

TWO-WAY SELECTION FOR BODY WEIGHT IN CHICKENS

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Two-Way Selection for Body Weight in Chickens

By M. A. Maloney, J. C. Gilbreath,
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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, the nation's broiler breeders are still confronted with the constant challenge of future requirements.

Some of the most extensive selection experiments in body size have been reported in laboratory animals by MacArthur (1944), Falconer (1953) and Robertson (1955). In comparison, however, there is little basic information on the effects of long-term selection for body size in young chickens, especially at broiler age. Even though body size is highly influenced by selection (Waters, 1931; Asmundson and Lerner, 1933; Gyles *et al.*, 1955; Martin *et al.*, 1953; Siegel, 1962) there is only a small amount of information available to suggest the maximum body size which might be obtained through selection.

Selection experiments for the improvement of certain traits have frequently resulted in the occurrence of a correlated response in an unselected trait (Mather and Harrison, 1949; Lerner, 1946, Lerner, 1950; Falconer, 1954). Since the occurrence of a correlated response is important in any selection program it would be advantageous to know the possible effect that long-term selection may have on other traits of economic importance.

This bulletin reports results of a study conducted to determine some of the influences of long-term selection for body size at twelve-weeks of age and its subsequent effects on other economic traits.

Experimental Procedure

This study involved ten generations of selection for high and low body weight at twelve weeks of age. A report on the effects of relaxed

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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 study included approximately 320 sires, 2,300 dams and 15,500 chicks.

The stock used in this investigation was the Silver Oklabar breed from the Oklahoma Agricultural Experiment Station. The Silver Oklabar was developed over a period of several years by Dr. R. George Jaap, poultry geneticist at Oklahoma State University from 1935 to 1946. The Silver Oklabar is a columbian-patterned bird 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 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.

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 inbreeding.

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

At six and 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 trap-nested 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 pedigree 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 12-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 expected selection differential was 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 high line was consistently higher than the low line with respect to the total selection differentials (Table I). 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 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 in this study, since there was very little difference between the weighted and the unweighted differentials.

Response to Selection. Figure 1 shows the response to selection for twelve week body weight of each line separately for the ten generations. The points plotted are the generation twelve-week weight means of the averages of the sexes combined. 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

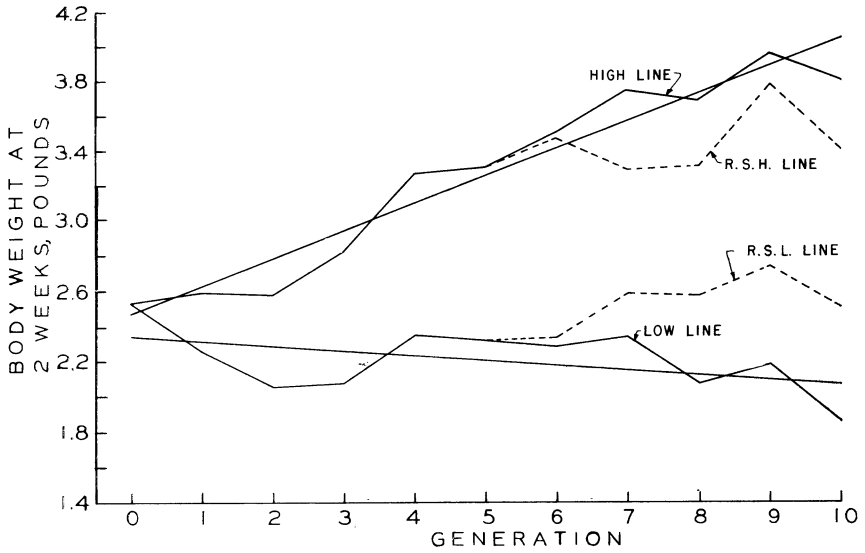


Figure 1. The effect of continuous selection on 12-week body weight

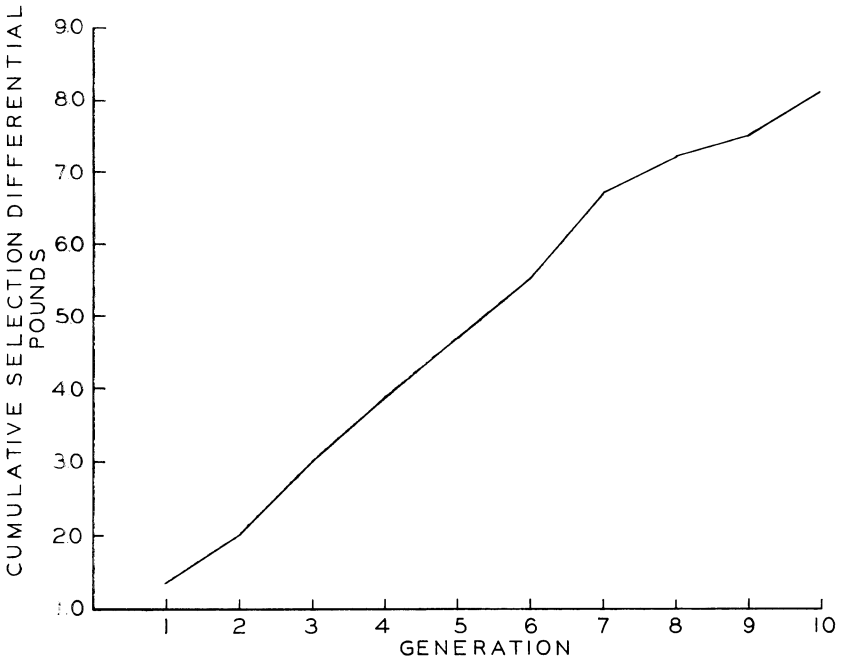


Figure 2. The cumulative selection differential in selection for 12-week body weight.

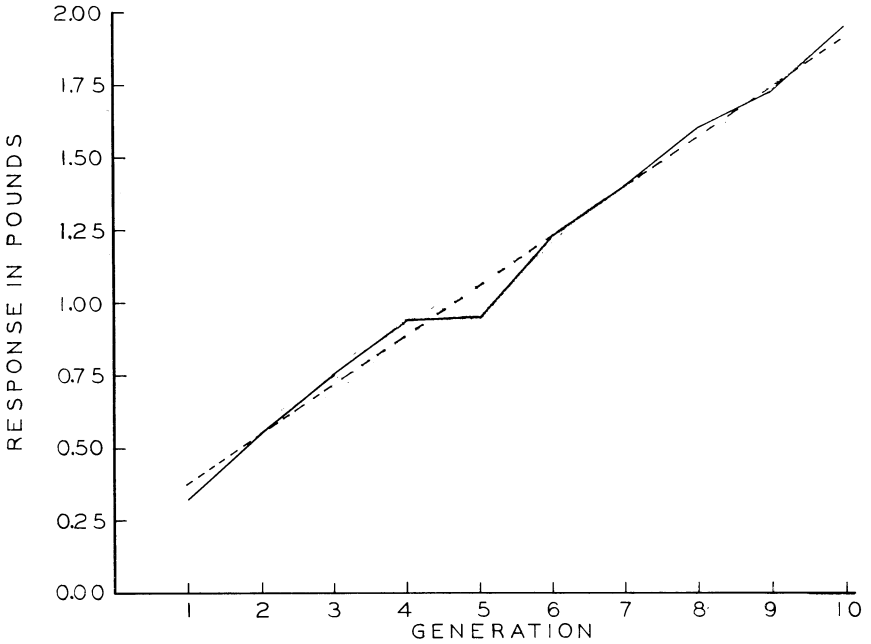


Figure 3. The effect of continuous 2-way selection on 12-week body weight. (Response measured as difference between high and low line 12-week body weight means.)

weeks of age. 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, but 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 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. 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 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 judgment 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 dif-

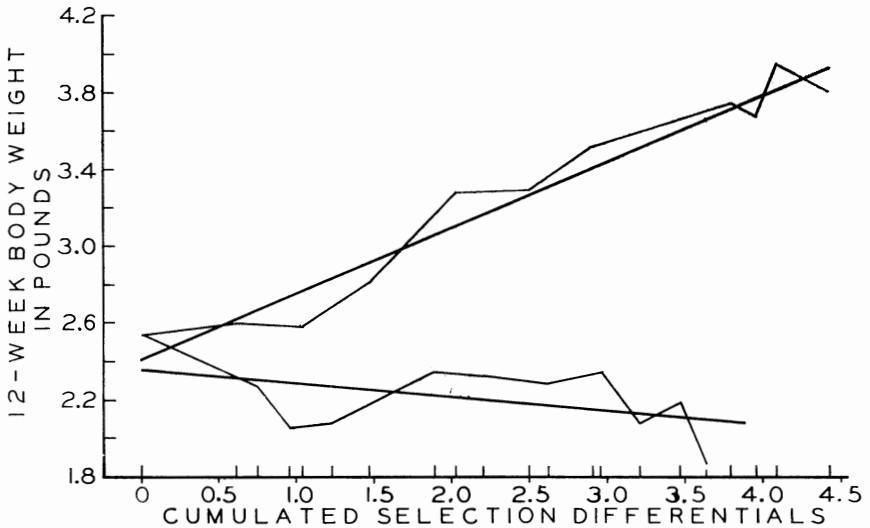


Figure 4. The high and low line realized heritability of 12-week body weight.

ference 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 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

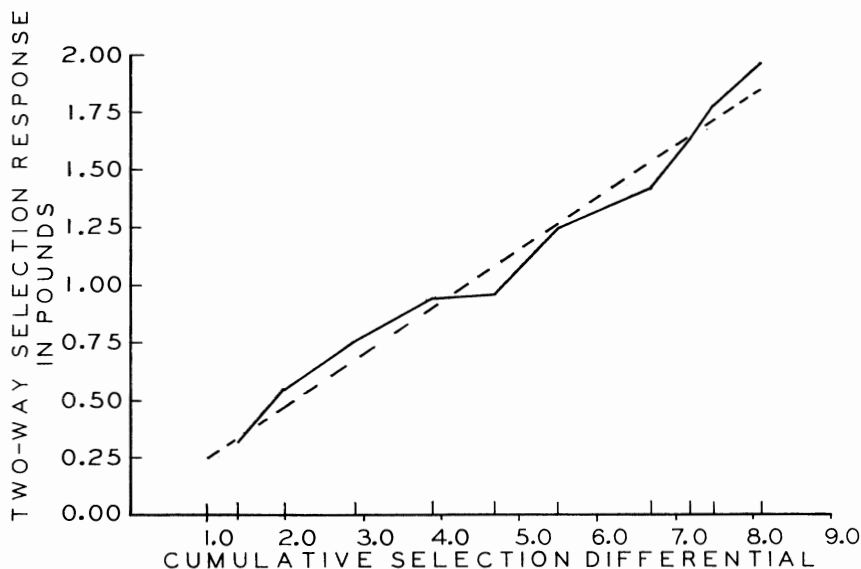


Figure 5. The 2-way selection realized heritability of 12-week body weight. (Response measured as difference between high and low line 12-week body weight means.)

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 per-

manent 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 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

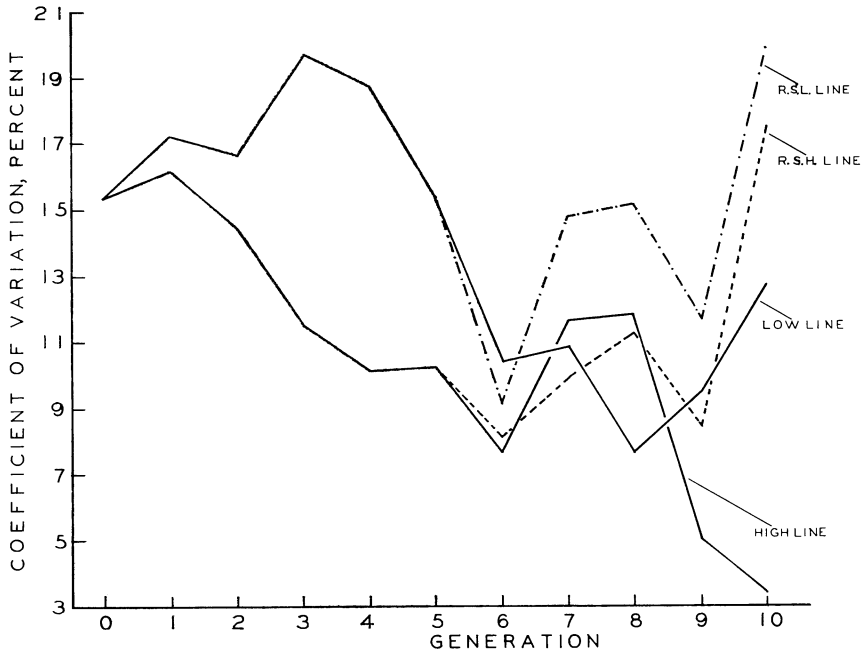


Figure 6. The effect of continuous selection on variability of 12-week body weight.

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 homostasis" by Lerner (1950).

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. 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

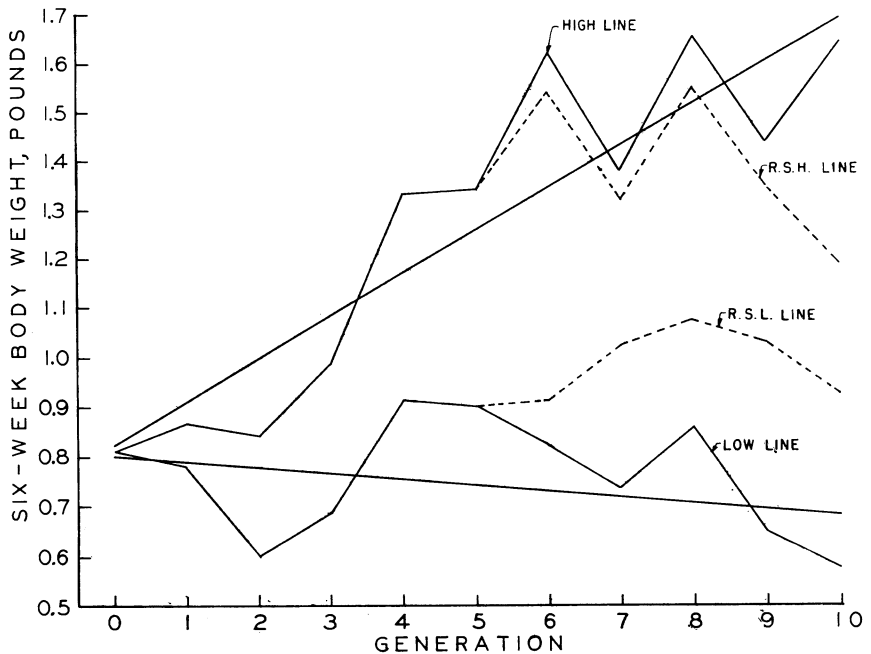


Figure 7. The effect of continuous selection for 12-week body weight on 6-week body weight.

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 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. 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

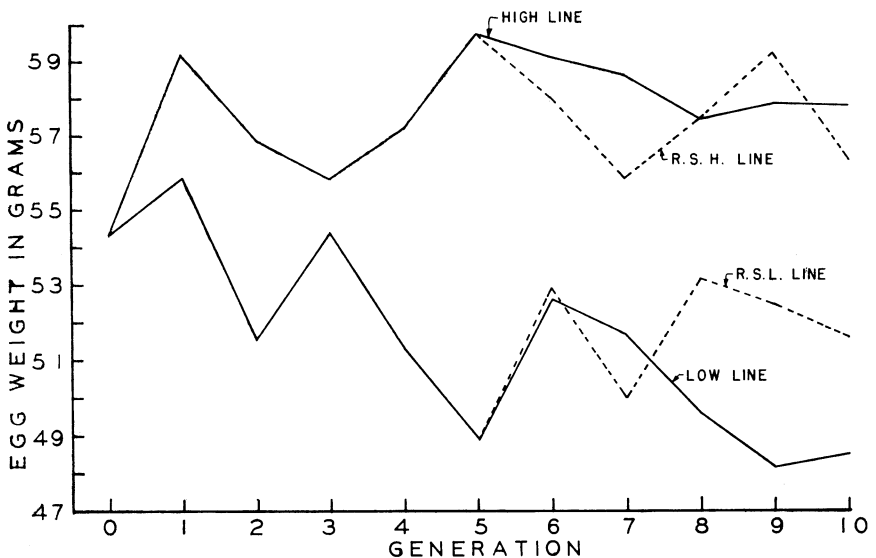


Figure 8. The effect of continuous selection for 12-week body weight on March egg weight.

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 ± 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 lines 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 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

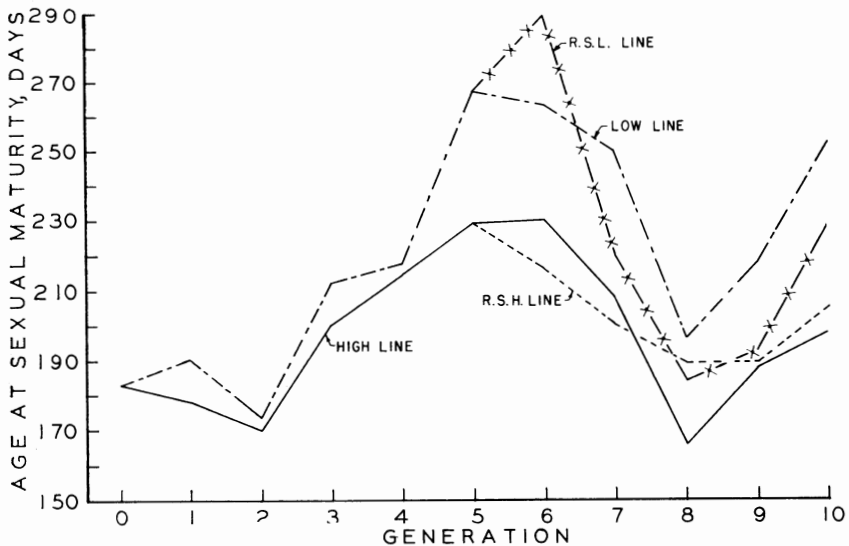


Figure 9. The effect of continuous selection for 12-week body weight on age at sexual maturity.

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, 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 from the high line do not concur 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 of 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 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 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-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.

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 dis-

cussed, 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 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.

Other Phenotypic Differences. 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.

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, 2,300 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.

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TABLE I
Selection Differentials

Gen.	Expected	High Line		Expected	Low Line	
		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	

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.

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)	±0.016	±0.016	±0.0049

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).

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

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

² Regression analysis of Figure 4.

³ Regression analysis of Figure 5.

Realized Heritability Estimates from Regression Analysis of Response to the Cumulated Selection Differential

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

¹ Realized heritability expressed in percentages.

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)	±0.015	±0.011

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

**Significant (P<.01).

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).

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 ($P < .01$).

TABLE X
Age at Sexual Maturity as Effected by
Selection for Twelve-Week Body Weight

Gen.	Selected Lines			Relaxed Selected Lines		
	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 the five generations together.

* Significant ($P < .05$).

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

TABLE XII
Reproductive Performance of the Selected Lines

Gen.	% Fertility			% Hatch of Fertile Eggs		
	High	Low	Difference	High	Low	Difference
0	81.0	---	---	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	09.1*	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 ($P < .01$).

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 ($P < .01$).

TABLE XIV
Egg Production in the Selected Lines

Gen.	Hen-Housed Production ¹			Survivor Production ²			% Egg Production ³		
	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 ($P < .01$).

TABLE XV
Egg Production in the Relaxed-Selected Lines

Gen.	Hen-Housed Production ¹			Survivor Production ²			% Egg Production 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 eggs produced by survivors of 500-day test period.

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

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

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

¹ Relaxed-selected-high line.

² Relaxed-selected-low line.

³ Correlation coefficients obtained from grouping the five generations together.

* Significant ($P < .05$).

Oklahoma's Wealth in Agriculture

Agriculture is Oklahoma's number one industry. It has more capital invested and employs more people than any other industry in the state. Farms and ranches alone represent a capital investment of four billion dollars—three billion in land and buildings, one-half billion in machinery and, one-half billion in livestock.

Farm income currently amounts to more than \$700,000,000 annually. The value added by manufacture of farm products adds another \$130,000,000 annually.

Some 175,000 Oklahomans manage and operate its nearly 100,000 farms and ranches. Another 14,000 workers are required to keep farmers supplied with production items. Approximately 300,000 full-time employees are engaged by the firms that market and process Oklahoma farm products.