding was approximately the same in the two lines.

When the actual selection differentials are applied to the calculation of heritabilities, the differentials of each mated pair must be weighted by the numbers of offspring of the pair that are measured in the next generation. This procedure is discussed by Falconer (1960). The weighted selection differential in pounds is shown in Table I. Two reasons for a possible difference between the weighted and the unweighted selection differentials are reported by Falconer (1953). The first is

TABLE I
SELECTION DIFFERENTIALS

Gen.	Expected	<u>High Line</u>		Expected	<u>Low Line</u>	
		Unweighted	Actual Weighted		Unweighted	Actual Weighted
1	0.634	0.638	0.633	0.596	0.722	0.717
2	0.557	0.405	0.403	0.514	0.239	0.247
3	0.495	0.536	0.535	0.626	0.408	0.410
4	0.506	0.459	0.449	0.680	0.483	0.492
5	0.461	0.456	0.451	0.369	0.357	0.366
6	0.465	0.415	0.420	0.381	0.352	0.341
7	0.776	0.875	0.878	0.624	0.349	0.365
8	0.642	0.143	0.193	0.255	0.287	0.281
9	0.289	0.130	0.103	0.270	0.235	0.240
10	0.221	0.365	0.383	0.359	0.194	0.182
Total	5.046	4.422	4.448	4.674	3.626	3.641

TABLE II
ANALYSIS OF VARIANCE OF SELECTION
DIFFERENTIAL MEASUREMENTS

Source	d. f.	S.S.	M.S.	F
Total	59	1.9033449		
Measurements	5	0.1621196		
High Line X Low Line	(1)	0.0650104	0.0650104	2.016
Within the Low Line	(2)	0.0721873	0.0360936	1.119
Within the High Line	(2)	0.0249219	0.0124609	0.386
Error	54	1.7412253	0.0322449	

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. This type of natural selection, however, did not occur to a great extent, since there was very little difference between the weighted and the unweighted differentials in this study.

Response to Selection. The results of the response to selection for twelve-week body weight are summarized in Figure 1. Figure 1 shows the response of each line separately for the ten generations. The points utilized in Figure 1 are the generation twelve-week weight means of the averages of the sexes combined. Figure 1 also shows a straight-line regression fitted to the generation means. Figure 2 gives a graphic interpretation of the cumulative selection differential of both of the selected lines combined. The cumulative selection differential at any one generation is the selection differential for the generation added to the sum of the differential for all previous generations. The divergence shown in Figure 3 is the difference in mean weights between the selected high and the selected low line for the ten generations.

In considering Figure 1, there is little doubt about the efficiency of selection in increasing and in decreasing body weight at twelve weeks of age. The magnitude of the change is considerable. The difference between the lines after ten generations of selection amounts to 77.08 percent of the initial weight. Progress in both selected lines appears erratic. This irregularity is similar to that reported in many selection experiments.

It is clear from a comparison of high- and low-line response in Figure 1 that much of the fluctuation is parallel, and is therefore

eliminated from the line of divergence shown in Figure 3. The irregularity of the response shown in Figure 1 makes it difficult to compare the rate of progress in the two directions by mere inspection. However, the graph suggests that progress was more rapid in the high line than in the low line. It was noted also in the discussion of the selection differentials that the total selection was greater in the high line than in the low line. From the comparisons of the response in each line, it appears that the heritability may have been greater for the upward direction than for the downward direction. This is particularly true when the total response of 1.28 pounds in the high line and 0.67 pounds in the low line is compared with their respective total selection differential of 4.45 pounds for the high line and 3.65 pounds for the low line.

The divergence line in Figure 3, which is free of much of the fluctuation noted in the separate lines in Figure 1, shows a fairly steady increase through the tenth generation of selection. An important conclusion to be drawn from an inspection of the divergence line is that the response to selection proceeds almost unchanged. This may mean that the heritability remains substantially unaltered by the continuous selection through the tenth generation. This concurs with the findings reported by Falconer (1953) and Robertson (1955).

The heritability for selection in this stock can be measured from the divergence in each generation, separately. Table III presents the selection differential, response and heritability for each generation. The heritabilities vary between rather wide limits. Although the graph in Figure 3 looks fairly regular, a single generation of two-way selection provides a very unreliable estimate of heritability in a

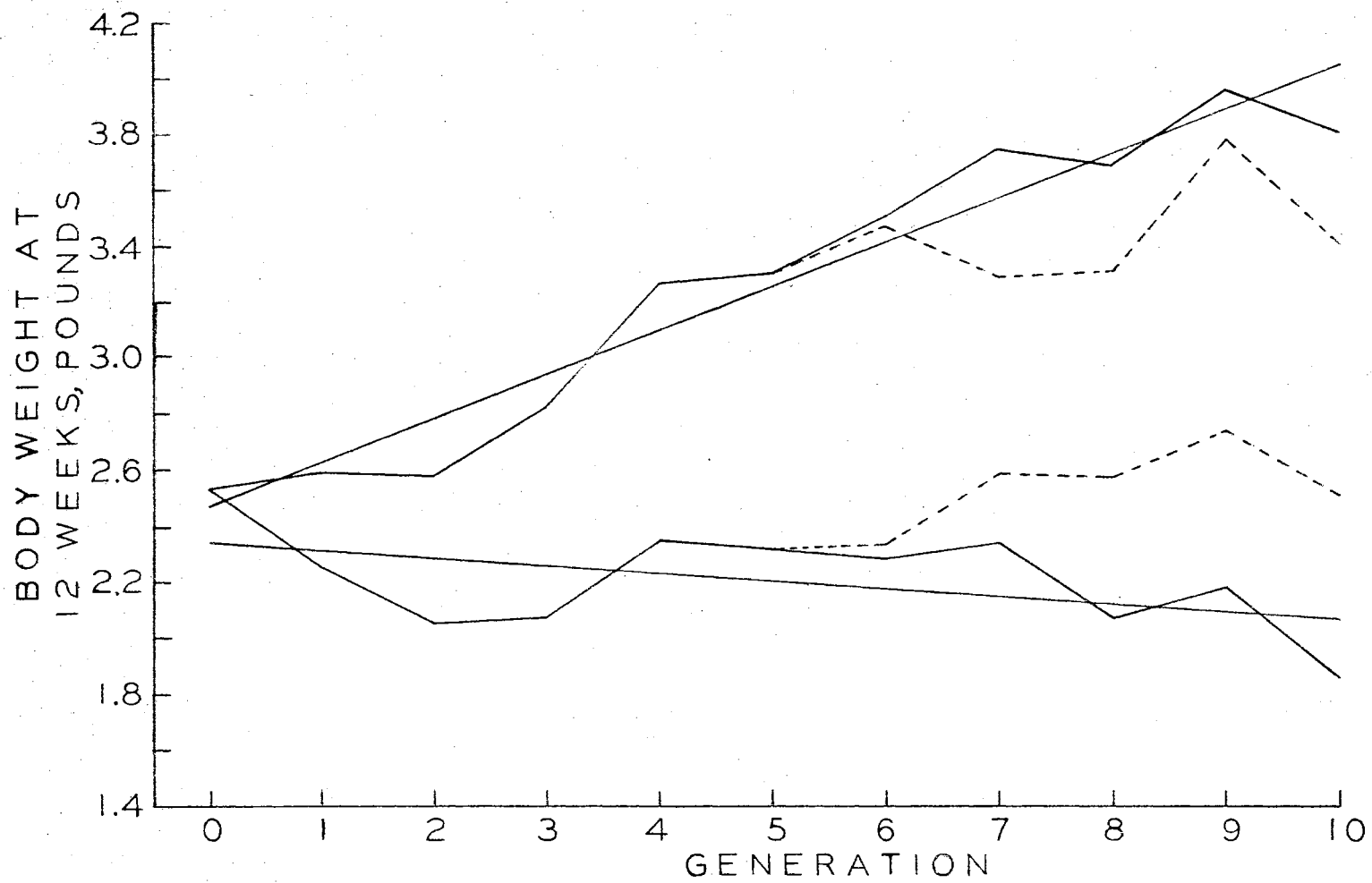


Fig. 1. The Effect of Continuous Selection on 12-week Body Weight.

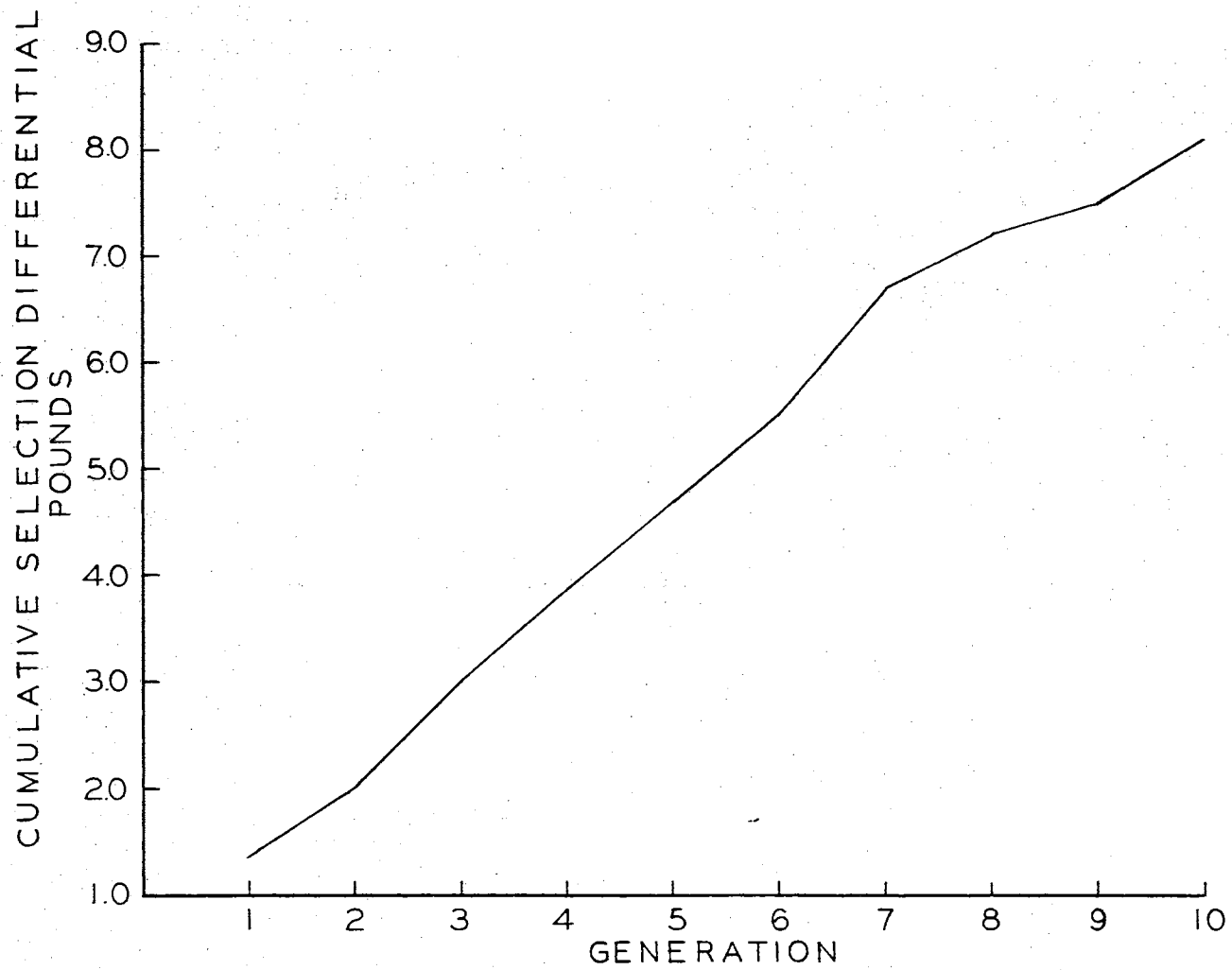


Fig. 2. The Cumulative Selection Differential in Selection for 12-week Body Weight.

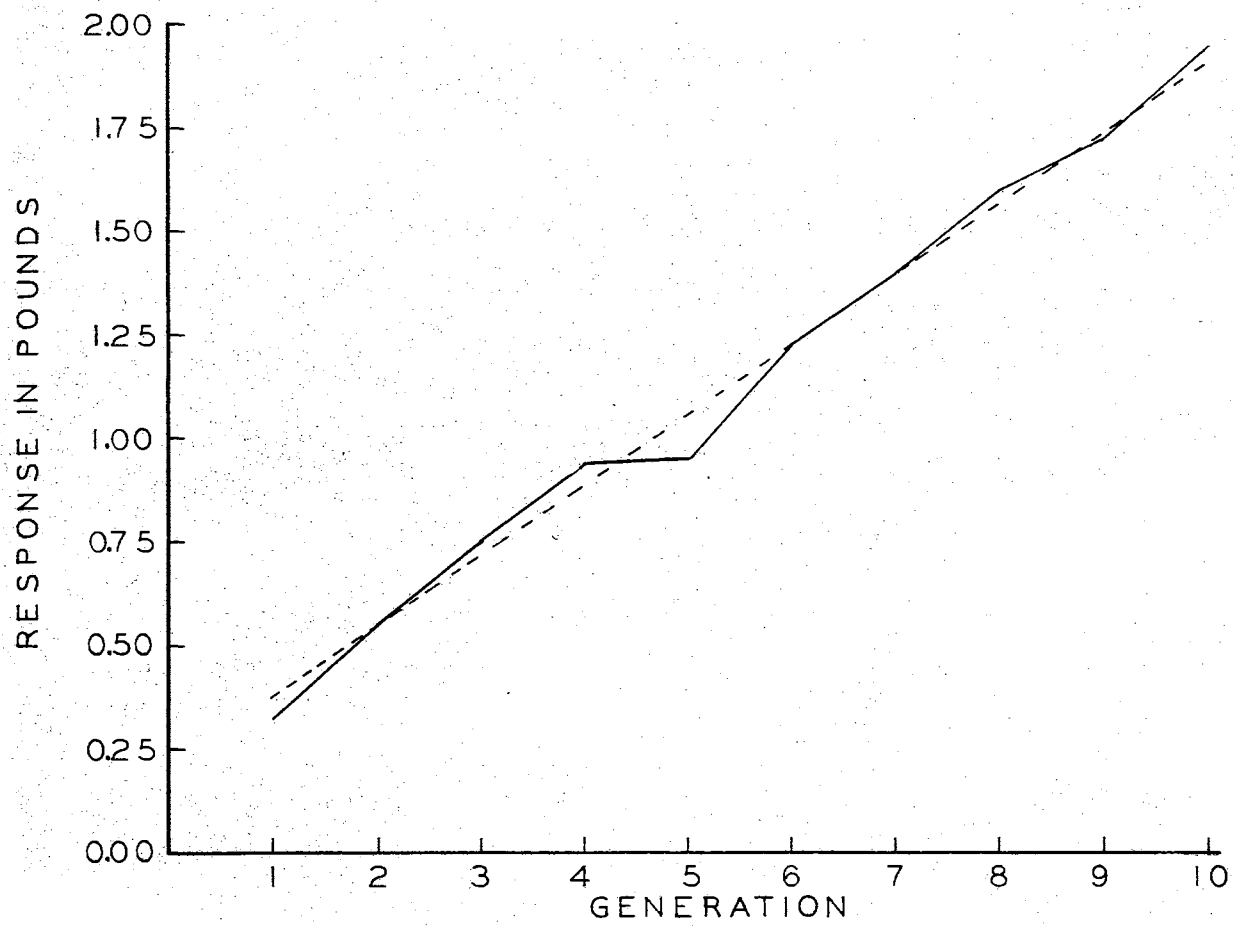


Fig. 3. The Effect of Continuous Two-Way Selection on 12-week Body Weight.
 (Response Measured as the Difference Between the High and the Low Line 12-week Body Weight Means.)

TABLE III
HERITABILITY ESTIMATES FROM THE DIFFERENCE
BETWEEN THE HIGH LINE AND THE LOW LINE

Gen.	Selection* Differential	Response**	Heritability (%)***
1	1.350	0.33	24.45
2	0.650	0.21	32.31
3	0.945	0.21	22.22
4	0.941	0.18	19.13
5	0.817	0.03	03.67
6	0.761	0.26	34.17
7	1.243	0.18	14.48
8	0.474	0.21	44.30
9	0.343	0.16	46.65
10	0.565	0.18	31.86
Total	8.089	1.95	24.11

* The selection differentials of both lines were added together to measure the total selection within each generation.

** The response measurement is the difference between the two lines.

*** Heritability is presented as the ratio of difference of response to the summed selection differential.

population of this size. As the generations proceed, the estimate from the total response becomes more and more reliable. The total response gives a heritability estimate of 24.1 percent. This, however, is still not the best estimate that can be obtained.

Statistical Analysis of Selection. In particular, standard errors are desired in measuring the rate of response and the estimates of heritability in the two lines and in the divergence. Also, statistical analysis is needed to assess the significance of the difference of response and of heritability between the two lines. The statistical analysis required to provide the confidence limits centers on an examination of the irregularities displayed by the graphs of response.

For the purpose of analysis, the true response may be regarded as straight lines about which the observed generation means fluctuate. This fluctuation is caused by different kinds of error variance. Regression lines may then be fitted to the generation means, and the error variance about the regression lines can be directly estimated. A part of the object of this analysis is to evaluate the different causes of this error variance. The assumption that the responses are essentially linear, upon which the regression analysis depends, appears to be justified by the actual observations over the period covered by the experiment.

The regression analyses of the two lines shown in Figure 1 and the divergence line shown in Figure 3 are given in Table IV. The calculations are based on the first ten generations of selection from generation zero to generation ten. From the data in Table IV certain specific conclusions may be drawn.

The response (with its standard error) in the high line was 0.157 ± 0.016 pound per generation, and the low-line response was 0.028 ± 0.016

TABLE IV
ANALYSIS OF RESPONSE BY GENERATION

	High Line ²	Low Line ²	Difference ³
Rate of Change (b) ¹	0.157**	0.028	0.177**
Variance of (b)	0.00026	0.00026	0.000024
Standard Error of (b)	<u>+0.016</u>	<u>+0.016</u>	<u>+0.0049</u>

¹ Slope of regression line expressed in pounds change per generation.

² Regression analysis of Figure 1.

³ Regression analysis of Figure 3.

**Significant (P < .01).

pound per generation. The difference of 0.129 ± 0.014 is nine times its standard error, and must therefore be judged as significant. The point of intersection of the two regression lines, when extrapolated backwards, provides an estimate of the level of the unselected population. This was demonstrated by Falconer (1953). The lines intersect at a weight of 2.38 pounds, which is fairly close to the observed mean of generation zero (2.53 pounds in the original population). Furthermore, the means of the final generation also lie close to their respective regression lines. The preliminary judgement based on the total response in the two lines, therefore, is substantially correct. The total change in the high line reflects a real difference in the rate of response to selection in the two directions.

The heritability is the ratio of the response (R) to the selection differential (S). The response may be measured either from the difference between the first and the last generation, or from the slope of the fitted regression line, with the response plotted against the cumulated selection differentials. The realized heritability for twelve-week body weight was estimated by plotting the generation means against the cumulated weighted selection differential, and a regression line was fitted to the points. The slope of the line measures the average value of R/S, the realized heritability. A graphic representation of R/S is shown in Figure 4 and Figure 5.

Using the slope of the regression line as a measure of the average value of R/S, the realized heritability for twelve-week body weight in this stock was found to be 34.4 ± 3.24 in the high line, and 7.20 ± 4.55 in the low line, and 22.15 ± 1.77 for the two-way selection. These results are shown in Table V. The difference in the realized heritability

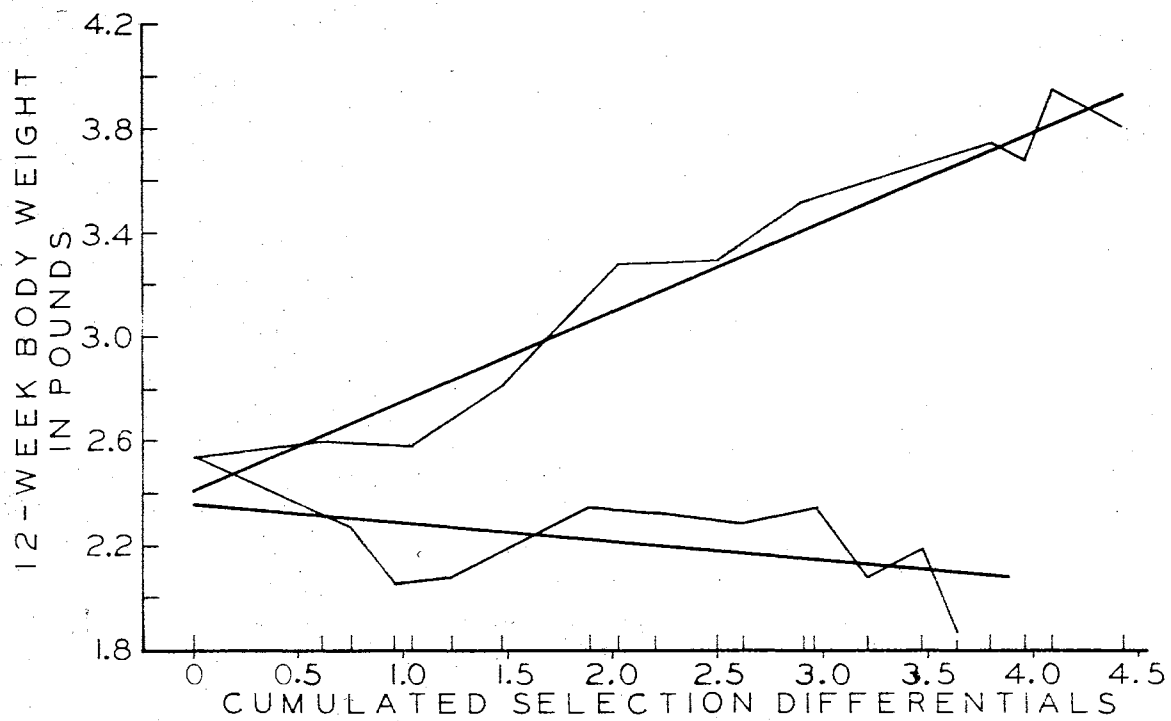


Fig. 4. The High and Low Line Realized Heritability of 12-week Body Weight .

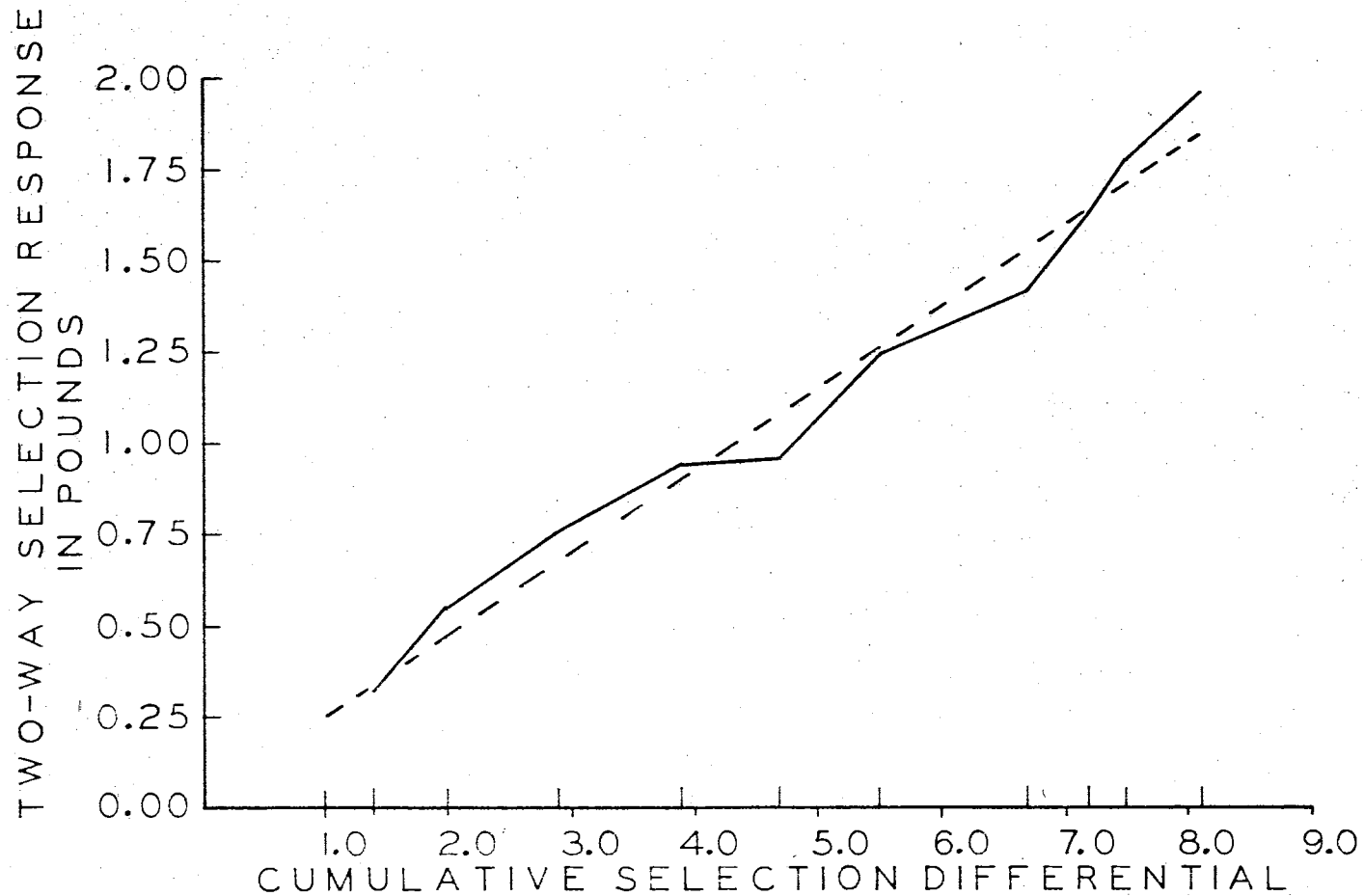


Fig. 5. The Two-Way Selection Realized Heritability of 12-week Body Weight. (Response Measured as the Difference Between the High and the Low Line 12-week Body Weight Means).

TABLE V
ANALYSIS OF RESPONSE TO THE CUMULATED
SELECTION DIFFERENTIALS

	High Line ²	Low Line ²	Divergence ³
Rate of Change (b) ¹	0.34405	0.07202	0.22148
Variance of (b)	0.00105	0.00207	0.00014
Standard Error of (b)	± 0.0324	± 0.0455	± 0.0117

¹Slope of regression line expressed as the rate of change in pounds.

²Regression analysis of Figure 4.

³Regression analysis of Figure 5.

REALIZED HERITABILITY ESTIMATES FROM REGRESSION ANALYSIS OF
RESPONSE TO THE CUMULATED SELECTION DIFFERENTIAL

	Realized Heritability ¹
High Line	34.41 \pm 3.24
Low Line	7.20 \pm 4.55
Divergence	22.15 \pm 1.17

¹Realized heritability expressed in percentages.

between the high and the low lines is 27.2 ± 4.65 . The difference in heritability is six times its standard error, and is thus well beyond the usual criterion of significance.

The Effects of Relaxed Selection on Twelve-Week Body Weight. Selection was relaxed in the high line and in the low line during the fifth generation. The procedure of relaxed selection has been described previously. The twelve-week mean body weights are shown graphically in Figure 1 as broken lines for both the relaxed-selected-high and the relaxed-selected-low lines. There is a noticeable and almost immediate response in the relaxed low line to return to the mean of the original population. The twelve-week mean of the low line in the fifth generation was 2.32 pounds as compared to 2.50 pounds after five generations of relaxed selection. The means of the second and third generations of relaxed selection were, respectively, 0.05 pound and 0.20 pound above the original mean. Since the low line showed a definite tendency to return to the original mean weight when selection was relaxed, it may be concluded that very little if any permanent change in body weight occurred during the first five generations of selection for low body weight.

The high line, however, did not exhibit the same tendency to return toward the original mean as occurred in the low line. Even though the means of the high line fluctuated extensively, a linear regression analysis showed a slight but not significant increase over the five generations of relaxed selection. It may be concluded that since the relaxed-selected-high line did not return toward the original mean, some permanent change in body weight occurred during the five generations of selection.

Changes in the Variance. It was noted that the response to the two-way selection continued almost undiminished throughout the ten generations

of the experiment. It was also noted that a greater response occurred in the high line. The heritability of the divergence remained substantially unchanged during this period. These observations suggest that the selection produced very little change in the variation of the population.

The within-generation variances were found to change with the mean weight, becoming smaller in the large line and somewhat unchanged in the small line. The effects of the changing means can be partially eliminated by expressing the variance as a coefficient of variation. The coefficients of variation may be determined by the formula

$$\frac{(\text{Standard deviation} \times 100)}{\text{Mean weight}} = \text{Coefficient of variation.}$$

This procedure was used by Falconer (1953) and Robertson (1955). The coefficients of variation, shown in Figure 6, are not equal for the two lines. The coefficients in the high line reflect the expected decline of variance which should occur as selection proceeds toward its limits.

This decline should also be accompanied by a decrease in heritability and a decrease in rate of response. These decreases, as noted earlier, did not occur. This may be due to a decrease in the non-genetic variance and not to a decline in the actual genetic variation.

The phenotypic variance in the low line did not exhibit the decline noted in the high line, but remained nearly the same as that of the original population until the fifth generation. The same type of phenotypic variance was also noted by MacArthur (1949), Falconer (1953) and Robertson (1955). However, the phenomenon of a sudden increase in the coefficients of variation for body weight, which was reported in mice by

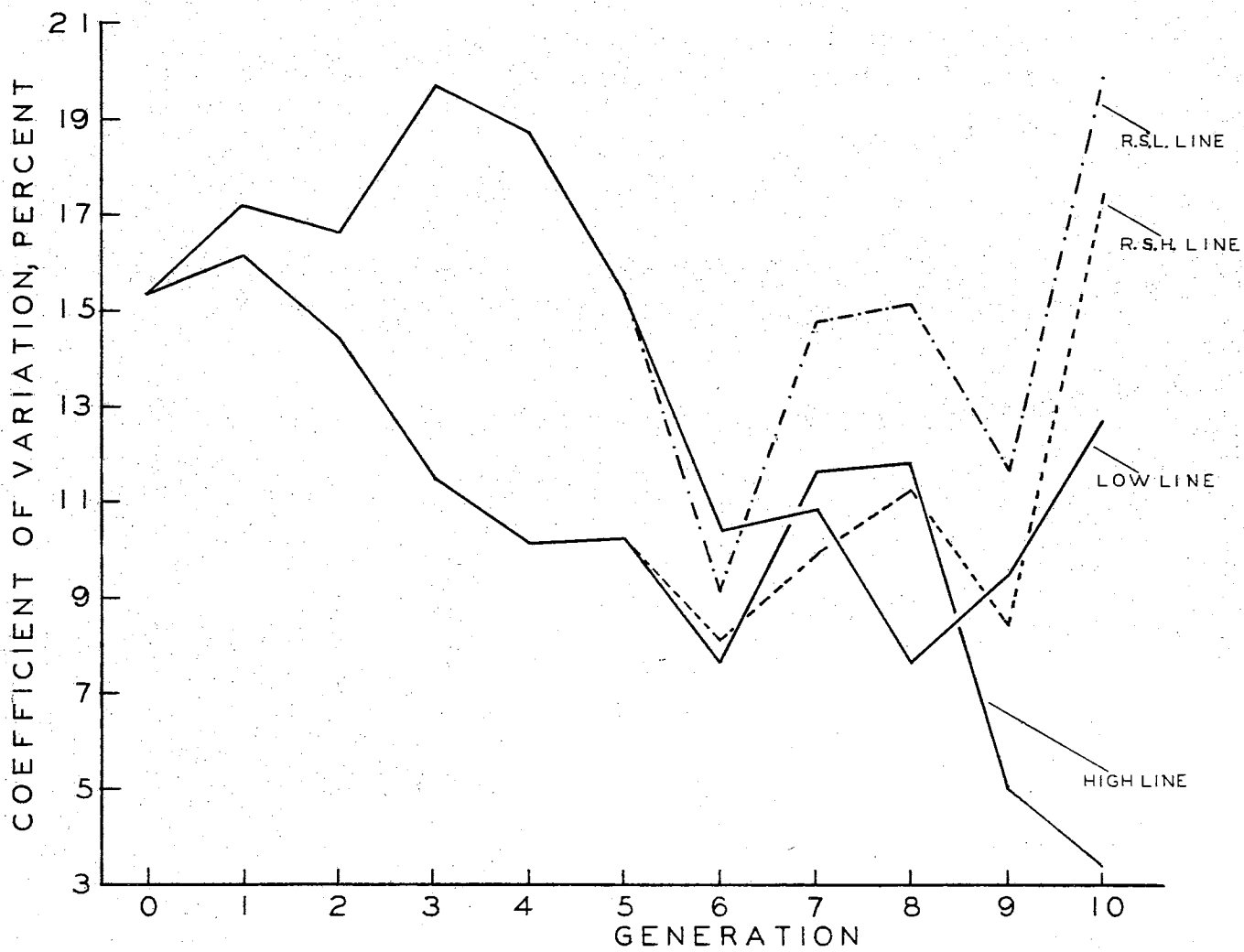


Fig. 6. The Effect of Continuous Selection on Variability of 12-week Body Weight.

MacArthur (1949) and Falconer (1953), did not occur in this experiment.

Effect of Selection on Other Traits

Measurements of several other characters of economic importance, in addition to twelve-week body weight, were made during the course of this experiment. There are several types of correlated response which may occur between a selected trait and an unselected trait. If two characters are uncorrelated genetically, then no correlated response would be expected. However, the secondary character may nevertheless show undirected departure from the normal following selection. Mather and Harrison (1949), in a study of Drosophila melanogaster, reported this type of correlated response in selection for bristle number. These changes which occurred were attributed by Mather and Harrison (1949) to the break up of balanced combinations of linked genes.

If the two characters are correlated genetically, the secondary character will show a direct change following selection for the primary character. This is the commonly observed type of correlated response. This type is exemplified by the correlated changes in body weight with selection for shank length in poultry, which was observed by Lerner (1946). A further example is the correlated response of tail length to selection for body weight in mice, which was reported by Falconer (1954).

Another type of correlated response exists if the secondary character forms an important component of the total fitness. Under these conditions the secondary character may be expected to decline in response to selection for the primary character, in either direction. This type of response has been termed "genetic homeostasis" by Lerner (1950).

The changes in secondary characters resulting from the selection

for twelve-week body weight are described in this section. The phenotypic correlation coefficients were obtained from the data collected during the last five generations of selection.

The IBM 650 computer program, "Beaton Correlation Routine", was used to calculate the correlation coefficients in this study. This program was designed by Beaton (1957). Correlation coefficients were obtained between all traits measured within each line within each of the last five generations. Correlations were also obtained within lines over the last five generations combined. These calculations were obtained in order to determine any possible change in the relationship between these traits which may have occurred during the last five generations of the experiment.

Six-Week Body Weight. The six-week body weights were measured as previously described. Figure 7 shows the means of the six-week body weight of each generation, as the arithmetic mean of the sexes combined. During the first six generations of selection, the high line increased fairly steadily; however, during the last five generations the change became very irregular. The low line, however, decreased fairly rapidly during the first two generations, then increased almost as rapidly above the value of the original mean by the fourth generation of selection. The low line declined during the last five generations of selection, with the exception of the eighth generation. In the last generation of selection in the low line, the six-week weight decreased to a value of 0.235 pound below the value of 0.810 for the original population.

The linear regression analysis of six-week body weight by generations is given in Table VI. The high line in this analysis exhibited a highly significant increase in six-week body weight per generation, since the

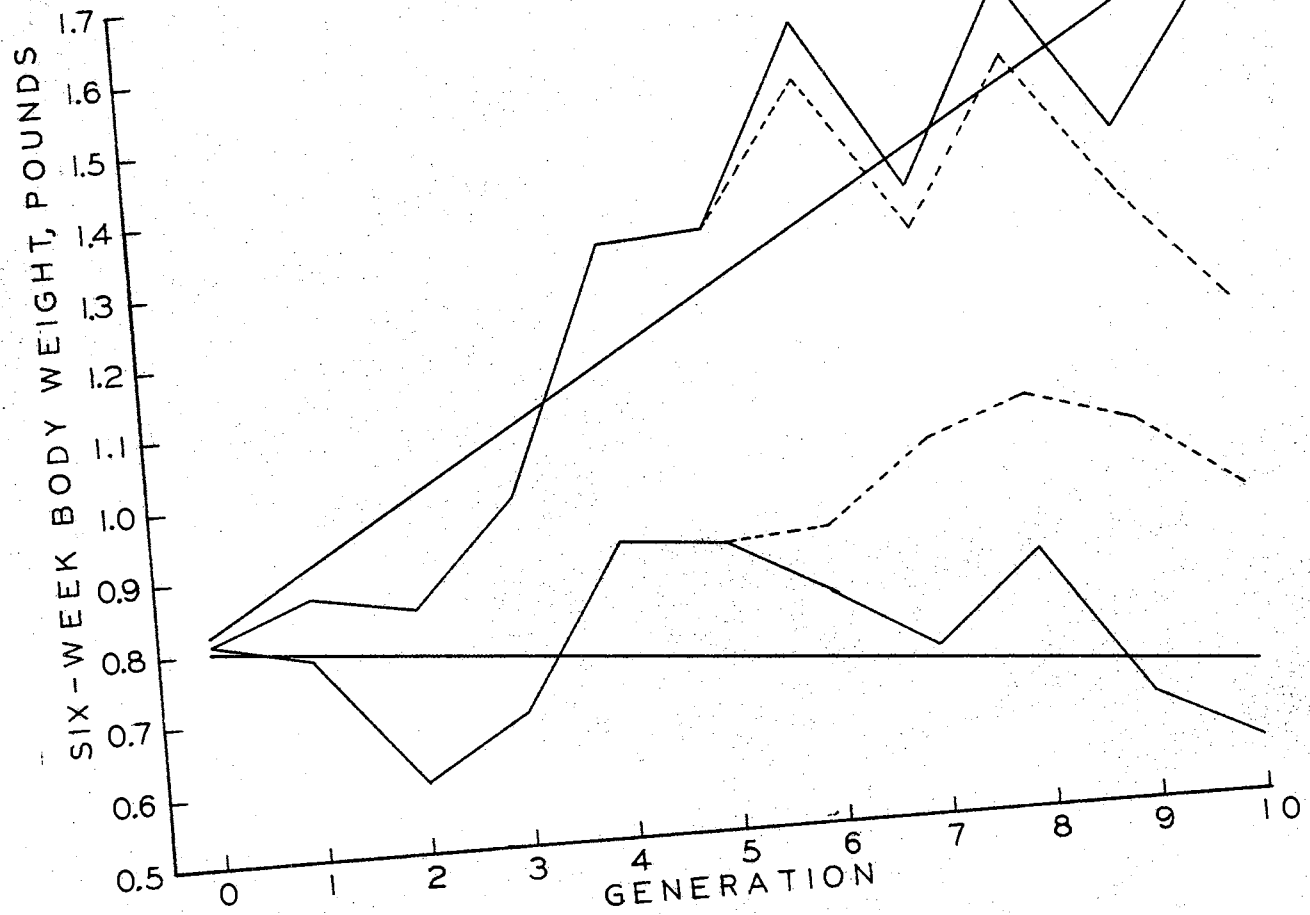


Fig. 7. The Effect of Continuous Selection for 12-week Body Weight on 6-week Body Weight.

TABLE VI
 LINEAR REGRESSION ANALYSIS OF SIX-WEEK
 BODY WEIGHT BY GENERATION

	High Line	Low Line
Rate of Change (b) ¹	0.0878**	-0.0079
Variance of (b)	0.0002	0.00012
Standard Error of (b)	<u>+0.015</u>	<u>+0.011</u>

¹ Slope of regression line expressed in pounds change per generation.
 Shown graphically in Figure 7.

**Significant ($P < .01$).

slope of the regression line was 0.088 ± 0.015 . The low line, however, did not show the same rate of response as the high line, since the slope of the regression line was only -0.008 ± 0.011 . This rate of change per generation was not significant.

The phenotypic correlation coefficients between weights at six weeks and weights at twelve weeks for each line are given by generation in Table VII. It may be noted that the low line had consistently higher correlations than did those of the high line. The variation from one generation to another may have been due to the varying number of observations used to calculate the coefficients. This variation also may have been due to an unstable genetic relationship, particularly in the high line. The apparent cessation of the response of the six-week weights in the high line after the sixth generation may possibly suggest a disruption of the genetic correlation with twelve-week weights. A similar response was also reported by Falconer (1954) in the effect of selection for large body size in mice on tail length. Since the correlation coefficients were not determined for the first five generations, the actual facts about this relationship are not clear enough to warrant more speculation on this point.

When the last five generations are combined, the correlation coefficients are 0.245 for the high line and 0.530 for the low line. Both of these correlations are statistically highly significant. On this basis it may be concluded that there may exist a positive significant correlation between six-week and twelve-week weight in the last five generations of this study.

After the initiation of relaxed selection in the relaxed-high line, six-week weights remained about the same as that of the fifth generation.

TABLE VII
 CORRELATION COEFFICIENTS BETWEEN
 TWELVE-WEEK BODY WEIGHT AND SIX-WEEK BODY WEIGHT

Gen.	High Line	Low Line	R.S.H. ¹	R.S.L. ²
6	0.250	0.573	0.365**	0.317*
7	0.421**	0.370	0.414**	0.505**
8	0.133	0.465**	0.408**	0.489**
9	0.568**	0.795**	0.663**	0.635**
10	0.641**	0.838**	0.229	0.324
Overall ³	0.245**	0.530**	0.250**	0.407**

¹ Relaxed-selected-high line.

² Relaxed-selected-low line.

³ Correlation coefficients obtained from grouping the five generations together.

* Significant ($P < .05$).

**Significant ($P < .01$).

However, the fifth generation did decline below this value of 1.34 pounds, but remained well above the value of 0.810 pound for the original population. The low-line, six-week mean weight at the fifth generation, prior to the relaxation of selection, was 0.09 pound above the original mean. During the five generations of relaxed selection, the six-week mean weight increased somewhat through the third generation, with very little decrease during the last two generations.

The decline noted during the fourth and fifth generations in both the relaxed-high and relaxed-low line failed to return to the original mean values. This indicates that possibly the genetic makeup controlling six-week weight was changed somewhat from that of the original population, especially in the high line.

March Egg Weight. The mean average egg weight in grams for each line by generations is shown in Figure 8. It should be noted that each generation mean for each line is the mean of all hens' average egg weights. These averages were obtained from all eggs laid during the first ten days of March. The mean egg weight in both the high line and the low line varied somewhat from generation to generation. Even with this irregularity, the response to selection tended to increase egg weight in the high line and decrease egg weight in the low line. There was a greater decrease in the low line than the increase in the high line. The mean egg weight of the low line for the tenth generation was 5.80 grams below the original mean of 54.3 grams. The increased egg weight for the high line was only 3.50 grams above the original mean value.

A linear regression analysis (Table VIII) of the mean egg weights of the high line indicated an average increase per generation of 0.200 ±

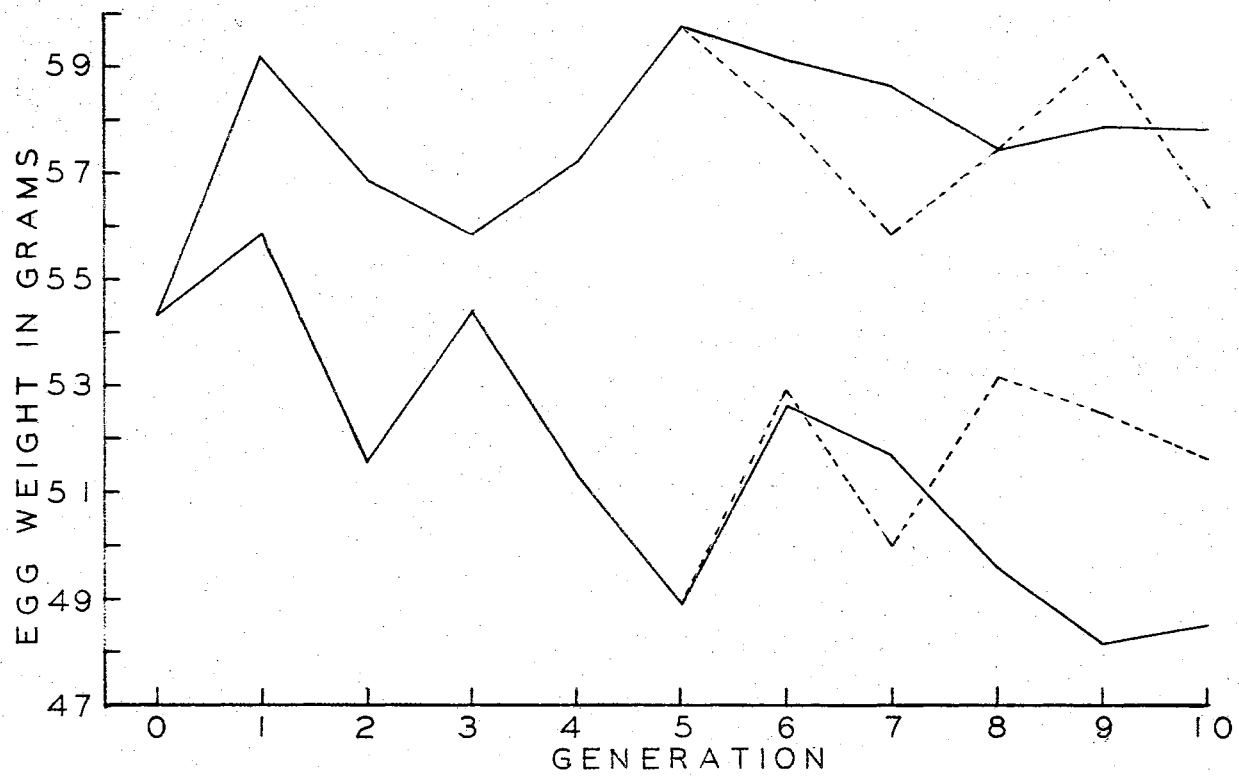


Fig. 8. The Effect of Continuous Selection for 12-week Body Weight on March Egg Weight.

0.144 gram, which was not statistically significant. The analysis of the low line, however, indicated that the mean egg weight in each generation decreased at the rate of 0.632 ± 0.149 gram per generation. This rate of decline was highly significant. This indicated that a possible linear relationship existed between body weight at twelve-weeks and mean egg weight in the low line.

Phenotypic correlation coefficients between body weight at twelve weeks of age and March egg weight, by generations, are summarized in Table IX. The high line was consistently positive in its correlations for most of the generations; however, only the ninth generation showed a statistically significant correlation of 0.430. The overall correlation coefficient of 0.086, determined by combining the last five generations, was not significant. This correlation indicates very little if any direct positive correlation between twelve-week body weights and March egg weights in the high line. The low line, however, did not show any significant correlation for any one generation, but the overall positive correlation coefficient of 0.158 was significant. The low-line overall correlation suggests that a small but consistent positive relationship may exist between twelve-week body weight and March egg weight. The correlations may not have been significant within each generation because of the small number of observations utilized to obtain them.

Neither the relaxed-selected-high nor the relaxed-selected-low line returned toward the original mean egg weight of 54.3 grams. The value for the relaxed high line in the tenth generation was 2.0 grams above the original mean, and the relaxed low line was 2.7 grams below the original mean. Even though the correlation coefficients obtained during the last five generations indicated very little relationship between twelve-week

TABLE VIII
 LINEAR REGRESSION ANALYSIS OF MARCH
 EGG WEIGHT BY GENERATIONS

	High Line	Low Line
Rate of Change (b) ¹	0.200	-0.632**
Variance of (b)	0.021	0.022
Standard Error of (b)	±0.144	±0.149

¹ Slope of the regression line expressed in grams change per generation.
 Shown graphically in Figure 8.

**Significant (P < .01).

TABLE IX
CORRELATION COEFFICIENTS BETWEEN
TWELVE-WEEK BODY WEIGHT AND MARCH EGG WEIGHT

Gen.	High Line	Low Line	R.S.H. ¹	R.S.L. ²
6	-0.026	0.209	0.109	0.029
7	0.218	0.148	0.034	0.201
8	0.210	0.210	0.296*	0.317
9	0.430**	0.107	0.022	0.029
10	0.288	-0.035	0.015	-0.060
Overall ³	0.086	0.158*	0.094	0.122**

¹ Relaxed-selected-high line.

² Relaxed-selected-low line.

³ Correlation coefficients obtained from grouping the five generations together.

* Significant ($P < .05$).

**Significant ($P < .01$).

body weight and March egg weight, the response to relaxed selection indicated that at least the genes which affect egg weight were recombined to some degree.

Sexual Maturity. Age at sexual maturity was determined as the number of days from the date of hatching to the date of the first egg. Age at sexual maturity is generally considered to be inherited. In reports of studies conducted by other workers, however, it is not always clear whether the age at first egg is inherited independently of body size or merely incidental to the inheritance of body size.

The mean age at sexual maturity by generations for each line is shown graphically in Figure 9. Although the generation means fluctuate to a great degree, the low line was consistently higher than the high line. Both lines indicated an overall increase in days required to reach sexual maturity. An analysis of the difference in age at sexual maturity between lines is given in Table X. It was noted that the difference between the high line and the low line was not significant during the first four generations of selection. The difference, however, was highly significant during the last six generations. This would indicate that, even though the overall trend for both lines was to increase, selection for small body size at twelve weeks of age may increase the age at sexual maturity more rapidly than selection for high twelve-week body weight.

The relaxed-selected lines in Figure 9 indicate an almost immediate return toward the original population mean. The relaxed-low line increased abruptly in the first generation and decreased in the second and third, returning almost to the original mean value of 182.5 days. The relaxed-high line, however, decreased consistently through the third generation. During the fourth and fifth generations of relaxed selection,

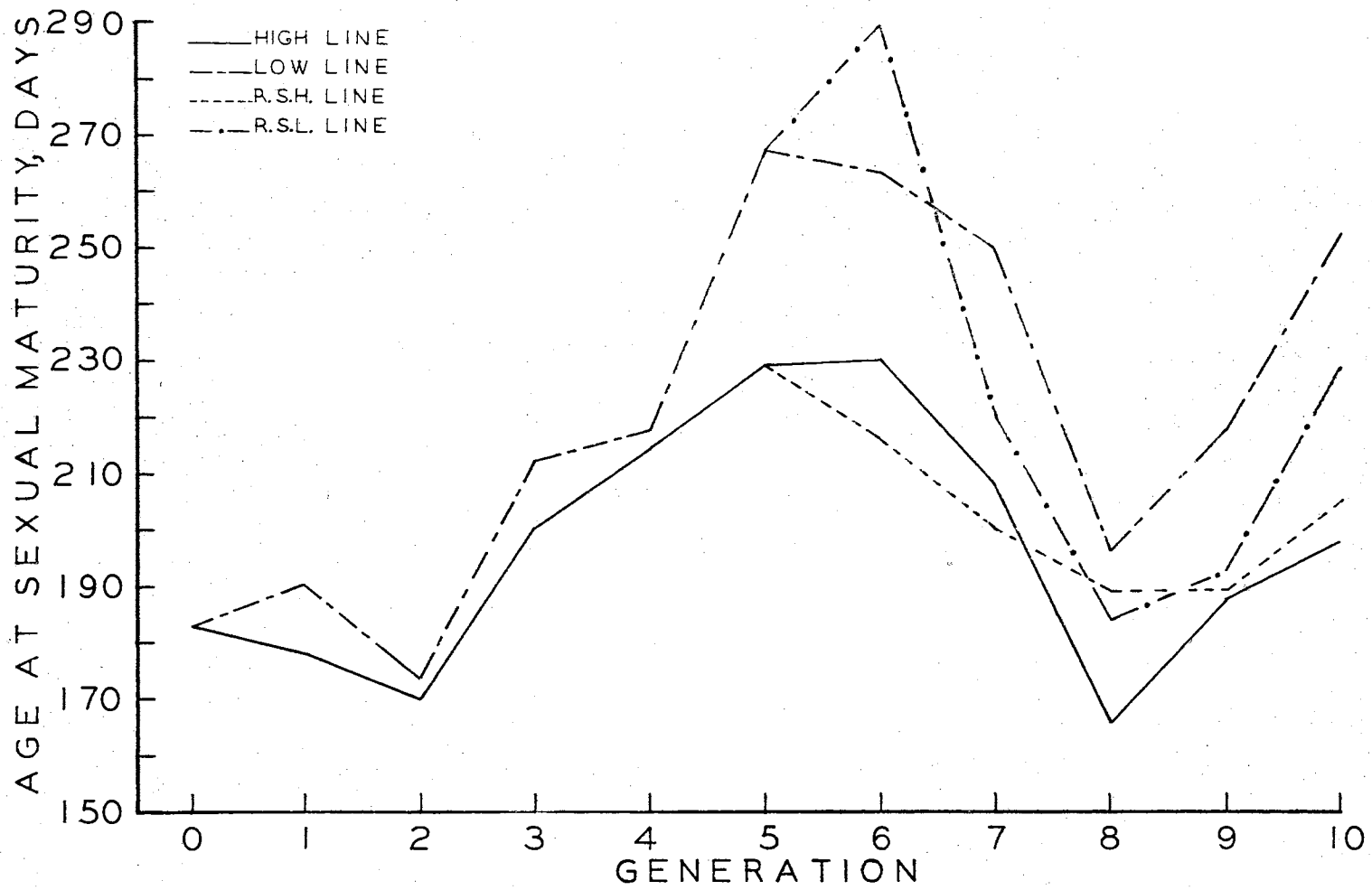


Fig. 9. The Effect of Continuous Selection for 12-week Body Weight on Age at Sexual Maturity.

both lines increased.

The analysis of the generation means (Table X) indicates that the difference between the relaxed high and relaxed low lines remained highly significant until the eighth and ninth generations. It appeared from the almost immediate decrease in both lines toward the original mean value that selection for body size during the first five generations may not have changed permanently the genes controlling sexual maturity.

The overall fluctuation of the selected lines, and the sudden increase observed in the relaxed selected lines, indicate that age at sexual maturity may have been influenced to a great degree by non-genetic variances in this experiment.

Correlation coefficients obtained in this study between twelve-week body weight and age at sexual maturity are shown in Table XI. Statistically significant correlations of -0.355 and 0.485 were determined during the sixth and the seventh generations of high-line selection. Significant correlations were also obtained in the second, fourth and fifth generations of relaxed-high line selection. These correlations were -0.399, -0.612 and 0.780, respectively. The correlations obtained between the selected-low line and the relaxed-selected low line were consistently small and non-significant. The overall correlation coefficients were negative in all lines. However, these correlations were not significant. Since the correlations ranged from significantly positive to significantly negative within lines, a permanent relationship of genetic origin probably does not exist between age at sexual maturity and high twelve-week body weight. This variation encountered, however, may tend to indicate high correlation due to environmental effects.

The results obtained in this study from the high line do not concur

TABLE X
 AGE AT SEXUAL MATURITY AS EFFECTED BY
 SELECTION FOR TWELVE-WEEK BODY WEIGHT

Gen.	<u>Selected Lines</u>			<u>Relaxed Selected Lines</u>		
	High	Low	Difference	High	Low	Difference
0	182.50	---	----	----	---	----
1	178.10	190.30	12.20	----	---	----
2	170.30	172.90	02.60	----	---	----
3	200.40	212.20	11.80	----	---	----
4	214.00	217.00	03.00	----	---	----
5	229.00	267.00	38.00**	----	---	----
6	230.08	263.11	33.03**	216.53	289.36	72.83**
7	208.11	250.08	41.97**	200.63	220.45	19.82**
8	165.65	196.16	30.51**	189.14	184.31	04.83
9	188.59	218.08	29.49**	189.04	192.83	03.79
10	198.12	252.82	54.70**	205.22	229.59	24.37**

**Significant ($P < .01$).

TABLE XI
CORRELATION COEFFICIENTS BETWEEN
TWELVE-WEEK BODY WEIGHT AND AGE AT SEXUAL MATURITY

Gen.	High Line	Low Line	R.S.H. ¹	R.S.L. ²
6	-0.355*	-0.106	0.110	0.090
7	0.485**	0.039	-0.399*	-0.227
8	0.087	-0.065	0.003	-0.052
9	-0.036	0.012	-0.612**	-0.165
10	-0.022	-0.133	0.780**	-0.156
Overall ³	-0.003	-0.030	-0.046	-0.022

1 Relaxed-selected-high line.

2 Relaxed-selected-low line.

3 Correlation coefficients obtained from grouping five generations together.

* Significant ($P < .05$).

**Significant ($P < .01$).

directly with the results reported by Godfrey and Jull (1935), Goodale (1936), and Lerner (1946). In these experiments, age at sexual maturity was automatically increased as a result of selection for greater body size. Similar results were obtained in this study during the first five generations of selection for high body weight at twelve-weeks of age. When all generations are considered, however, the effect of selection for increased twelve-week body weight was lowered to a great degree by the negative response of age at sexual maturity to selection for increased body weight during the last five generations. The same response is also exhibited for selection for low twelve-week body weight. The overall results and the low correlation coefficients obtained in this study tend to indicate that age at sexual maturity is more highly influenced by environmental changes than by change in body weight at twelve weeks of age. These results are similar to those obtained by Hays and Sanborn (1939) and Waters (1934), which indicated that age at sexual maturity was influenced by genes apart from those affecting body weight.

Reproductive Performance. The data on reproductive performance of the two selected lines are summarized in Table XII. Measurements of percentage fertile eggs, and percentage hatch of fertile eggs, were described previously.

The data on percentage of fertile eggs, as shown in Table XII, indicate a significant difference in fertility in the third, fifth, seventh and eighth generations of selection. It should be noted, however, that in considering all generations, neither line indicates a superiority of fertility over the other line. The average percentage of fertility over all generations was 84.4 percent for the high line and

TABLE XII
REPRODUCTIVE PERFORMANCE OF THE SELECTED LINES

Gen.	% Fertility			% Hatch of Fertile Eggs		
	High	Low	Difference	High	Low	Difference
0	81.00	---	----	94.0	---	----
1	91.5	90.0	01.5	76.6	71.8	04.8
2	93.1	90.0	03.1	91.2	87.6	03.6
3	84.2	76.1	08.1*	88.5	75.0	13.5*
4	90.0	82.3	07.7	92.4	89.0	03.4
5	77.1	88.9	11.8*	82.2	82.0	00.2
6	88.8	90.9	02.1	74.2	70.1	04.1
7	92.3	76.3	16.0*	79.3	75.6	03.7
8	71.4	96.0	24.6**	70.2	78.5	08.3
9	69.7	78.2	10.3	77.6	86.2	08.6
10	85.8	93.4	07.6	77.5	76.7	00.8

*Significant (P < .05).

**Significant (P < .01).

86.2 percent for the low line. In comparison to the original mean of 81.0 percent, the data for both lines indicate that percentage fertility was increased. The increase, however, was not significant.

An analysis of the percentage hatch of fertile eggs indicates that a significant difference did not exist between the two selected lines, with the exception of the third generation. The high line, however, was consistently higher than the low line. When comparing the selected lines to the original mean, both the high and the low lines indicate a non-significant decrease in percentage hatch of fertile eggs.

The data on percentage of fertility and percentage hatch of fertile eggs for both the relaxed-selected high and the relaxed-selected low lines are summarized in Table XIII. Due to the large amount of fluctuation in the relaxed high line, an accurate account of the influence of relaxed selection could not be determined. This fluctuation may possibly have been due to extreme environmental conditions exerted against the reproductive performance of the relaxed lines. Although the variation was not as great in the relaxed-selected-low lines, the difference between the two relaxed-selected lines was not significant, except for the ninth generation. The relaxed-low line indicated that percentage fertility remained above the original mean, with the exception of the seventh generation. In comparisons of the performance of the relaxed-selected-low line to the performance of the fifth generation of selection for low body weight, the relaxed line decreased; however, this decrease was not statistically significant. The comparisons of the overall generation means of the relaxed-high line and the fifth generation of selection for high body weight indicate no significant difference.

In comparing the percentage hatch of fertile eggs the relaxed-

TABLE XIII
REPRODUCTIVE PERFORMANCE OF THE RELAXED LINES

Gen.	% Fertility			% Hatch of Fertile Eggs		
	High	Low	Difference	High	Low	Difference
6	90.0	82.3	07.7	89.7	90.2	00.5
7	61.9	66.3	04.4	78.9	87.3	08.4
8	83.5	84.8	01.3	75.7	86.5	10.8
9	58.9	85.2	26.3**	77.2	81.9	04.7
10	78.8	83.2	04.4	80.3	83.8	03.5

**Significant ($P < .01$).

selected-high and relaxed-selected-low lines showed no significant difference during the five generations. The overall comparison of these lines to the original mean indicates that there was no tendency to return toward the original mean. It may be noted that both of the relaxed lines remained at about the same level as that of the fifth generation of the selected lines. This would tend to indicate that relaxation of selection may not have changed the overall reproductive performance of these lines.

Egg Production. In this study, egg production records were maintained through 500 days of age. Three measurements of egg production are given in Table XIV. Hen-housed egg production was determined as the average egg production of all pullets housed. Survivor egg production was the average number of eggs produced by only those hens which lived through the 500th day of age. Percentage of egg production was determined as the average percentage egg production per production day. In order to obtain this measurement, the days of age at sexual maturity were subtracted from the smaller of two numbers, either the number of days lived or 500 days. This was determined to be the number of production days for each hen. The percentage egg production for each hen was determined from the number of eggs laid during her production days. The average of these percentages determined the average percentage production for the line in question.

An analysis of the difference between the high line and the low line, in hen-housed egg production (Table XIV), indicates that the difference was not significant until the seventh generation. Even though several earlier generations showed a high mean difference, it was not significant because the variance within lines was greater than the variance between lines.

TABLE XIV
EGG PRODUCTION IN THE SELECTED LINES

Gen.	<u>Hen-Housed Production¹</u>			<u>Survivor Production²</u>			<u>% Egg Production³</u>		
	High	Low	Difference	High	Low	Difference	High	Low	Difference
0	122.0	---	-----	-----	---	-----	45.0	---	-----
1	149.7	78.8	70.9	154.2	87.9	66.3	47.3	33.0	14.3**
2	111.5	122.4	10.9	126.6	139.2	12.5	40.3	44.8	04.5
3	128.6	127.5	01.1	133.3	130.9	02.3	49.4	49.3	00.1
4	89.3	99.2	09.9	128.6	124.1	04.6	49.9	47.1	02.8
5	99.0	76.0	23.0	112.0	108.0	04.0	44.7	47.9	03.2
6	132.0	87.0	45.0	134.0	107.0	27.0	52.8	50.3	02.5
7	105.0	78.0	27.0**	117.0	91.0	26.0**	47.4	44.2	03.2
8	118.0	102.0	16.0	131.0	121.0	10.0	47.5	45.0	02.5
9	117.0	86.1	30.9**	130.3	98.5	31.8**	44.1	37.8	06.3**
10	135.4	70.9	64.5**	139.0	78.6	60.4**	46.3	33.0	13.3**

¹ Average number of eggs produced by all pullets housed, 500-day test period.

² Average number of eggs produced by survivors of 500-day test period.

³ Average percentage of production per production day (see text).

* Significant (P < .05).

**Significant (P < .01).

Similar results were also obtained in the analysis of survivor egg production (Table XIV). In this analysis, however, only three of the last four generations indicated a significant difference. The differences obtained were smaller than those obtained from the analysis of hen-housed egg production.

All sources of variation which are measured by hen-housed egg production and survivor egg production should be considered. In measuring hen-housed production, not only egg production is measured but also mortality during the laying period and the effects of age at sexual maturity. Survivor egg production may be a better measure of egg production than hen-housed egg production, since it is not influenced by the mortality during the laying period. In this study, as previously discussed, age at sexual maturity was increased by each succeeding generation of selection. Thus, the influence of sexual maturity may have caused both hen-housed and survivor egg production measurements to be biased. The transformation of egg numbers to percentages would remove most of the variation due to age at sexual maturity and mortality during the laying period.

The analysis of the percentage of egg production, as given in Table XIV, indicated that a highly significant difference was obtained during the first, ninth and tenth generations only. Since the percentage of egg production is influenced to a lesser degree by age at sexual maturity than either hen-housed or survivor egg production, this analysis may be considered more conclusive in determining the actual differences. This would tend to indicate that selection for twelve-week body weight may have very little influence on egg production directly. This is substantiated by the analysis of the effects of relaxed selection (Table

TABLE XV

EGG PRODUCTION IN THE RELAXED-SELECTED LINES

Gen.	<u>Hen-Housed Production</u> ¹			<u>Survivor Production</u> ²			<u>% Egg Production</u> ³		
	High	Low	Difference	High	Low	Difference	High	Low	Difference
6	89.3	99.2	09.9	128.6	124.1	04.5	50.7	50.6	00.1
7	110.0	92.0	18.0	148.1	107.1	41.0	47.6	47.8	00.2
8	119.0	103.0	16.0**	144.1	138.1	06.0	42.2	52.4	10.2**
9	108.0	126.0	18.0**	125.1	155.1	30.0**	41.6	44.1	02.5
10	107.8	112.9	05.1	131.1	128.5	02.6	44.9	45.5	00.6

¹ Average number of eggs produced by all pullets housed, 500-day test period.

² Average number of egg produced by survivors of 500-day test period.

³ Average percentage of production per production day (see text).

**Significant (P < .01).

XV). If selection for twelve-week body weight had exerted a permanent change in egg production, then the relaxed-selected lines would have remained subsequently unchanged from that of the fifth generation of selection. The results as shown in Table XV suggest that neither the relaxed-high nor the relaxed-low line remained at the proposed consistent level of production.

The fluctuation exhibited by the relaxed-selected lines, however, was very similar to that shown by the regular selected lines. The fluctuation may be caused by non-genetic influences and therefore may overshadow any effects due to genetic sources.

In the analysis of the simple correlations (Table XVI) obtained between twelve-week body weight and percentage of egg production, two generations of the relaxed-selected low line were significant. These coefficients were 0.328 in the seventh generation and 0.287 in the tenth generation. The overall correlation coefficients obtained in the high line, the low line, the relaxed-high line and the relaxed-low line were 0.018, 0.048, 0.003 and 0.032, respectively. This would seem to provide additional evidence that a correlation did not exist between body weight at twelve-weeks of age and subsequent percentage of egg production in this study.

TABLE XVI
 CORRELATION COEFFICIENTS BETWEEN TWELVE-WEEK
 BODY WEIGHT AND PERCENTAGE OF EGG PRODUCTION

Gen.	High Line	Low Line	R.S.H. ¹	R.S.L. ²
6	0.007	0.052	0.021	-0.105
7	-0.178	0.110	0.304	0.328*
8	0.029	-0.170	-0.253	0.008
9	-0.043	0.249	0.024	-0.156
10	0.310	0.196	0.034	0.287*
Overall ³	0.018	0.048	0.003	0.032

¹Relaxed-selected-high line.

²Relaxed-selected-low line.

³Correlation coefficients obtained from grouping the five generations together.

*Significant ($P < .05$).

SUMMARY

Data were collected from ten generations of selection for high and low twelve-week body weight and for five generations of relaxed selection for twelve-week body weight in the Silver Oklabar chicken. This study involved approximately 320 sires, 2300 dams and 15,500 chicks.

The results of the two-way selection study indicated that the response to selection for high and low twelve-week body weight tended to be asymmetrical. Selection produced a greater change in the high line than in the low line. The rate of change per generation in twelve-week body weight, based on the regression analysis, was 0.16 pound in the high line and only 0.03 pound in the low line. The average response per generation for the two-way selection was 0.18 pound. The rate of change was highly significant in the high line; in the two-way selection, however, the rate of change in the low line was not significant.

The heritability of body weight at twelve-weeks of age, determined as the realized heritability, was 34.4 percent in the high line, 7.2 percent in the low line and 22.2 percent for the two-way selection. The difference of 27.2 percent obtained between the high line and the low line was highly significant.

During this selection experiment the phenotypic variation (coefficient of variation) was decreased from 15.0 percent, exhibited in the original stock, to about 4.0 percent in the tenth generation of the high line. The phenotypic variation in the low line increased greatly during the first five generations of selection, and subsequently the variation in

the tenth generation was unchanged from that of the original stock.

After the initiation of relaxed selection during the fifth generation of selection, the high line showed a non-significant increase in body weight at twelve weeks of age. The relaxed-selected-low line returned almost immediately toward the mean of the original stock.

Several traits measured in this study exhibited a correlated response to selection for twelve-week body weight. The regression analysis of six-week body weight indicated a highly significant increase of 0.09 pound per generation in the high line. The low line six-week body weight decreased at a non-significant rate of 0.01 pound per generation. A correlated response was also noted in March egg weight. The regression analysis of the March egg weight means of the high line indicated an increase of 0.2 gram per generation. This rate of increase was not statistically significant. The analysis of the low line, however, indicated that the March egg weight mean was decreased 0.6 gram per generation. This rate of decline was highly significant.

It was further noted that age at sexual maturity also exhibited a correlated response; however, this response was not as definite as the response of March egg weight or the response of six-week body weight. The tendency over all generations was to increase age to sexual maturity in both lines during the first five generations and to decrease this age during the last five generations.

Highly significant phenotypic correlations were obtained between body weight at twelve weeks of age and body weight at six weeks of age in both selected lines. These correlations were 0.245 in the high line and 0.530 in the low line. A significant phenotypic correlation of 0.158 was also obtained between twelve week body weight and March egg

weight in the low line. The correlation of 0.090 in the high line was not significant. The phenotypic correlations obtained in this study between twelve-week body weight and age at sexual maturity were not significant in either selected line.

The average percentage of fertile eggs set over all generations was 84.4 percent for the high line and 86.2 percent for the low line. Both the high line and the low line exhibited a small but non-significant increase in percentages of fertile eggs over the original stock. An analysis of the percentage hatch of fertile eggs indicated that the two selected lines decreased when compared to the original mean. This decrease, however, was not significant.

A significant difference did not occur between the two selected lines in percentage of egg production, until the last two generations. The average percentage of egg production was 47.0 percent in the high line and 43.0 percent in the low line.

Other phenotypic differences between the high line and the low line were also observed. Considerable variation was noted in the egg shell color of the high line, whereas the low line was uniformly colored. Although the original stock was assumed to be "pure" for the silver gene, gold plumage color has been observed in some of the high-line females. The gold gene has not been observed in the low line, however. A further difference has also been observed in the activity exhibited by the two lines. The high line has become less active and more docile, while the activity and nervousness of the low line have increased considerably.

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