Genetic progress through a mating system involving alternating intensive inbreeding with wide outbreeding

by Darrel Gene Keller

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE IN Animal Science
Montana State University

Abstract:
A selection experiment was undertaken with White Leghorn chickens and Japanese quail as the experimental species. Two replicated experimental groups under selection were set up in each species. In treatment 1, the mating procedure involved alternating generations of inbreeding and outbreeding. Treatment 2 involved random mating. In these trials the controls in the two species differ as follows; The chicken genetically stabilized Cornell population is reproduced on a one for one basis at Purdue from where the hatching-eggs are obtained to synchronize with experimental generations. The locally reared Japanese quail control population, while chosen at random with respect to merit and mated at random with respect to relationship, is hatched proportionate to the number of eggs produced by each female during the hatching-egg saving period.

In the chickens and quail, the primary concern was with the changes in 8 quantitative measurements relative to treatments and generations.

The 8 measurements (traits) are bird weight, shank length, shank width, total egg weight (average egg weight x total egg number), total egg number, index (total egg weight/body mass), average egg weight, and shank length x shank width, The nested classification in analysis of variance was used on the data to test the difference among treatments. Duncan’s Multiple Range test was used to interpret the difference between breeding treatments. Linear regressions of all traits on generations (time) were calculated to examine time trends.

In the quail experiment, the data indicate there is no consistent trend in treatments 1 and 2 that is different from the controls. The lack of response to selection may be due to the loss of heterozygosity in treatments 1 and 2 since they were the result of an outbred foundation stock while the controls were from a straightbred line. Likewise, the alternating inbred generations clearly exhibited inbreeding depression in all traits.

There are not enough generations in the chicken study to exhibit definite trends in any trait excepting the observed inbreeding depression in the treatment 1 index.

Currently, in the continuing breeding project, the quail and chicken data indicate progress in the selection criterion (index) may have been confounded by environment and/or natural selection.

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ABSTRACT

A selection experiment was undertaken with White Leghorn chickens and Japanese quail as the experimental species. Two replicated experimental groups under selection were set up in each species. In treatment 1, the mating procedure involved alternating generations of inbreeding and outbreeding. Treatment 2 involved random mating. In these trials the controls in the two species differ as follows: The chicken genetically stabilized Cornell population is reproduced on a one for one basis at Purdue from where the hatching-eggs are obtained to synchronize with experimental generations. The locally reared Japanese quail control population, while chosen at random with respect to merit and mated at random with respect to relationship, is hatched proportionate to the number of eggs produced by each female during the hatching-egg saving period.

In the chickens and quail, the primary concern was with the changes in 8 quantitative measurements relative to treatments and generations. The 8 measurements (traits) are bird weight, shank length, shank width, total egg weight (average egg weight x total egg number), total egg number, index (total egg weight ÷ body mass), average egg weight, and shank length x shank width.

The nested classification in analysis of variance was used on the data to test the difference among treatments. Duncan's Multiple Range test was used to interpret the difference between breeding treatments. Linear regressions of all traits on generations (time) were calculated to examine time trends.

In the quail experiment, the data indicate there is no consistent trend in treatments 1 and 2 that is different from the controls. The lack of response to selection may be due to the loss of heterozygosity in treatments 1 and 2 since they were the result of an outbred foundation stock while the controls were from a straightbred line. Likewise, the alternating inbred generations clearly exhibited inbreeding depression in all traits.

There are not enough generations in the chicken study to exhibit definite trends in any trait excepting the observed inbreeding depression in the treatment 1 index.

Currently, in the continuing breeding project, the quail and chicken data indicate progress in the selection criterion (index) may have been confounded by environment and/or natural selection.

INTRODUCTION

Flower (1966) indicated that inbreeding reduces productivity in most selection systems, yet produces dependability in crossing. Cycles of inbreeding and synthesis of converged population have yielded progress in both the succeeding cycles of inbreds and of synthetics. It is proposed that increment in inbreeding per generation rather than total amount of inbreeding may provide opportunity for a combination of genetic drift and selection to exert maximum effect in producing and choosing genotypes yielding progress toward chosen goals. Alternating generations of intense inbreeding with wide outcrossing in a closed population maximizes or near-maximizes this increment, yet hedges effectively against reduction in frequency of genes which increase productivity.

The present experiment compares selection progress when alternating inbreeding and outbreeding in closed populations of Japanese quail and White Leghorn chickens with random mating in similar populations.

REVIEW OF LITERATURE

There have been many different breeding schemes developed in recent years that have contributed to the productiveness of domesticated animals. The present experiment is concerned with the effects of alternating full sib mating with wide outcrossing in succeeding generations with selection in each generation; therefore the following will be reviewed for their effect on many important characteristics that are affected by controlled breeding programs: (a) Classical work on inbreeding and linecrossing in guinea pigs, (b) inbreeding in Japanese quail, (c) inbreeding and linecrossing in chickens, (d) evidence of opportunity for progress in the present experiment from corn breeding.

The Effects of Inbreeding and Linecrossing on Guinea Pigs

Wright (1922) looked at the possible effects of inbreeding on age of maturity, fertility, rate of growth, mortality among the young, resistance to tuberculosis, the production of monstrosities, and coat color in guinea pigs. With respect to fertility, both the size and frequency of litters were considered.

The data on the rate of growth up to the age of weaning (33 days) were studied. The principle observations used in this connection were the weight at birth of all the young born, the birth weight of those which survive to 33 days, and the gain between birth and 33 days. The losses among the young are considered under two headings, death at or before birth and death between birth and weaning. The characters used are the percentage born and found alive and the percentage raised to 33 days of those born alive. The product of these two, namely, the total percentage raised, was used. A decline in vigor in all the characteristics studied during the course of 13 years of full sib inbreeding of the guinea pigs was reported. The decline was most marked in the frequency of litter and the size of litter. The decline was greater in the post-natal gains than in the birth weight, and greater in the percentage raised of the young born alive than in the percentage born alive. The ability to raise large litters was reduced much more than ability to raise small litters.

Wright reported that the comparison of the inbred guinea pigs with a control stock raised under identical conditions without inbreeding, and derived from the same linebred stock as the inbred families, indicates that the inbreds suffered a genetic decline in vigor in all characteristics. The decline in fertility was again shown to be most marked. Experimental inoculation with tuberculosis showed that the inbreds were inferior, on the average, to the controls in disease resistance.

Differentiation Among the Inbreds

Wright (1922) found that a certain color or pattern tended to become fixed automatically in each line of decent. In certain cases, an entire family came to breed true to a given color and pattern.

Relatively few monstrosities were produced either by the inbreds or the controls. The tendency to produce a given type of monstrosity was characteristic of certain families.

The study illustrates that one of the most important results of inbreeding is the bringing to light and fixing of characteristics in a family.

Crosses Between Highly Inbred Families

Wright (1922a) reported that crosses between inbred families resulted in a marked improvement over both parental stocks in every respect. The relatively small improvement in crossbred matings in each separate trait is compounded into an increase of over 80 percent in the combination. This goes well beyond the superiority of the random-bred control stocks over the inbreds.

The fundamental effect of inbreeding is the increase in homozygosis. Wright concluded that the average decline in vigor is the consequence of the observed fact that recessive factors, more extensively brought into expression by an increase in homozygosis, are more likely to be deleterious than their dominant alleles. The differentiation among the families is due to the chance fixation of different combinations of the factors present in the original heterozygous stock. Crossing results in improvement, because each family in general supplies some dominant factors lacking in the others. Dominance or imperfect dominance in each unit character is built up into a pronounced improvement over both parental stocks in the complex characters actually observed.

Inbreeding in Japanese Quail

Sittmann, Abplanalp, and Fraser (1966) have reported on the inbreeding depression in Japanese quail. Their experiment was designed to assess the response of Japanese quail to rapid inbreeding. By full-sib mating, these workers report that there is a complete loss of reproductive fitness by the third generation ($Fx = 0.5$) due to inbreeding depression. They also studied hatchability, variability and fertility in connection with inbreeding. They stated that the probability of zygote reaching maturity and leaving offspring was reduced from 0.3 in the controls to 0.1 by one generation of full-sib mating and practically zero by three generations. Hatchability declined by 7 percent and fertility by 11 percent for each 10 percent increment in inbreeding of the progeny.

Inbreeding in Poultry (Chickens)

Hays (1935) reported that in general, the daughters of individual males showed little consistent reduction in variability in different characters that could be traced to the degree of inbreeding of their sire. The data does show a slightly reduced variability for such characters as sexual maturity, body weight, and egg weight in daughters of inbred males with no reduction in variability of annual egg production. Annual egg production was significantly lowered by the use of inbred males.

Waters and Lambert (1936) reported the effects of 10 years of inbreeding in White Leghorn fowl with the intention of developing inbred lines homozygous for a number of characters. The full-sib matings of one family were maintained successfully for nine generations. The inbreeding coefficients for the birds in a most recent generation in three families reported was approximately 41, 61 and 83 percent and there was no selective elimination.

The fertility did not decrease for all the inbreds as the inbreeding coefficient increased. The percentage hatchability of fertile eggs for all the inbreds decreased slightly, but in only one case did it go below 62 percent. There was a slight decrease in both 200-day egg production and for annual egg production in the more highly inbred groups. Egg weight remained fairly constant throughout the entire inbreeding program.

Shoffner (1947) reports that there is an average reduction of 0.4 percent in hatchability and an average decrease in egg production of 0.9 percent of an egg for every one percent increase in the inbreeding coefficient. He reported that there is no correlation between inbreeding and egg weight.

Crossing Inbred Lines in Chickens

Maw (1941) reported little improvement in the progeny from crosses between related families. Crosses between unrelated inbred lines gave a progeny whose records were considerably better than the parental stock and random bred controls.

Corn Breeding

Mass Selection

According to Allard (1960) in mass selection, desirable plants are chosen, harvested and the seed composited without progeny test to produce the following generation. Since selection is based on the maternal parent only, and there is no control over pollination, mass selection amounts to a form of random mating with selection. The purpose of mass selection is to increase the proportion of superior genotypes in the population. Allard reported that the efficiency with which this is accomplished under system of random mating with selection depends primarily on gene numbers and heritability.

Mass selection has been effective in increasing gene frequencies for characters which are easily seen or measured. In corn, it was possible by mass selection to develop varieties differing in color of grain, plant height, size of ear, placement of ear on the stalk, date of maturity, the percentage of oil and protein. Mass selection has thus been useful in developing varieties for special purposes in changing the adaptation of varieties to fit them to new production areas.

On the other hand, mass selection has not been effective in modifying characters, such as yield, that are governed by many genes and cannot be accurately judged on the basis of the appearance of single plants. Thus this method of breeding has proved to be almost powerless to affect the yield of adapted varieties, at least in short-term breeding projects.

The ineffectiveness of mass selection in increasing the yield of adapted varieties results from three main causes: (1) Inability to identify superior genotypes from the phenotypic appearance of single plants, (2) uncontrolled pollination, so that selected plants are pollinated by both superior and inferior pollen parents, and (3) strict selection leading to reduced population size, which leads in turn to inbreeding depression.

Sprague (1955) reports that the effectiveness of mass selection for several ear characters are presented by Williams and Welton (1915). The results from one of their experiments involving selection for ear length in one corn variety were presented. An examination of these data indicates that the selection for ear length was not effective in separating the original population into two distinct groups, nor did the selection have any important effect on yield. Two of the factors which led to the ineffectiveness of the selection practiced were small selection differential and lack of parental control (interpollination). These two forces might be sufficiently important to mask the effects of the selection practiced.

Inbreeding and Crosses in Corn

According to Sprague (1955), the first inbreeding experiments which led to an interpretation of inbreeding depression and the restoration of vigor upon crossing were reported by Shull.

Shull (1909) concluded from his experiments with Indian corn that (1) in an ordinary field of corn, the individuals are generally very complex hybrids and (2) the deterioration which takes place as a result of self-fertilization is due to the increase in homozygosis.

East (1908) presented data on the inbreeding and crossbreeding of maize. He found that the crosses between inbred lines were more vigorous than the parental lines and that some corn species thrive under inbreeding while others appear to deteriorate (1909). He further stated that maize is reduced in vigor in one generation, so that the difference between selfed and crossed plants is noticeable in seedlings two weeks old.

Jones (1918) reported on the effects of inbreeding in his experiments with the following points: (1) Continued inbreeding results in segregation of a variable complex into a number of diverse types which are uniform within themselves; (2) the change in size, structures, or function and reduction in variability is most noticeable in the earlier generations of inbreeding, rapidly becomes less and the surviving inbred strains are uniform and constant; (3) no single effect can be attributed to inbreeding other than reduction of variability.

Jones (1918) also summarized his work on crossbreeding with the following points: (1) Heterosis accompanies heterogeneity in germinal constitution whether or not the organisms crossed are from the same stock or diverse stocks; (2) heterosis is shown as an increase in the size of parts rather than the increase in the number of parts; (3) heterosis may have a stimulating effect on some characters and depressing effect on others in the same organism.

Jones and Mangelsdorf (1925) reported that during the process of inbreeding in corn, with the resulting segregation , recombination and the automatic elimination of heterozygous combinations of factors, selection for particular characters is somewhat effective. By choosing tall plants as progenitors in each generation, tall strains can be produced. Best productiveness, yield of grain, which is due to the plant's entire energies show no simple relation. Promising strains during the first generations may be very unproductive or undesirable in some respects when finally reduced to uniformity and constancy. This emphasizes the fact that effective selection must be based upon the performance of the plants after homozygosity is attained.

Jenkins (1935) reported the effects of inbreeding and selection within inbred lines of maize upon the hybrids made after successive generations of selfing. Two progenies from the first to the eighth generation of inbreeding inclusive, except for the seventh, of 14 inbred lines each of Lancaster Surecrop and of Iodent were topcrossed with Krug. One of these progenies from each inbred line in each generation was the selected progeny representing the direct line of descent. The other represented a sister progeny, chosen at random from among those discarded in favor of the one selected to continue the pedigree.

Selection between sister progenies was effective in isolating those progenies whose crosses were slightly but consistently more productive than those of their discarded sibs. Selection was ineffective in isolation strains whose crosses differed from those of their parents in productiveness or in any of the later characters studies.

The inbred lines acquired their individuality as parents of topcrosses very early in the inbreeding processes and remained relatively stable thereafter.

The data indicated that selection for performance should be based upon the appearance of the parent lines.

The early individuality of the lines in crosses should permit their early testing, possibly after the first and certainly after the second generation of inbreeding. The early stability of their lines in crosses is explained on the basis of the number of dominant genes present as well as the particular genes present. Essentially equal numbers of dominant alleles will be preserved throughout the successive generation of selfing.

Richey (1925) reported that the yield of 70 F_1 crosses between lines of corn self-fertilized for six generations before crossing ranged from considerably less to considerably more than the yield of the parent variety.

The average yield of three of these crosses was 30 percent more than that of the parent variety, and the consistency of the data showed clearly that this superiority was not due to chance.

Comparisons between successive generations of self-fertilized lines and between crosses following self-fertilization for different numbers of generations showed the importance of selection in obtaining larger yields by the methods followed, and indicates that the principle role of self-fertilization is to isolate definite lines differing from each other among which selection may be practiced.

The data indicated that there is little or no relation between the productiveness of the self-fertilized lines and that of their crosses and that the final value of the lines for crossing must be determined by comparisons of the productiveness of their crosses.

Hayes and Johnson (1939) produced inbred lines of corn by the pedigree method from crosses between inbreds where one parent at least of each cross, was outstanding in ability to withstand lodging and in smut resistance. The inbreds produced by the pedigree method was studied in inbred-variety crosses to determine their combining ability. The evidence indicated that lines of good combining ability are attained more frequently from crosses between inbreds that themselves are good combiners than from crosses between inbreds that are low in combining ability.

Lonnquist and McGill (1956) reported on the performance of corn synthetics in advanced generations of synthesis and after two cycles of recurrent selection.

These workers found that synthetic varieties of corn produced by intercrossing selective S_1 lines of high combining ability as determined in topcross combinations can be expected to maintain their improved productivity in advanced generations through mass selection procedures. Visual selection of the plants resulted in slight improvement in yield from syn-2 to syn-4 for several synthetics studied.

Four second cycle synthetics averaged 96 percent of hybrid U. S. 13 in yield as compared with 82 percent for the first cycle populations over a two-year period of testing. Moisture at harvest averaged 105 percent and 103 percent of hybrid U. S. 13.

MATERIALS AND EXPERIMENTAL PROCEDURES

I. Experimental Animals

A. *Coturnix coturnix japonica*

The foundation stocks for this study was the result of a cross between birds from the University of California, Davis, California and birds obtained from Dr. D. Douma, Bozeman, Montana. However, the controls for the quail study were strictly birds from the University of California. For more detail on the foundation stocks, one can refer to the Doctorate dissertation written by Mahn (1968).

B. White Leghorn Chickens

The foundation stocks for the project involving the chickens came from Hyline Poultry Farms, Johnston, Iowa. These birds were the result of crossing four inbred lines. In each generation, the control hatching-eggs were the Cornell random bred strain obtained from Purdue University.

II. Experimental Materials

A. Quail

The Montana Agricultural Experiment Station, Bozeman, Montana maintains facilities for 768 pair of Japanese quail. Mated quail are kept in individual cages (Figure 1) during their laying period. They are housed at random with respect to treatments and replications in 8 banks, each of which contains 96 cages with 12 cages per row and 8 rows per bank (Figure 2). The quail are housed at 4 weeks of age in a room approximately 20' x 20' x 8' under continuous light, forced draft ventilation, and at a temperature of approximately 70^{o} F. The quail eggs are incubated at 99.5^{o} F for 19 days with an average humidity of 87 percent. As soon as the keets are hatched, they are banded and their identifications are recorded. The keets are transferred to gas heated batteries (Figure 4), for 10 days at 100° F and at about 80° F for the remaining 18 days. After this time, the quail are sexed and assigned to laying cages (Figure 1). The temperature of the quail brooder room is kept at 80° F for about the first two weeks of brooding and then is reduced to approximately 72° F for the remaining brooding period.

B. Chickens

The Montana Agricultural Experiment Station, Bozeman, Montana, maintains facilities for 576 chicken hens for this project. The chickens are assigned at random to cages in 12 banks, each containing 12 cages per row and 4 rows per bank (Figure 3). The chickens are housed in a room about 32' x 60' x 8' and are maintained at a temperature approximating 65° F under continuous light, with pressure controlled ventilation. The chicken eggs are incubated at 100° F for the first 14 days and at 99° F for the remaining 7 days with an average humidity of 87 percent (Figure 6). The chicks are transferred to floor brooders (Figure 5) under continuous light, gas heated, and ventilation by a forced draft ventilation system. The chicks are reared in the floor brooders for one week at 90° F then the temperature is reduced one degree F per week until they are 18 weeks of age, at which time they are assigned to laying cages. The chickens are sexed at 12 weeks of age. The temperature of the brooder rooms are maintained at 80° F for the first 2 weeks of brooding and then it is reduced to about 72° F for the remaining brooding period.

III. Rations

All rations for the chickens and quail for their various levels of development were formulated by Newman and Beeckler (1968) and are presented in Tables I - V (see appendix).

IV. Breeding Procedures

A. White Leghorns

The breeding procedure involved 48 full-sib families of White Leghorn chickens averaging five pullets each, separated into two replicate lines. They were housed in cages in each of two mating programs. Mass selection for egg weight per unit of body weight is applied at 58 weeks of age. Additional production is measured at 82 weeks of age and the index recomputed at that time for statistical analyses. Males are chosen on the mean of female sibs' index. In one program, matings were at random with respect to genetic relationship, while in the other, a generation of full-sib matings was alternated with a generation of wide outbreeding as computed by genetic covariance, and within the limits imposed by selection. Since the matings to produce the inbred group in alternate generations require that each selected female be mated to a full sib, selection of males for this generation was necessarily modified accordingly.

The first generation matings in both groups were made at random with respect to relationship, since individual pedigrees were not available for the four-line incross hybrid White Leghorn foundation birds.

Additionally approximately 96 Cornell random-bred control White Leghorn hens were housed under the same environment. These pullets were furnished in each cycle by means of eggs procured from Purdue to serve as a control to assess genetic changes in the two experimental groups. Hatching dates were synchronized with all groups.

B. Coturnix coturnix japonica

Female selections in the quail study are comparable with the chickens on the project when approximately one-fifth of the females are mass selected.

All males are mated for life with single contemporary females within treatment and replication. The only selection applied to them is the result of the fact they are offspring of selected females in the random mated group, and from the fact that they are not descended from selected females, but also full-sibs of one or more of the selected females in the inbred phase. Thus, no selection computations are necessary in the males except to assure that they are descended from selected females, represent the appropriate replication within treatments, and are appropriately inbred or outbred in the two phases of alternating-generation treatment. In the outbred phase, males will be chosen within progeny groups from approximately the upper 10 percent of the dams. Random bred controls are housed under the same conditions as the other experimental groups. One-half of the total eggs from each female that are gathered during the collection period were incubated and at four weeks of age the birds were randomly mated to become the controls for the next generation.

Family performance is measured by the index =

$$\frac{\text{Egg number x mean egg weight}}{\text{Body weight of the female}}$$

This is tabulated, placed in an array within replications within treatments, The means of the indexes were summarized by sibships and placed in an array at the same time for choosing the males in the chickens.

For additional details concerning the breeding procedures, one can refer to the project outline of Flower (1966).

V. Traits Studied and Experiment Groups

In the experiment to date, the primary concern was with the changes in the 8 quantitative measurements relative to treatments and generations. The 8 measurements are bird weight, shank length, shank width, total egg weight (average egg weight x total egg number), total egg number, index = $\frac{\text{(total egg weight)}}{\text{body weight}}$ average egg weight, shank length x shank width. In both the chickens and quail, data from the base populations were not included in the analyses. The means for the 8 traits are reported in the chickens, but the means in the quail were unavailable for generation I. The experimental groups in this study are as follows; Treatment 1 (alternating generations of inbreeding and outbreeding with selection), treatment 2 (random mating with selection), and treatment 3 (controls under random mating).

STATISTICAL METHODS

The nested or hierarchal classification of analysis of variance was used on all the data to test for difference between breeding treatments. Duncan's Multiple Range test was used to interpret which breeding treatments were different. Linear regressions of all traits on generations were calculated in both the chickens and quail to examine time trends. Analysis of variance for testing the difference between two regression coefficients was used. These procedures are described by Steel and Torrie (1960). The inbreeding coefficients were calculated with the aid of a computer program introduced to Monana State University by Harvey (1968).

RESULTS AND DISCUSSION

Coturnix coturnix japonica Data

Bird Weight

There are significant differences ($P. < 05$) between the mean bird weights of the three treatments in all generations excepting generation II. There is a definite trend inidcating that body weight has decreased from generation II through generation VI (Figure 7). The linear regression coefficients of all traits on generations in all treatments were calculated, however, in treatment 1, they were calculated from data in only generations II, IV and VI (outbred generations). In treatment 1 and 2, the linear regression coefficients were not significantly different ($P > .05$) from the regression coefficient of the controls. It may be that natural selection or management is active in reducing body mass because treatments 1 and 2 have responded in much the same manner as the controls that are random mated with no selection pressure applied.

There is considerably more variation as indicated by the standard deviation in treatment 1 than in treatment 2 which suggests that there may be more room for progress in treatment 1 than in the latter treatment.(Table I). However, there has not been any selection pressure applied to treatment 1 up to generation V because the birds in this treatment have been intolerant to inbreeding. Although in generation V about 80 percent of the females that had an index were selected. There may be selection in favor of small bird weight in all treatments since very large eggs are often lost due to breakage..

Shank Length

The means for shank length between the treatments are significantly different ($P < .01$) in generation II through VI. The data indicates (Figure 8) that treatment 2 is responding in an opposite manner than treatment 1 and treatment 3 (controls). The regression coefficients for treatments 1 and 3 are not significantly different and they are both positive. Since treatment 1 has had virtually no selection pressure applied, it may be presumed that it would be affected by environment and natural selection in much the same manner as the controls. Applied selection in treatment 2 appears to have been effective in decreasing shank length from generation II through generation VI (Table I).

Shank Width

The means for shank width among treatments are significantly different ($P < .05$) in all generations excepting generation IV. It appears (Figure 9) that shank width has decreased from generation II to generation VI. The regression coefficients show no significant differences ($P > .05$). While the biology of the situation is not apparent, natural selection and/or environment may be affecting shank width to produce a narrow shank that may be favored in genetic adaption to the small cages in which the quail are confined. These data are presented in Table I.

Total Egg Weight

The means for total egg weight among the treatments are significantly different ($P < .05$) in all generations. The means for total egg weight have increased (Figure 10) for generation II through generation III. The regression coefficients show no significant difference (Table I). This may indicate that applied selection has not yet been effective in differentially changing the total egg weight. The data indicates that inbreeding, in the odd generations (III, V), reduces reproductive performance which is in close agreement with Sittmann, Abplanalp, and Fraser (1966).

Total Egg Number

The mean total egg number has responded in much the same manner as the mean total egg weight. The mean total egg number was significantly different ($P < .05$) in generation II through generation VI but the regression coefficients among treatments show no significant differences (Table I). It appears (Figure 11) that the three treatments responded at approximately the same rate. The increase in total egg number appears to have been affected almost entirely by natural selection and/or by improvement of environmental conditions.

Index

The mean index among the treatments are significantly different ($P < .05$) in every generation. The effects of inbreeding in treatment 1 (full-sibs) are quite pronounced in alternate generations III and V. In these generations, the indexes decrease but in the immediately following generation it appears that the heterotic effects are quite adequate in restoring the index to a level that is higher than the previous outbred generation. It may be presumed that the mean indexes for treatment 1, in the outbred phases in later generations, will continue to increase to a level that will be superior to the mean indexes of treatment 2 since selection pressure will be available, and treatment variability greater. The regression coefficients show no significant differences ($P > .05$) at this point in the experiment. It appears that the mean index of all treatments (Figure 12) is increasing at approximately the same rate. It is presumed that natural selection and/or an improvement in environmental conditions has been the major force in causing the indexes to increase in this similar manner from generation II to generation VI. The standard deviation in treatment 1 in outbred generation VI is slightly more than that of treatment 2 (Table I). The variability in treatment 1 is considerably greater (8-10%) than the other treatments in the odd generations (inbred generations). Such increased variability will tend to give treatment 1 greater selection differentials over treatment 2 in later generations if reproductive rate continues to improve in treatment 1.

Average Egg Weight

The mean of average egg weights among the treatments are significantly different ($P < .05$) from generation II through generation VI. Investigation of the linear regressions (Figure 13) indicates that treatment 1 is responding in a very different manner than treatments 2 and 3. However, there were no significant difference ($P > .05$) between the regression coefficients. The mean for treatment 1 has remained relatively constant while the other treatments decrease slightly (Table I).

Shank Length x Shank Width

There is a highly significant difference ($P < .01$) among the means for shank length x shank width among treatments in all generations. The regressions of this measurement on generations (Figure 14) indicates that treatment 1 and treatment 3 have decreased at about the same rate. However, the rate at which treatment 2 declines differs from the controls significantly. The selection criterion (index) may have affected the decrease in shank length x shank width mean in treatment 2. It seems evident that natural selection may have played the sole role in treatments 1 and 3, since there is no significant difference between these treatments Table I). This is also in line with the fact that selection pressure, other than natural adaption, has been essentially nil in treatment 1.

Chicken Data

Bird Weight

Mean bird weights among treatments show significant differences ($P < .01$) in both generation I and generation II. Mean bird weight in treatments 1 and 2 have decreased while treatment 3 has slightly increased (Figure 15).

Comparison of the quail data with the chicken data clearly indicates that chickens are tolerant to inbreeding. Waters and Lamber (1936) support this by reporting that fertility and hatchability are not affected to any great extent by one generation of close inbreeding.

The data indicates that selection for the index decreased bird weight. Comparisons of the regression coefficient of weight on generations indicate that treatments 1 and 2 decreased at approximately the same rate while the controls remained nearly the same between generations I and II (Table II). At this point, it would be only speculation to predict that there will be any significant changes occurring in rate of change between treatments 1 and 2 in later generations.

Shank Length

Mean shank lengths among the treatments in generation I and generation II show a significant difference ($P<.01$). The selection criterion may have been responsible for the reduction in shank length since both the treatment groups responded in an opposite direction from the controls (Figure 16). The regression coefficients of treatments 1 and 2 are negative and are not significiantly different but they both significantly differ from the positive regression of the controls (Table II).

Shank Width

There are significant differences among treatment means for shank width in Generations I and II. Shank width increased in all treatments from generation I to generation II (Figure 17) with the controls exhibiting the sharpest increase. If environment has been the major reason for the increase in the mean of the controls and this effect is presumed to be constant over all treatments, then the selection pressure in treatments 1 and 2 which has resulted in a slower increase in the means of the latter two treatments. The regression coefficients were all positive and significantly different from each other at the 5 percent level of significance (Table II).

Total Egg Weight

The treatment means for total egg weight are significantly different in generation I and II. The data indicates (Figure 18) that the mean total egg weight in the controls has increased while treatments 1 and 2 have decreased. The regression coefficients of treatments 1, 2 and 3 are significantly different ($P<.01$). It appears that the index selection may have reduced the means in treatments 1 and 2 and the controls seem to have responded positively to environment and/or natural selection, and consequently have an increase in total egg weight (Table II). It is also apparent that treatment 1 has had a decrease in total egg weight since generation I produced birds with a planned reduction of heterozygosity from inbreeding. Also treatment 2 birds in generation I were offspring from planned hybrids and they may also be losing heterosis thus producing a negative regression coefficient. Again treatment 1 contains more variability than treatment 2 in the inbred phase (generation II) which hopefully provides opportunity for an increased selection differential in that treatment.

Total Egg Number

The means and regression coefficients for total egg number have responded in much the same manner as the mean for total egg weight and possibly for the same reasons (Figure 19). Variability in treatment 1 is also greater than the variability in treatment 2 (Table II).

Index

There are significant differences ($P < .01$) among the treatment mean indexes in generations I and II. The mean index of treatment I has decreased from generation I to generation II but this may be due to a depressing effect of inbreeding in this group. Later generations are needed to show the true effect of the treatment 1 mating system in comparison to that of treatment 2. At this point, the regression coefficients of treatments 2 and 3 show no significant difference. Since the slope of treatment 2 shows no significant difference from the slope of treatment 3, it may be possible that the positive effect from selection pressure is confounded with the negative effect from loss of planned heterozygosity thus producing a slope that is responding to environment or other natural pressure much like the control group (Figure 20). It may be expected that the inbreeding in alternate generations may tend to continue to increase variability and possibly increase the response of treatment 1 to selection in later generations over that of treatment 2 (Table II).

Average Egg Weight

There are significant differences among the treatment means for average egg weights in generation I but the means are not significantly different in generation II. It appears that the regression coefficients are negative in treatments 1 and 2 and positive in treatment 3.

The regressions coefficients are all significantly different among the treatments. The data (Figure 21) indicate that treatments 1 and 2 may be responding to selection while treatment 3 is being affected by environment since the regression coefficients of treatments 1 and 2 are negative while the regression coefficient is positive in the controls. Again the variability in treatment 1, generation II inbreds is greater than the variable of treatment 2 of the same generation Table II).

Shank Length x Shank Width

Means for this trait show no significant difference in generation I but treatments 1 and 2 are significantly different from the controls in generation II. The regression coefficients of treatments 1 and 2 are significantly different from the controls. Even though the regression coefficient of treatment 1 is positive and that of treatment 2 is negative, they show no significant difference (Table II). This may indicate that these means are remaining relatively constant in the treatments where selection pressure is being applied (Figure 22).

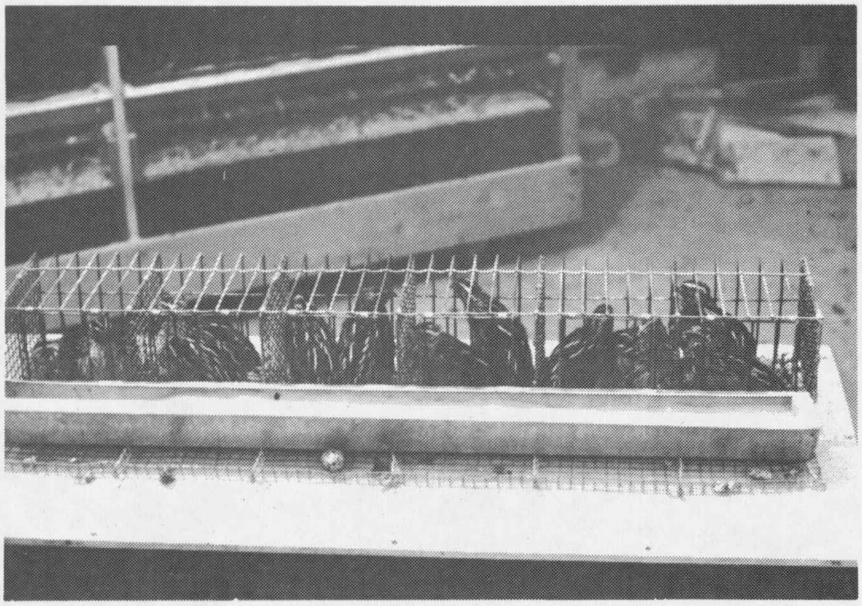


Figure 1. Quail laying cages.

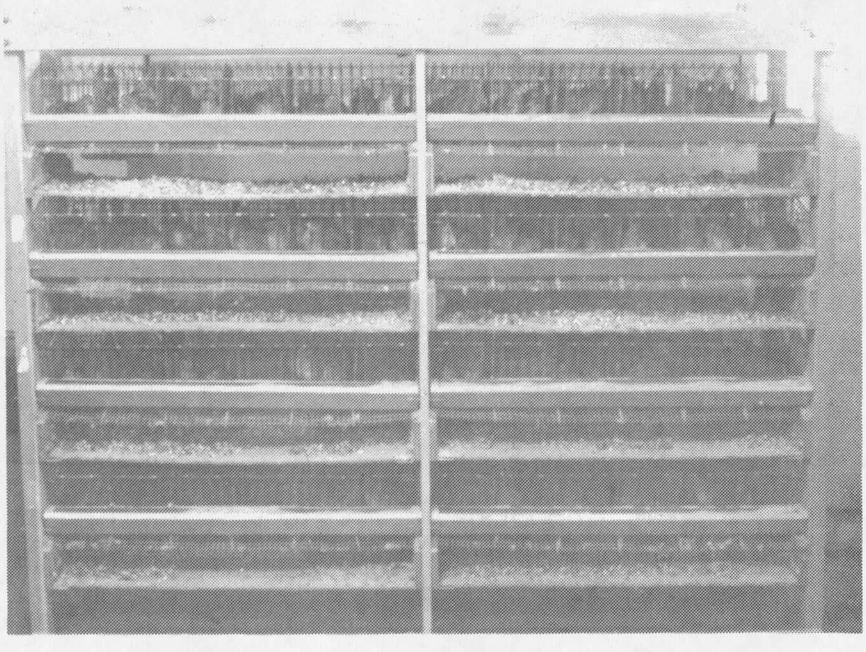
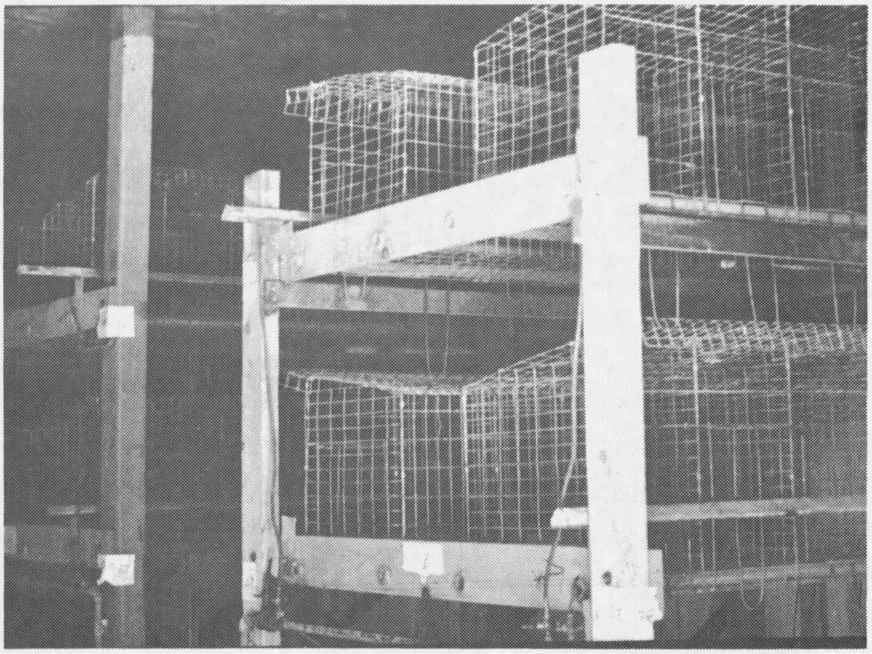


Figure 2. Quail banks (96 cages).



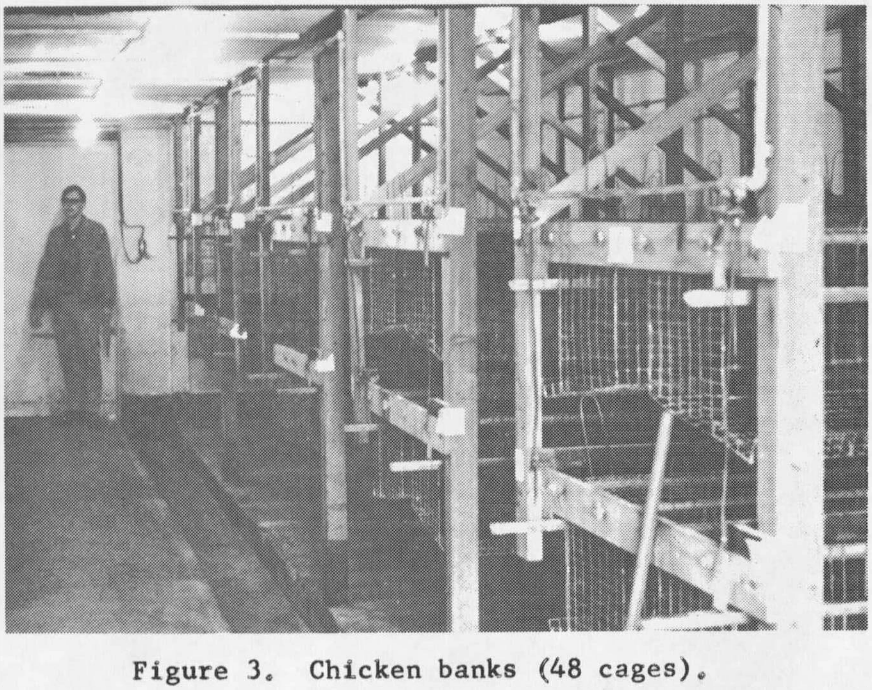


Figure 3. Chicken banks (48 cages).

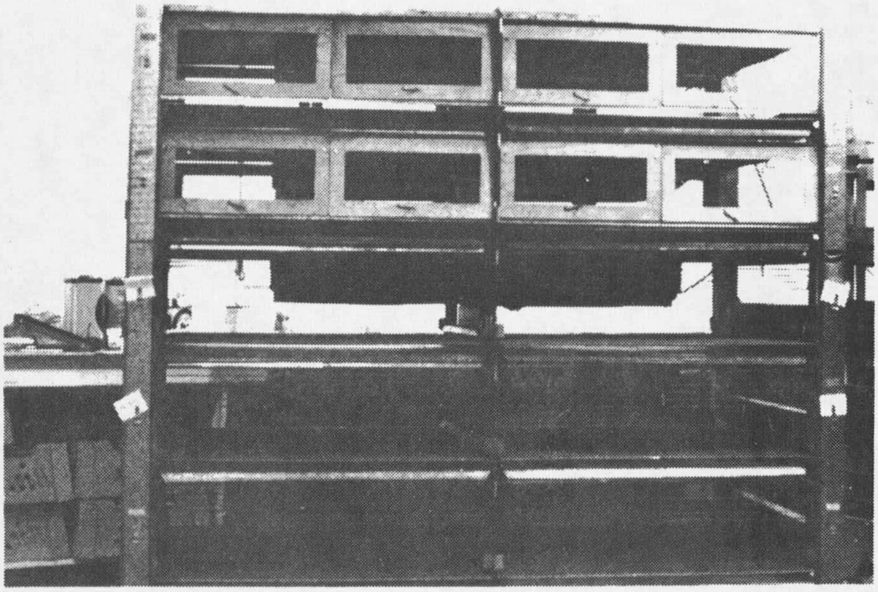


Figure 4. Gas heated batteries for the keets.

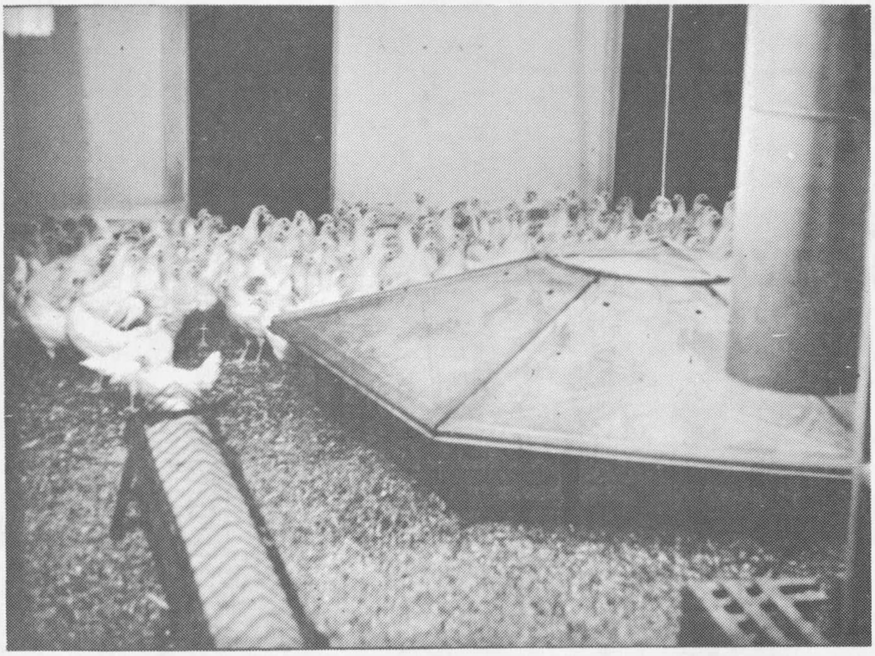
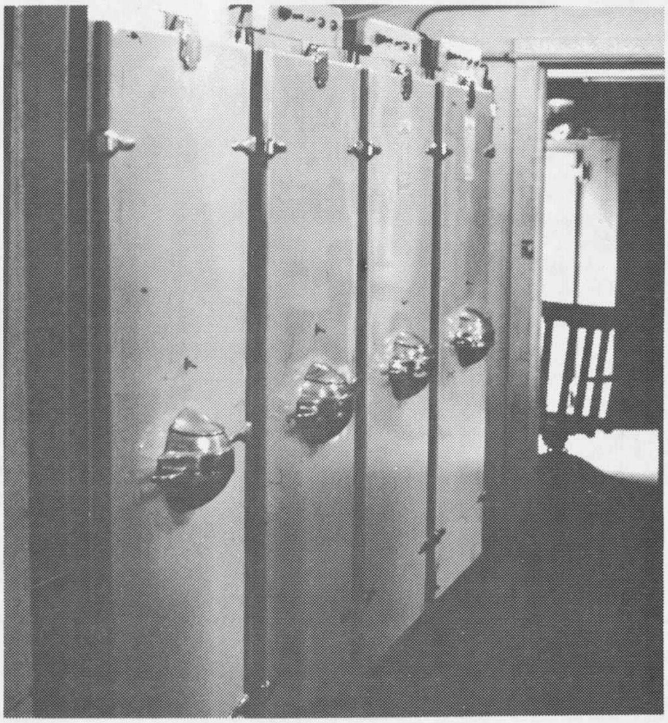


Figure 5. Chicken floor brooders.



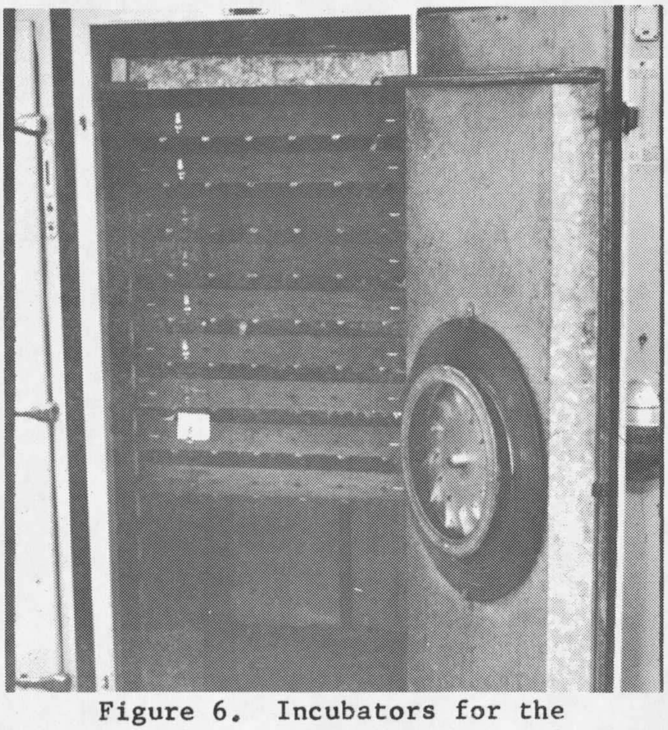


Figure 6. Incubators for the chickens and quail eggs.

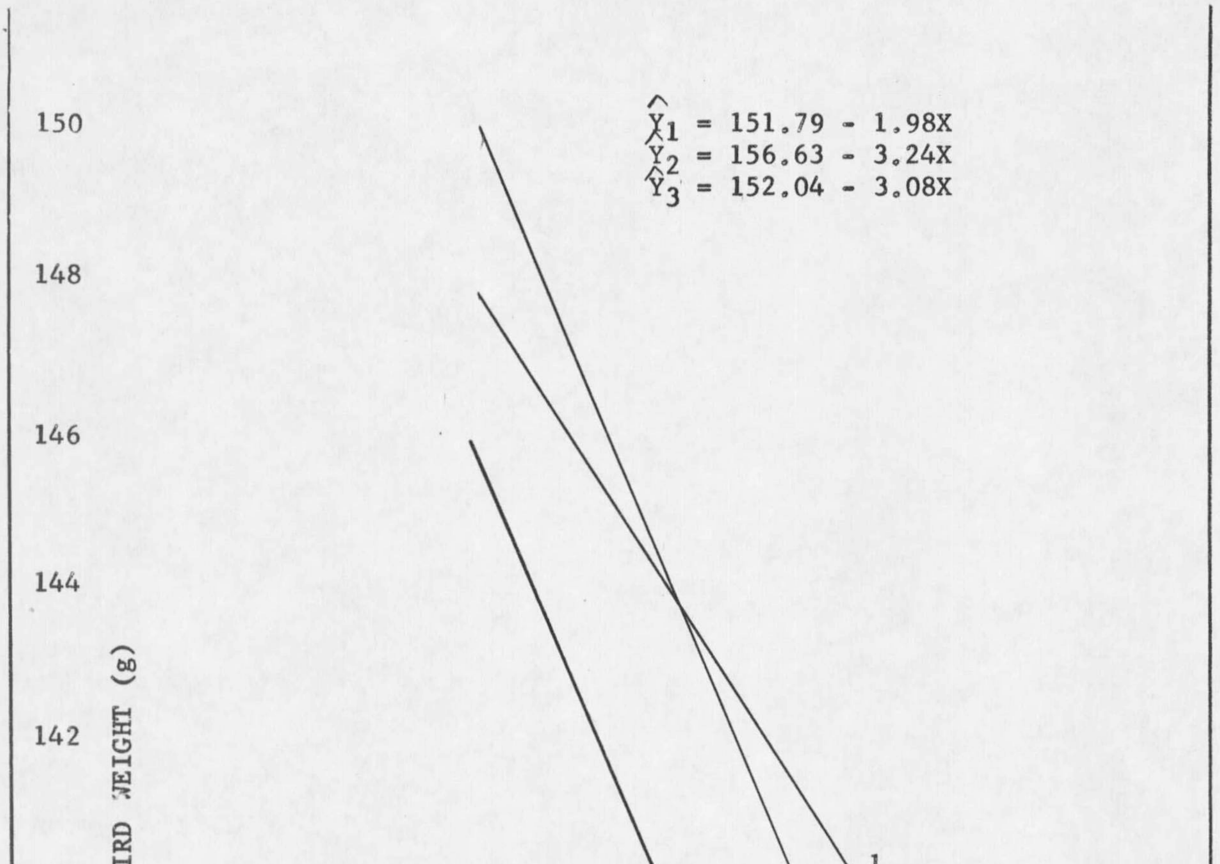


Figure 7. Regression of bird weight on generation (quail).

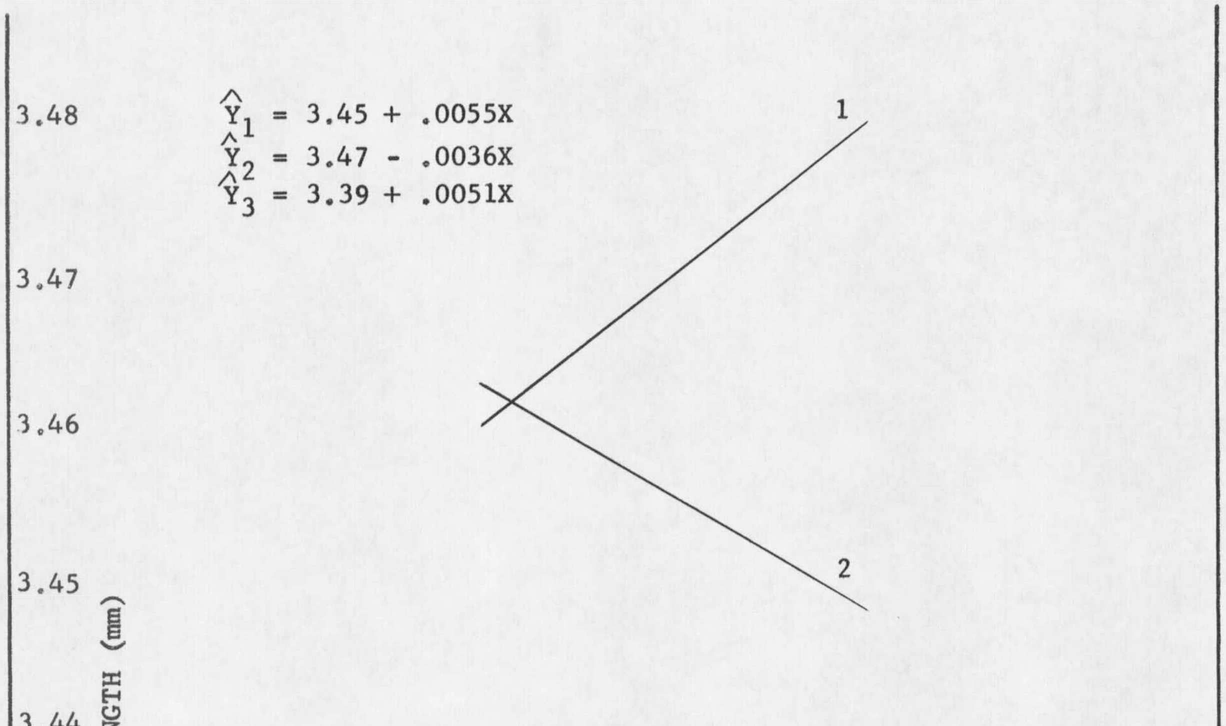


Figure 8. Regression of shank length on generation (quail).

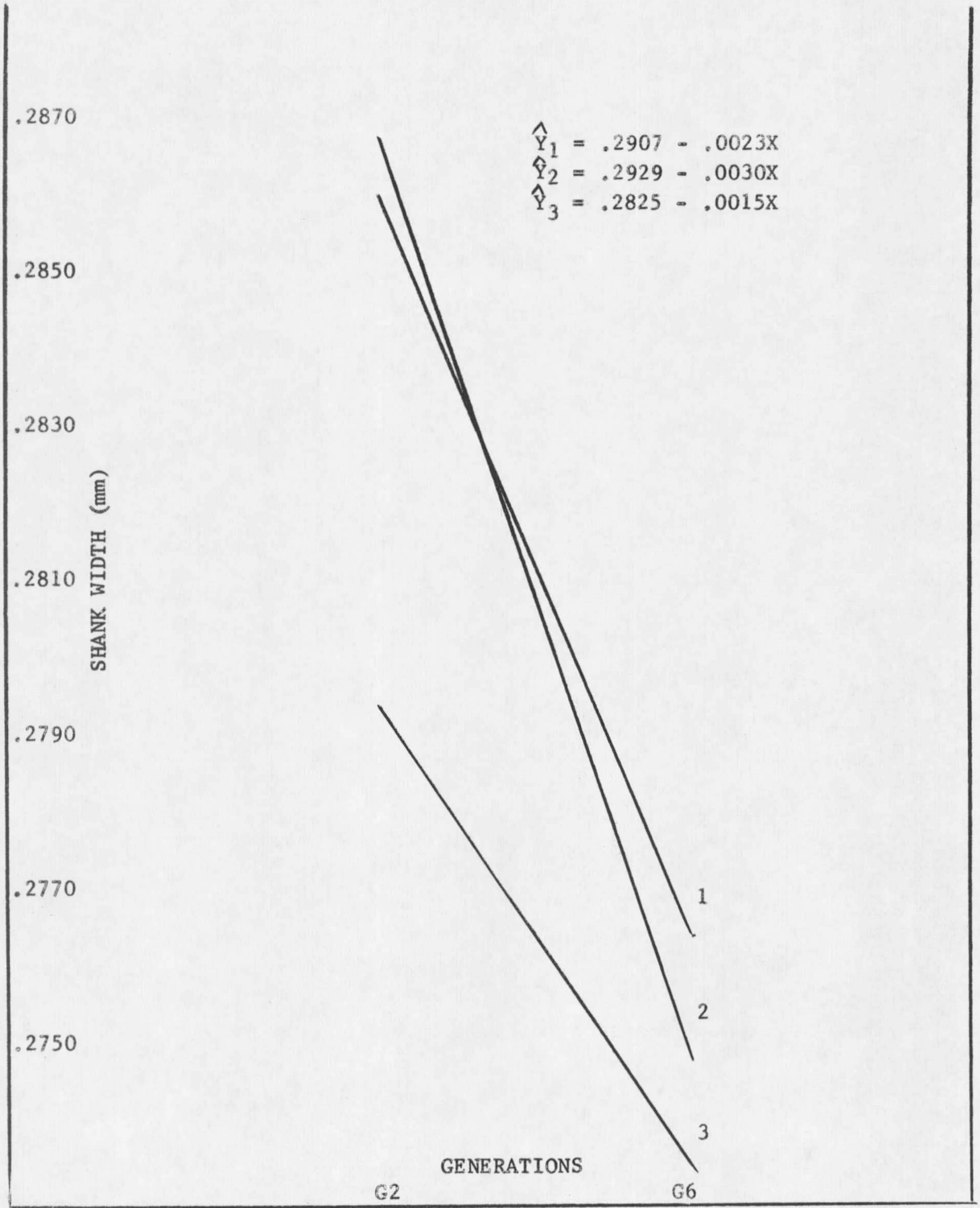


Figure 9. Regression of shank width on generation (quail).

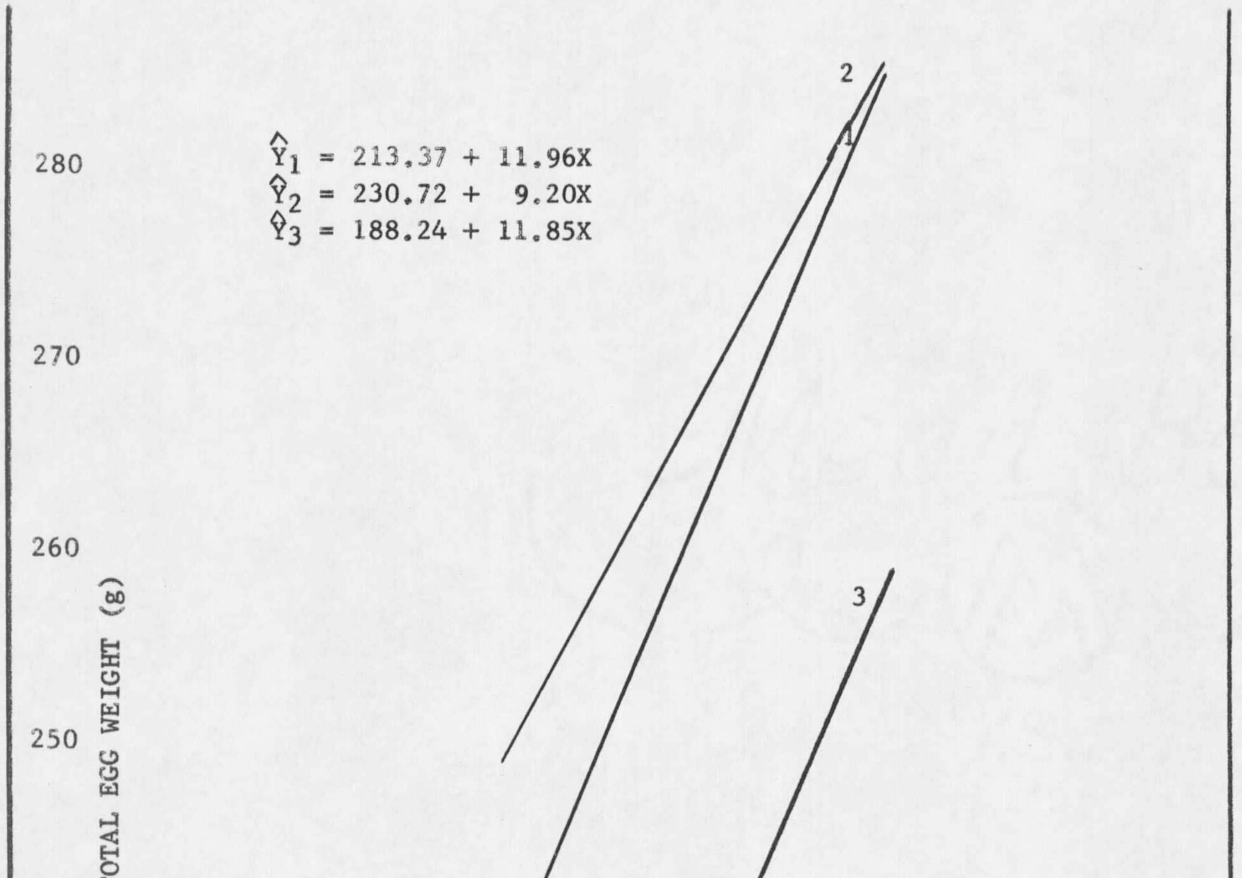


Figure 10. Regression of total egg weight on generation (quail).

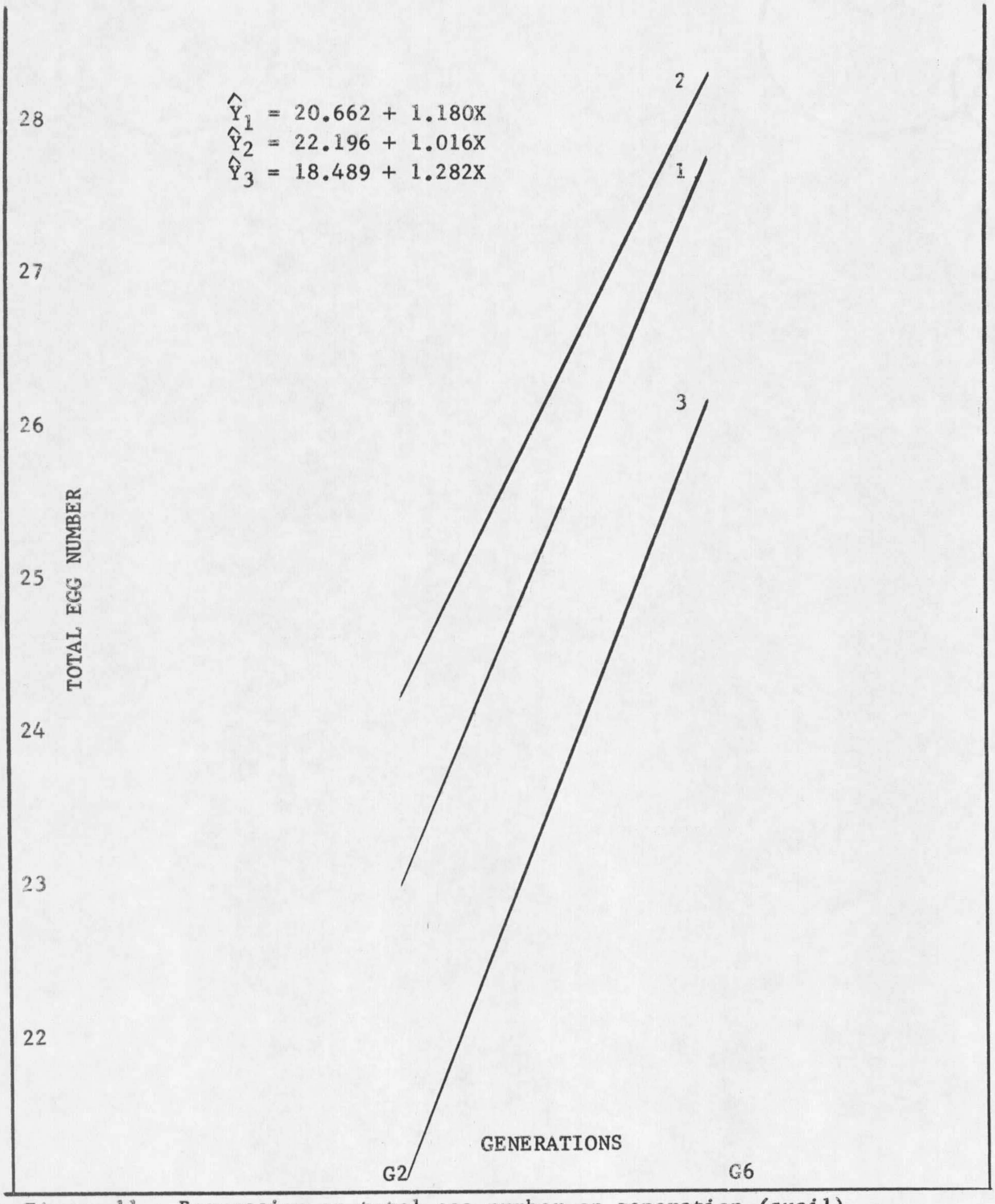


Figure 11. Regression on total egg number on generation (quail).

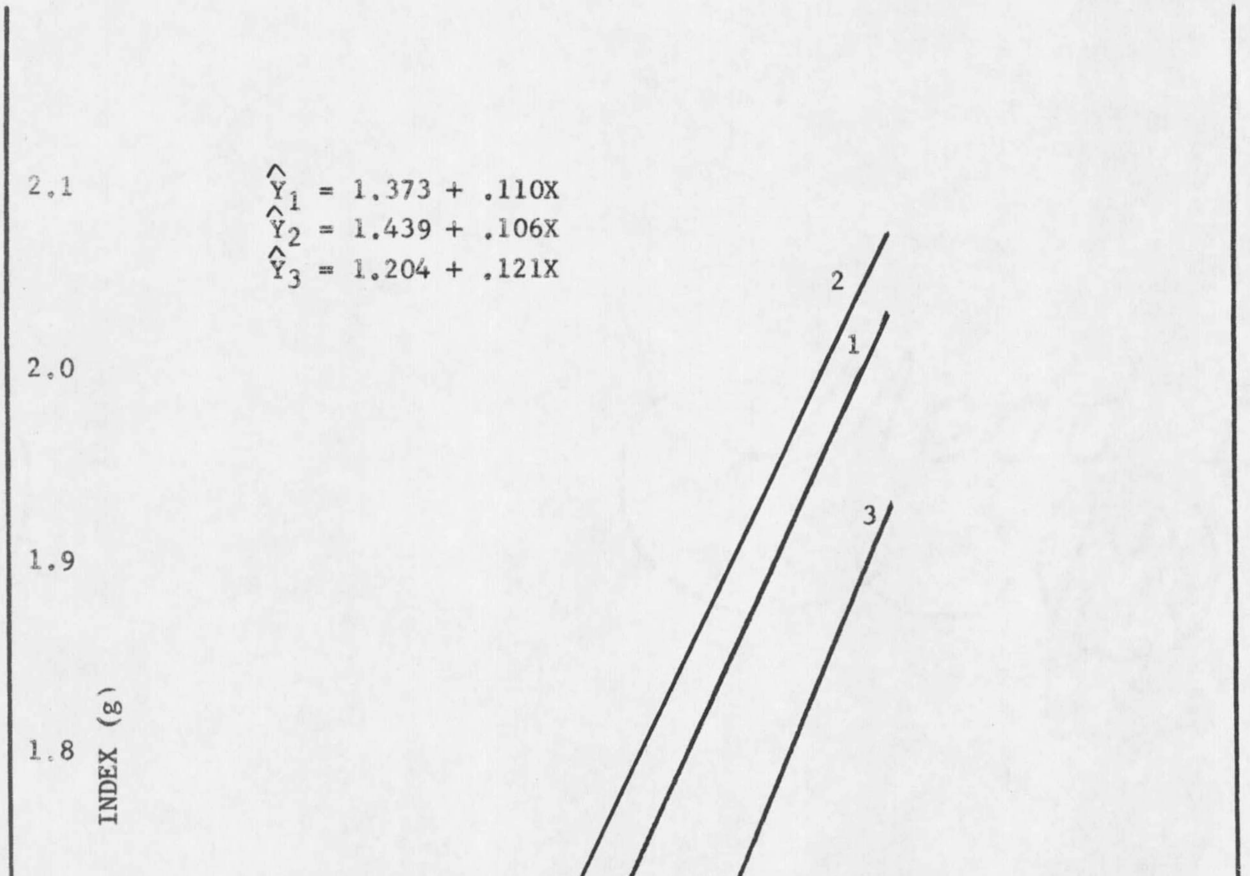


Figure 12. Regression on index on generation (quail).

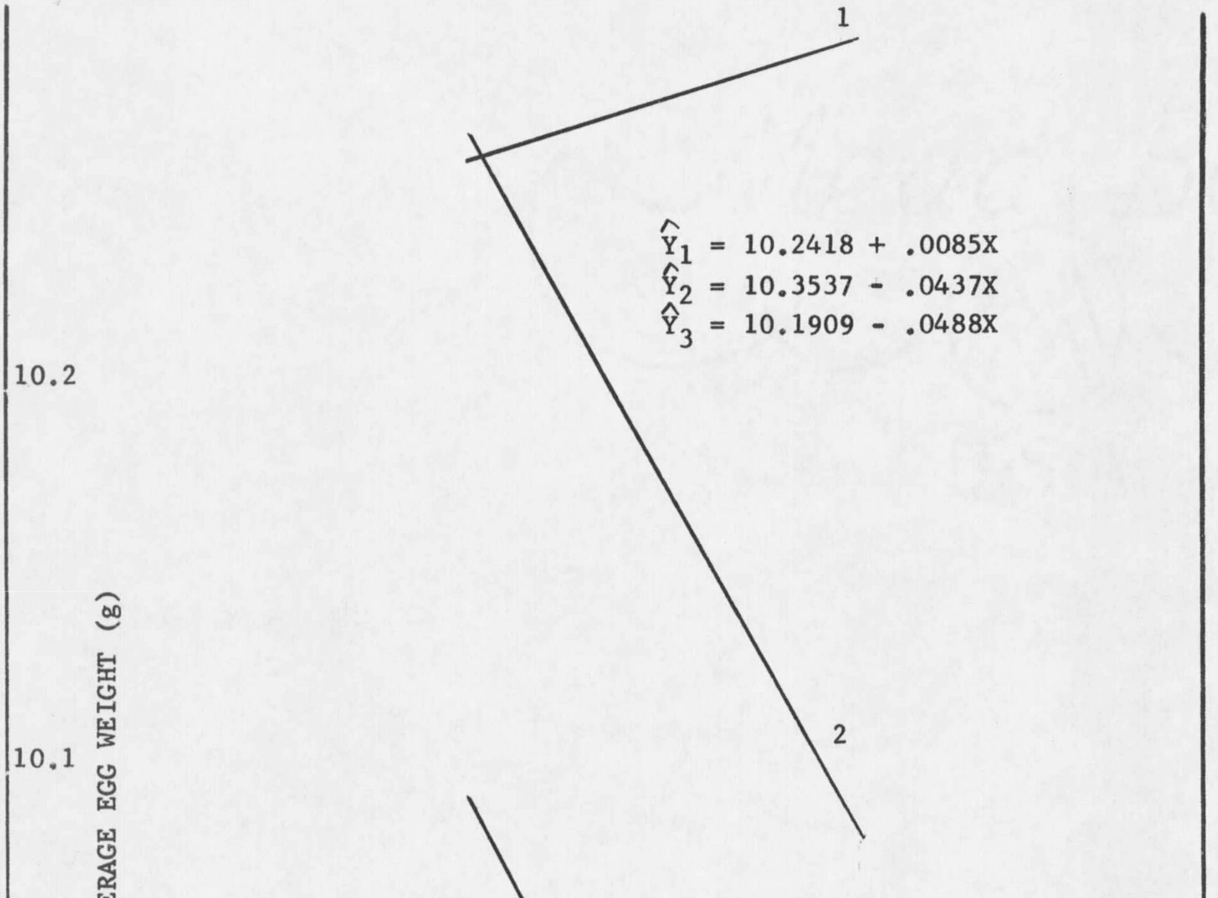


Figure 13. Regression on average egg weight on generation (quail).

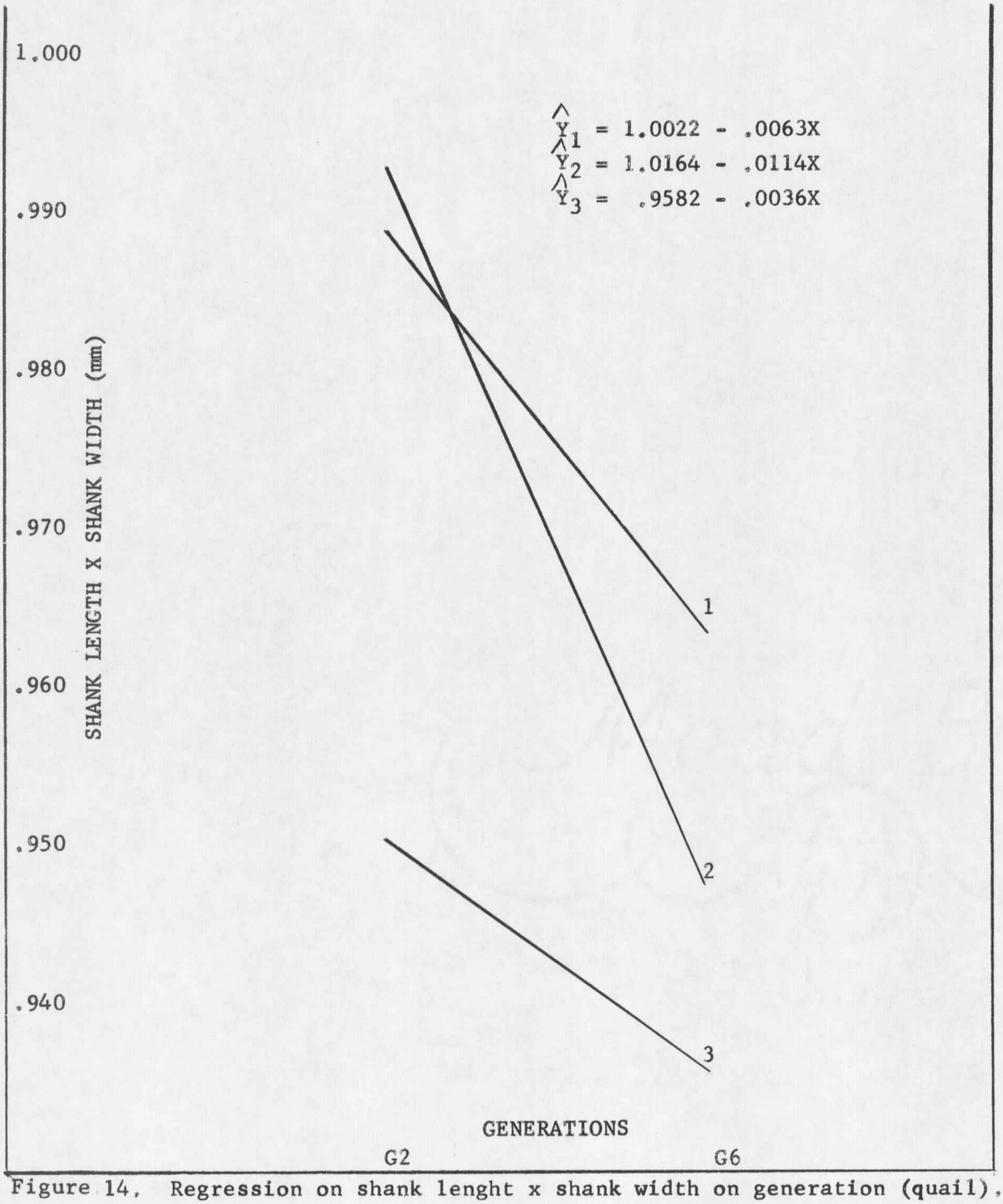


Figure 14, Regression on shank lenght x shank width on generation (quail),

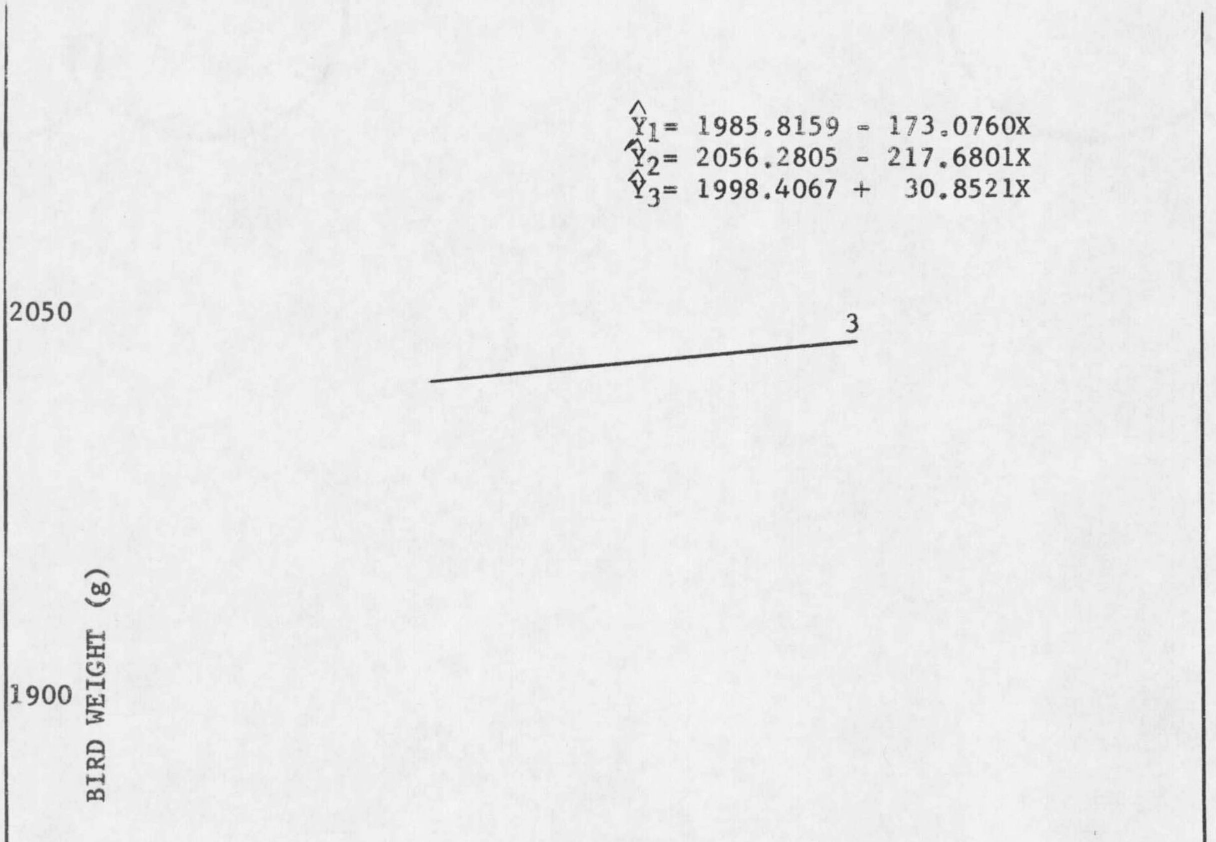


Figure 15. Regression of bird weight on generation (chickens).

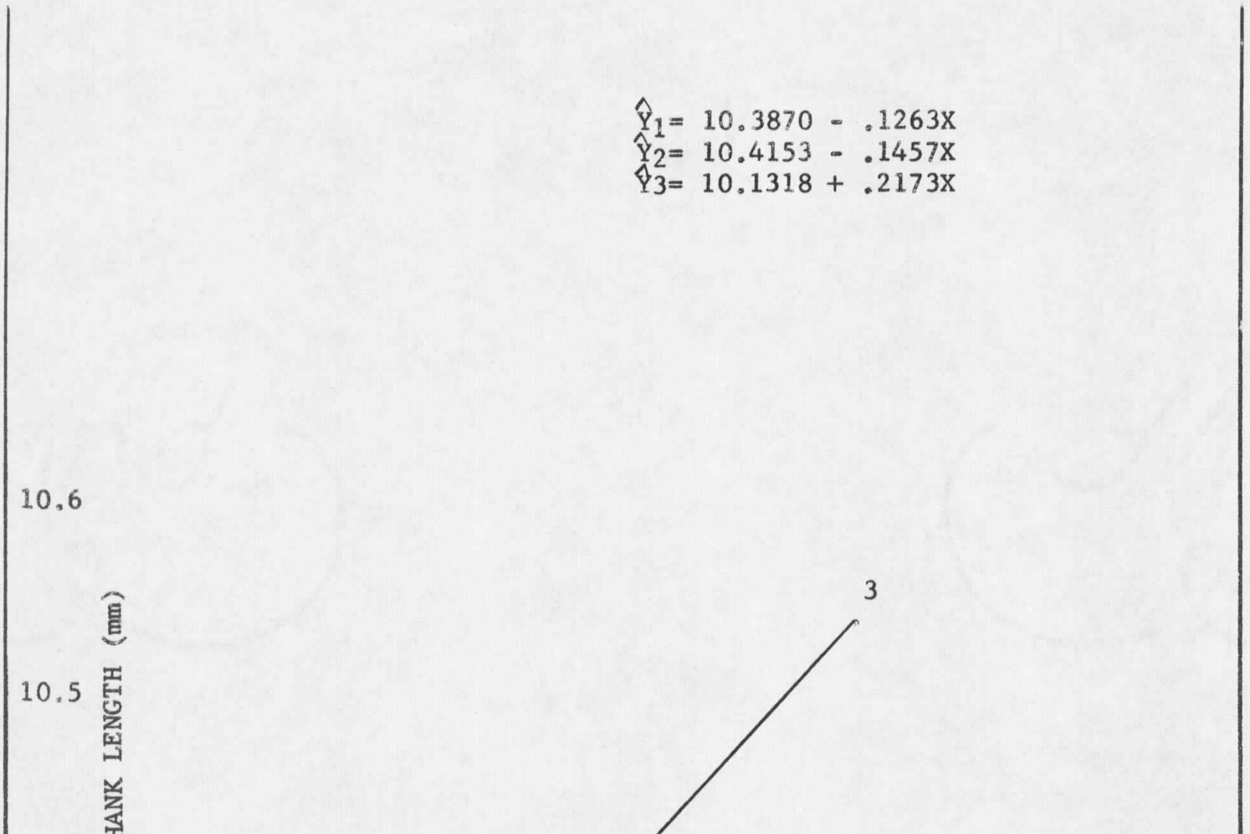


Figure 16. Regression of shank length on generation (chickens).

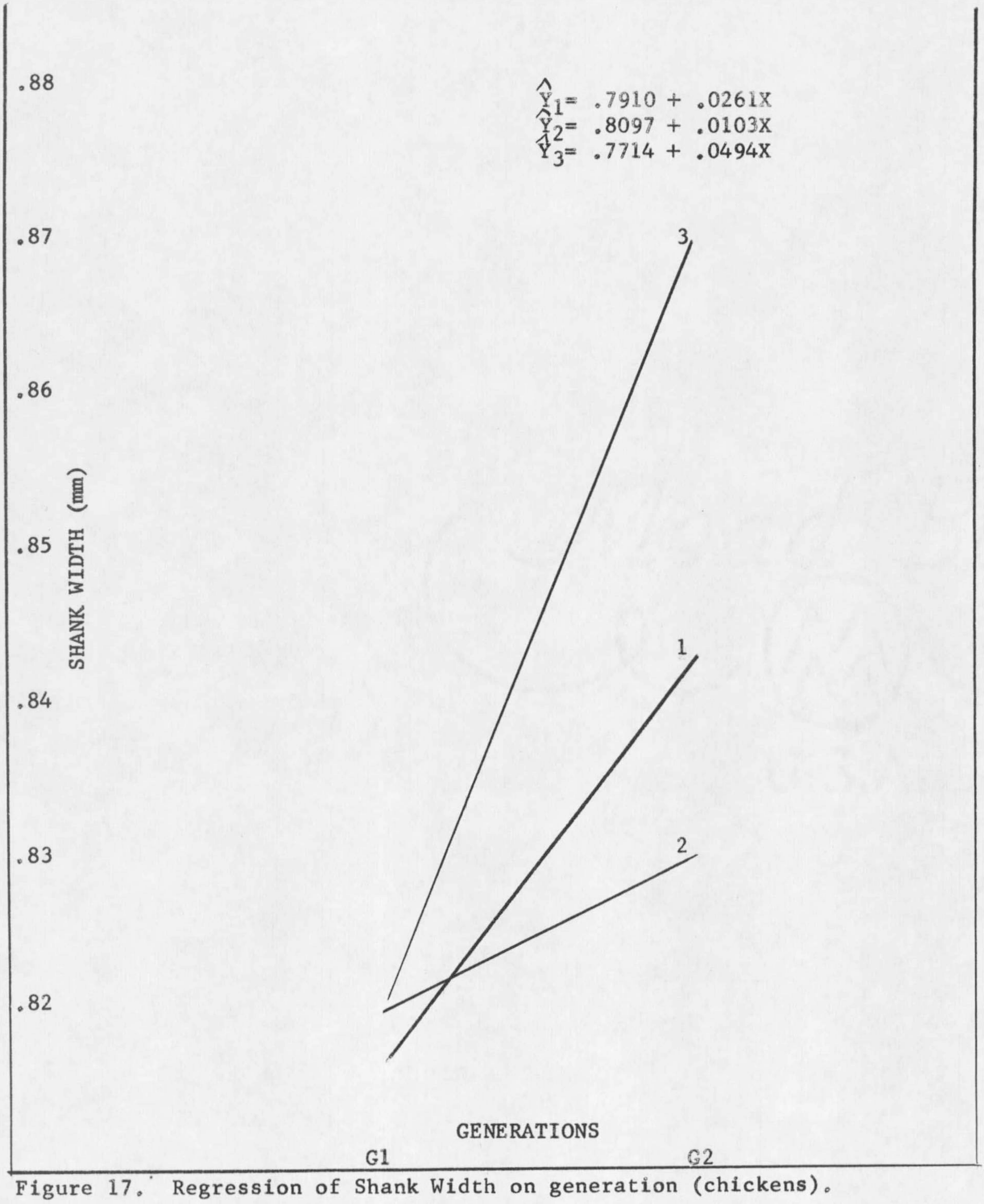


Figure 17. Regression of Shank Width on generation (chickens).

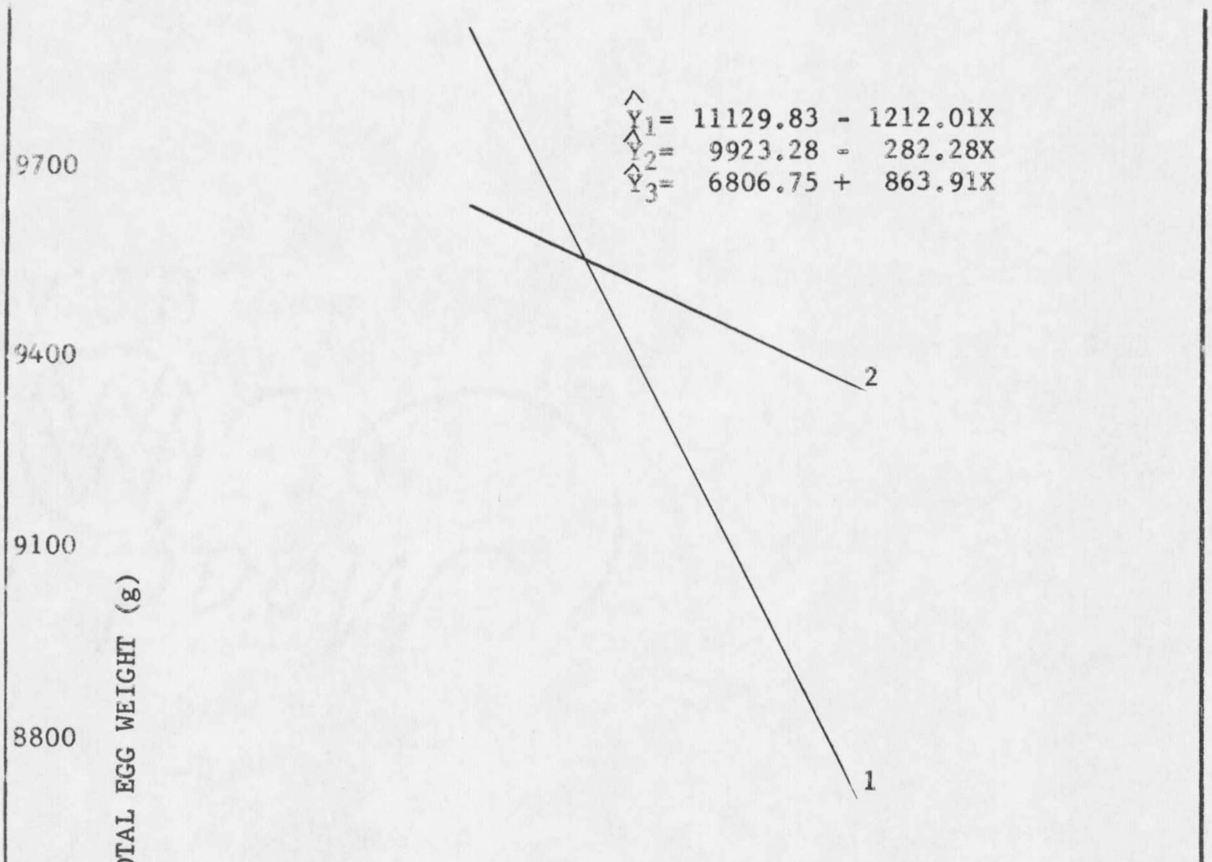


Figure 18. Regression of total egg weight on generation (chickens).

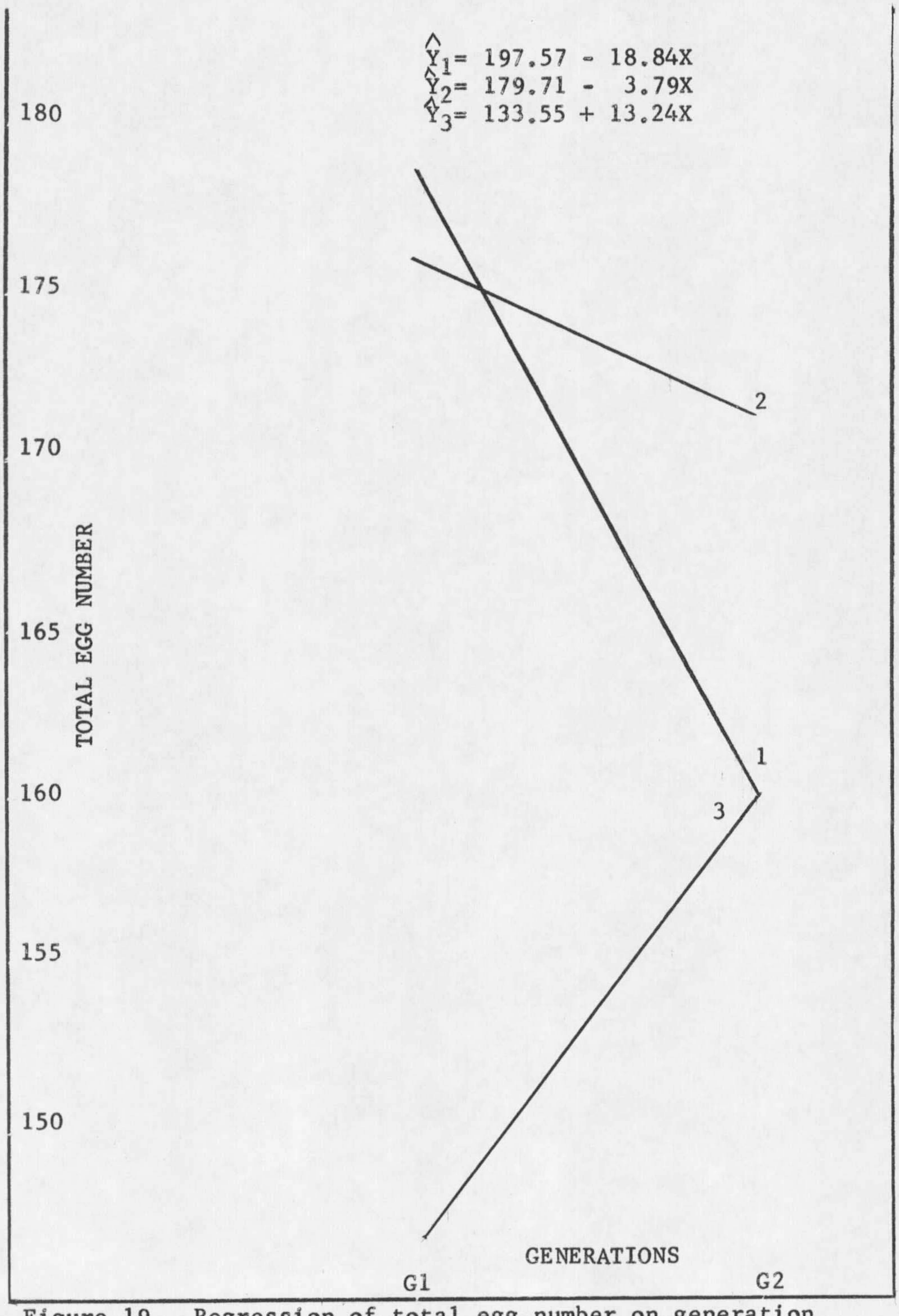


Figure 19. Regression of total egg number on generation (chickens).

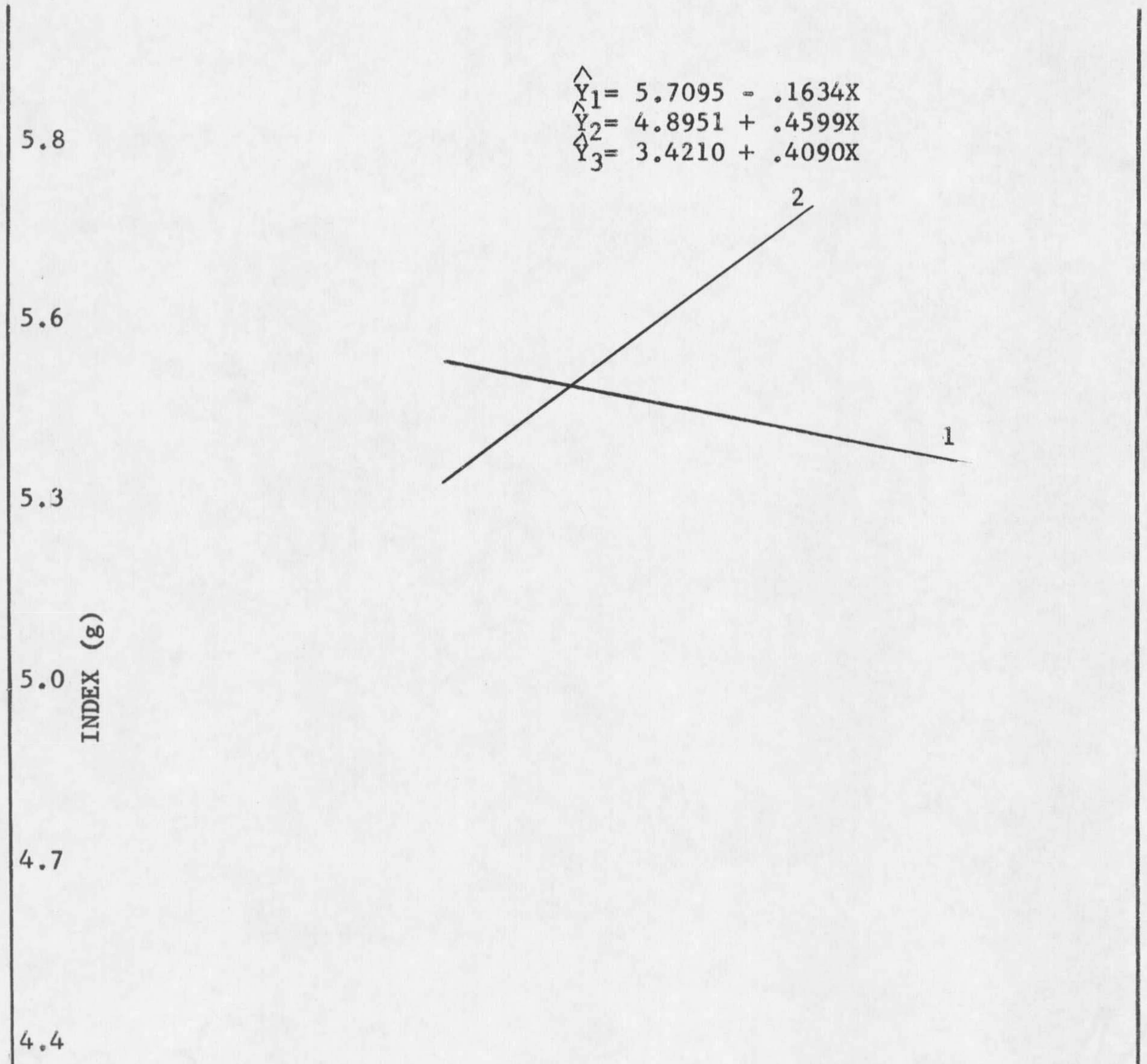
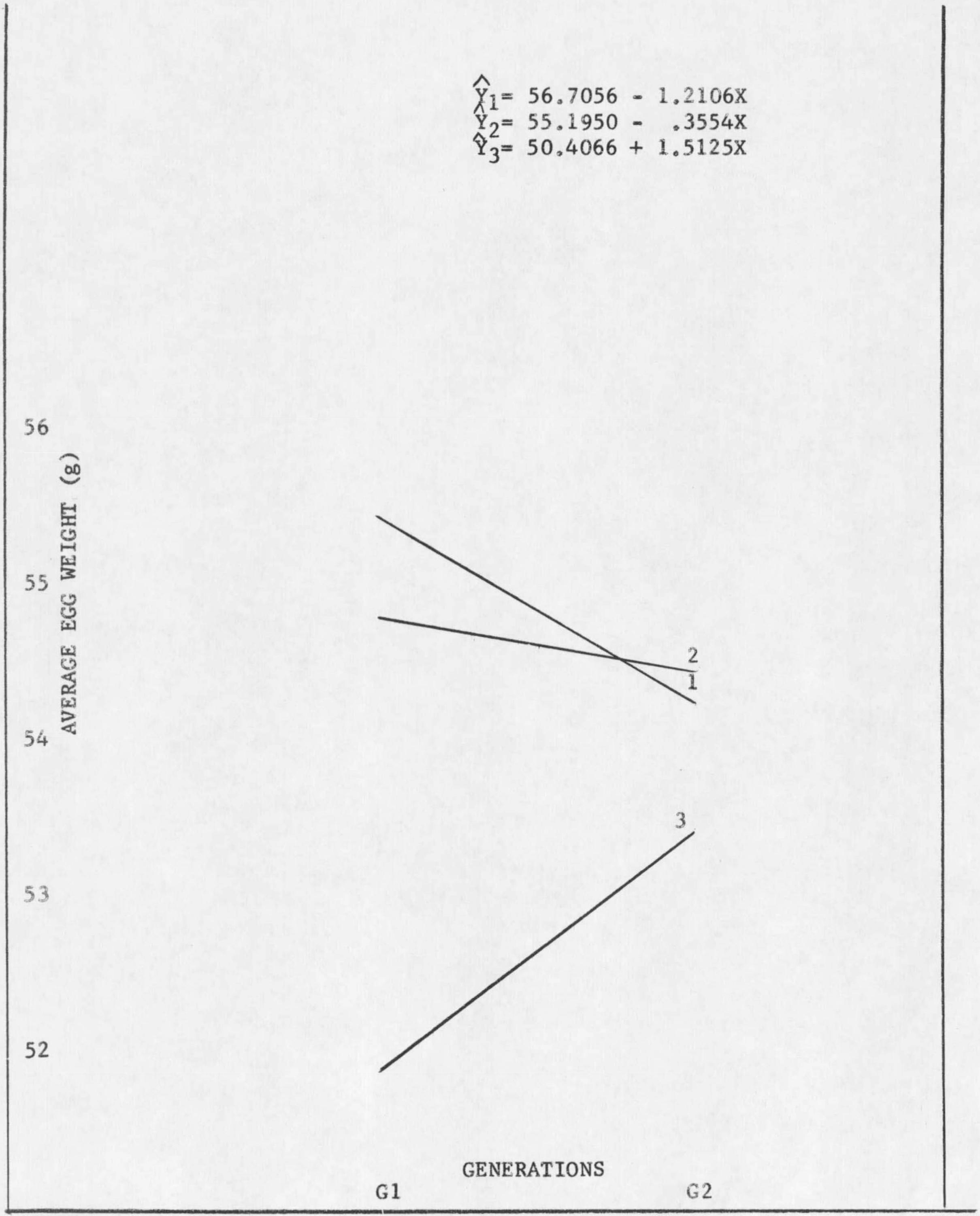


Figure 20. Regression of index on generation (chickens).



$$\hat{Y}_1 = 56.7056 - 1.2106X$$
$$\hat{Y}_2 = 55.1950 - .3554X$$
$$\hat{Y}_3 = 50.4066 + 1.5125X$$

Figure 21. Regression of average egg weight on generation (chickens).

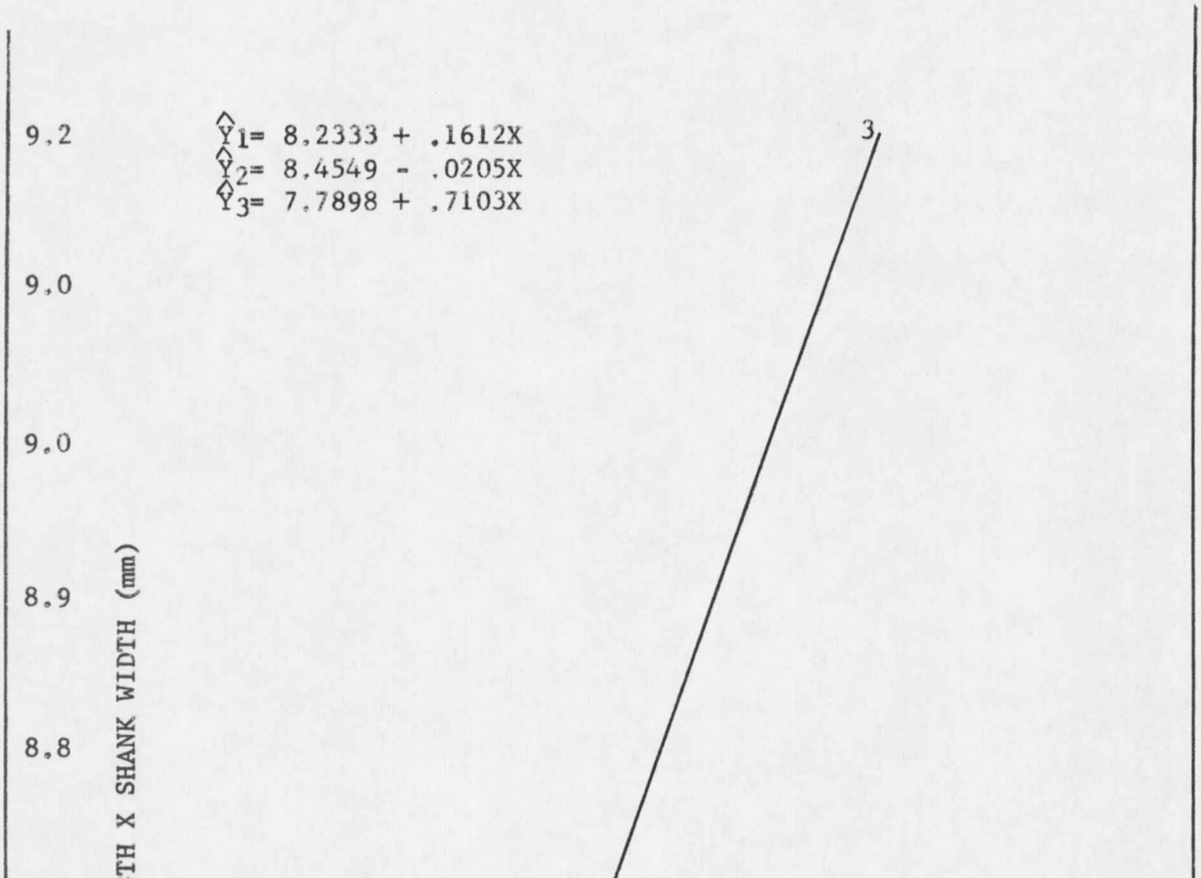


Figure 22. Regression of shank length x shank width on generation (chickens).

TABLE I. INBREEDING COEFFICIENTS, MEANS, DUNCAN'S MULTIPLE RANGE TESTS (D), NUMBER OF BIRDS (N), F TEST, AND STANDARD DEVIATIONS OF QUAIL DATA.

Generation II Trait	F_x	Treatment	Mean	D	N	F Test	S. D.
Bird Weight (g)	.0	T_1	149.22	a	134		16.81
	.0	T_2	150.95	a	126		15.09
	.0	T_3	146.50	a	78		16.18
Shank Length (mm)	.0	T_1	3.47	a		**	0.15
	.0	T_2	3.49	a			0.10
	.0	T_3	3.40	b			0.10
Shank Width (mm)	.0	T_1	0.2858	a		**	0.0177
	.0	T_2	0.2882	a			0.0326
	.0	T_3	0.2770	b			0.0161
Total Egg Weight (g)	.0	T_1	231.93	a		**	85.14
	.0	T_2	242.90	a			84.18
	.0	T_3	199.58	b			77.99
Total Egg Number	.0	T_1	22.58	a		**	7.88
	.0	T_2	23.58	a			7.87
	.0	T_3	20.10	b			7.71
Index (g)	.0	T_1	1.56	a		**	0.57
	.0	T_2	1.62	a			0.55
	.0	T_3	1.37	b			0.52
Average Egg Weight (g)	.0	T_1	10.22	a		**	0.84
	.0	T_2	10.27	a			0.89
	.0	T_3	9.94	b			0.67
Shank L. x Shank W. (mm)	.0	T_1	0.99	a		**	0.07
	.0	T_2	1.01	a			0.12
	.0	T_3	0.94	b			0.06

* Probability of chance occurrence (P∠.05)

** Probability of chance occurrence (P∠.01)

Duncan's Test: When the letters and the numbers are the same between treatments, then the treatments show no significant differences.

TABLE I. (CONTINUED)

Generation III Trait	F_x	Treatment	Mean	D	N	F Test	S. D.
Bird Weight (g)	.25	T_1	145.65	a	69	**	15.81
	.0	T_2	150.78	b	250		16.29
	.0	T_3	144.78	a	97		16.67
Shank Length (mm)	.25	T_1	3.38	a		**	0.11
	.0	T_2	3.45	b			0.11
	.0	T_3	3.40	a			0.11
Shank Width (mm)	.25	T_1	0.2836	a		*	0.0179
	.0	T_2	0.2820	a			0.0164
	.0	T_3	0.2786	b			0.0154
Total Egg Weight (g)	.25	T_1	224.47	a		*	94.44
	.0	T_2	269.91	b			84.53
	.0	T_3	234.90	a			93.05
Total Egg Number	.25	T_1	21.78	a		**	9.06
	.0	T_2	25.96	b			7.80
	.0	T_3	23.09	a			9.12
Index (g)	.25	T_1	1.55	a		**	0.65
	.0	T_2	1.80	b			0.57
	.0	T_3	1.63	a			0.64
Average Egg Weight (g)	.25	T_1	10.28	a_1		*	0.70
	.0	T_2	10.39	a_2			0.91
	.0	T_3	10.18	b_1			0.88
Shank L. x Shank W. (mm)	.25	T_1	0.96	a_1		**	0.07
	.0	T_2	0.97	a_2			0.07
	.0	T_3	0.95	b_1			0.06

* Probability of chance occurrence ($P < .05$)

** Probability of chance occurrence ($P < .01$)

Duncan's Test: When the letters and the numbers are the same between treatments, then the treatments show no significant differences.

TABLE I. (CONTINUED)

Generation IV Trait	F_x	Treatment	Mean	D	N	F Test	S. D.
Bird Weight (g)	0.0	T1	140.79	b	120	*	12.16
	0.0096	T2	137.98	a	241		11.50
	0.0130	T3	137.27	a	108		11.25
Shank Length (mm)	0.0	T1	3.45	a		**	0.11
	0.0096	T2	3.43	b			0.12
	0.0130	T3	3.40	c			0.10
Shank Width (mm)	0.0	T1	0.2823	a			0.0164
	0.0096	T2	0.2810	a			0.0158
	0.0130	T3	0.2784	a			0.0164
Total Egg Weight (g)	0.0	T1	273.21	a		*	85.34
	0.0096	T2	265.03	a			80.67
	0.0130	T3	244.53	b			82.05
Total Egg Number	0.0	T1	26.37	a		*	7.96
	0.0096	T2	26.43	a			7.67
	0.0130	T3	24.32	b			8.38
Index (g)	0.0	T1	1.90	a		*	0.60
	0.0096	T2	1.87	a			0.58
	0.0130	T3	1.74	b			0.61
Average Egg Weight (g)	0.0	T1	10.36	b		**	0.76
	0.0096	T2	10.01	a			0.79
	0.0130	T3	10.12	a			0.74
Shank L. x Shank W. (mm)	0.0	T1	0.97	a2		**	0.07
	0.0096	T2	0.96	a1			0.07
	0.0130	T3	0.95	b1			0.06

* Probability of chance occurrence ($P < .05$)

** Probability of chance occurrence ($P < .01$)

Duncan's Test: When the letters and the numbers are the same between treatments, then the treatments show no significant differences.

TABLE I. (CONTINUED)

Generation V Trait	F_x	Treatment	Mean	D	N	F Test	S. D.
Bird Weight (g)	0.3138	T_1	133.80	a	162	**	13.03
	0.0123	T_2	137.91	b	226		11.76
	0.0219	T_3	134.34	a	111		12.84
Shank Length (mm)	0.3138	T_1	3.43	a		**	0.12
	0.0123	T_3	3.46	b			0.11
	0.0219	T_3	3.44	a			0.09
Shank Width (mm)	0.3138	T_1	.2818	a		**	0.0154
	0.0123	T_2	.2818	a			0.0145
	0.0219	T_3	.2778	b			0.0147
Total Egg Weight (g)	0.3138	T_1	188.04	a		**	89.32
	0.0123	T_2	257.36	b			70.52
	0.0219	T_3	235.67	c			73.14
Total Egg Number	0.3138	T_1	19.38	a		**	8.83
	0.0123	T_2	25.97	b			7.01
	0.0219	T_3	24.22	c			7.66
Index (g)	0.3138	T_1	1.39	a		**	0.63
	0.0123	T_2	1.88	b			0.53
	0.0219	T_3	1.76	c			0.57
Average Egg Weight (g)	0.3138	T_1	9.62	b_1		**	0.87
	0.0123	T_2	9.92	a_2			0.73
	0.0219	T_3	9.77	a_1			0.74
Shank L. x Shank W. (mm)	0.3138	T_1	.97	a		**	0.07
	0.0123	T_2	.97	a			0.06
	0.0219	T_3	.96	b			0.06

* Probability of chance occurrence (P∠.05)

** Probability of chance occurrence (P∠.01)

Duncan's Test: When the letters and the numbers are the same between treatments, then the treatments show no significant differences.

TABLE I. (CONTINUTED)

Generation VI Trait	F_x	Treatment	Mean	D	N	F Test	S. D.	b	D
Bird Weight (g)	.0254	T_1	141.14	a	152	**	13.30	- 1.98	a_2
	.0230	T_2	140.74	a	245		10.17	- 3.24	b_1
	.0417	T_3	136.23	b	101		10.20	- 3.08	a_1
Shank Length (mm)		T_1	3.49	a		**	.12	0.0055	a
		T_2	3.46	b			.10	- .0036	b
		T_3	3.41	c			.09	0.0051	a
Shank Width (mm)		T_1	0.2768	b		**	.0161	- .0022	a
		T_2	0.2729	a			.0160	- .0030	a
		T_3	0.2705	a			.0127	- .0015	a
Total Egg Weight (g)		T_1	280.42	a		**	77.79	11.96	a
		T_2	297.54	b			78.16	9.20	a
		T_3	261.60	c			89.59	11.84	a
Total Egg Number		T_1	27.36	a		**	7.50	1.18	a
		T_2	28.92	b			7.24	1.02	a
		T_3	26.19	a			8.53	1.28	a
Index (g)		T_1	2.00	a		**	.58	0.110	a
		T_2	2.12	b			.57	0.106	a
		T_3	1.92	a			.66	0.121	a
Average Egg Weight (g)		T_1	10.26	a		**	.73	0.0085	a
		T_2	10.28	a			1.01	- .0436	a
		T_3	9.94	b			.81	- .0488	a
Shank L. x Shank W. (mm)		T_1	0.97	a		**	.07	- .0062	a_1
		T_2	0.94	b			.06	- .0114	a_2
		T_3	0.92	c			.05	- .0036	b_1

* Probability of chance occurrence ($P < .05$)
** Probability of chance occurrence ($P < .01$)

Duncan's Test: When the letters and the numbers are the same between treatments, then the treatments show no significant differences.

TABLE II. INBREEDING COEFFICIENTS, MEANS, DUNCAN'S MULTIPLE RANGE TESTS (D), NUMBER OF BIRDS PER TREATMENT, F TEST, STANDARD DEVIATIONS AND LINEAR REGRESSION COEFFICIENTS OF CHICKEN DATA

	Generation 0				Generation 1						
Trait	Treatment	F_x	Mean	N	Treatment	F_x	Mean	D	N	F	S. D.
Bird Weight (g)	T_1	.0	1773.64	44	T_1	.0	1812.74	a	209	**	230.38
	T_2	.0	1779.57	44	T_2	.0	1838.60	a	228		255.11
	T_3	.0	1980.02	287	T_3	.0	2029.26	b	81		291.87
Shank Length (mm)	T_1	.0	10.37		T_1	.0	10.26	a		**	0.4499
	T_2	.0	10.09		T_2	.0	10.27	a			0.4889
	T_3	.0	10.24		T_3	.0	10.34	b			0.4358
Shank Width (mm)	T_1	.0	0.8198		T_1	.0	0.8171	a		**	0.0461
	T_2	.0	0.8208		T_2	.0	0.8199	b			0.0534
	T_3	.0	0.8289		T_3	.0	0.8207	b			0.0949
Total Egg Weight (g)	T_1	.0	11666.38		T_1	.0	9917.57	a		**	1497.72
	T_2	.0	11615.70		T_2	.0	9640.77	a			1775.88
	T_3	.0	9342.69		T_3	.0	7670.59	b			2269.60
Total Egg Number	T_1	.0	200.57		T_1	.0	178.73	a		**	25.47
	T_2	.0	201.62		T_2	.0	175.92	a			32.43
	T_3	.0	171.62		T_3	.0	146.79	b			42.43
Index (g)	T_1	.0	6.62		T_1	.0	5.55	a		**	1.02
	T_2	.0	6.56		T_2	.0	5.35	a			1.23
	T_3	.0	4.81		T_3	.0	3.83	b			1.22
Average Egg Weight (g)	T_1	.0	58.33		T_1	.0	55.49	a			3.73
	T_2	.0	57.67		T_2	.0	54.84	a			3.83
	T_3	.0	54.33		T_3	.0	51.92	a			4.57
Shank L. x Shank W. (mm)	T_1	.0	8.53		T_1	.0	8.39	a		**	0.7367
	T_2	.0	8.29		T_2	.0	8.43	a			0.8366
	T_3	.0	8.50		T_3	.0	8.50	b			1.0912

TABLE II. (CONTINUED)

Generation II Trait	Treatment	F_x	Mean	D	N	F	S. D.	b	D
Bird Weight (g)	T_1	.25	1639.66	a	143	**	198.40	- 173.08	a
	T_2	.0	1620.92	a	164		142.46	- 217.68	a
	T_3	.0	2060.11	b	90		299.78	30.85	b
Shank Length (mm)	T_1	.25	10.13	a		**	.4399	- .1263	a
	T_2	.0	10.12	a			.3376	- .1457	a
	T_3	.0	10.57	b			.4720	0.2173	b
Shank Width (mm)	T_1	.25	0.8432	a		**	.0492	0.0261	a
	T_2	.0	0.8302	b			.0538	0.0103	b
	T_3	.0	0.8701	c			.0595	0.0494	c
Total Egg weight (g)	T_1	.25	8705.70	a		**	1684.64	- 1212.01	a
	T_2	.0	9358.56	b			1389.93	- 282.28	b
	T_3	.0	8534.54	a			1670.24	863.91	c
Total Egg Number	T_1	.25	159.88	a		**	30.61	- 18.84	a
	T_2	.0	172.13	b			26.08	- 3.79	b
	T_3	.0	160.03	a			30.66	13.24	c
Index (g)	T_1	.25	5.38	a		**	1.22	- .16	a
	T_2	.0	5.81	b			.98	0.46	b
	T_3	.0	4.24	c			1.04	0.41	b
Average Egg Weight (g)	T_1	.25	54.28	a			5.80	- 1.21	a
	T_2	.0	54.48	a			3.94	- .36	b
	T_3	.0	53.43	a			3.85	1.51	c
Shank L. x Shank Width (mm)	T_1	.25	8.56	a		**	.74	0.1612	a
	T_2	.0	8.41	a			.72	- .0205	a
	T_3	.0	9.21	b			.7103	0.7103	b

SUMMARY

Quail Data

It appears that any response to applied selection in treatment 2 is being masked by or compounded by environment and/or natural selection since no progress has been made as indicated by the index and most of the other traits. The base populations for treatments 1 and 2 were assumed to have more heterozygosity than the controls. If this assumption is correct, it may be that the birds in these treatments might be decreasing in heterozygosity thus canceling the effects of any selection differential and consequently responding much like the controls. Treatment 1 has had very little applied selection pressure due to its intolerence to inbreeding, thus natural selection and/or environment which is affecting the controls probably is affecting treatment 1 in the same manner.

If the selection pressure can be increased in later generations in treatment 1, it may be possible to get a clearer picture of the real genetic potential of the alternating generations mating system.

Chicken Data

The data seems to indicate that the chickens are responding to the selection criteria (index), in that, most of the measurements taken have responded positively and in the opposite direction from the controls. The inbred generation (II) shows, more variability in all means except shank width. By increasing variability by inbreeding in treatment 1 over treatment 2 in alternate (inbred) generations, it may be possible to get more response to selection in treatment 1 than in treatment 2 in later generations, thus acquiring greater progress in treatment 1 than treatment 2. It may be presumed that the positive mean regressions exhibited by the controls in many of the traits effect either sampling error and/or environmental effect since the stock is considered to be genetically stable (Gowe _et_ _al_. 1959).

The data indicates that more generations are needed to reveal the true breeding worth of alternating inbreeding with wide outbreeding with selection.

APPENDIX

APPENDIX TABLE I. BIRD WEIGHT - ANALYSIS OF VARIANCE IN QUAIL.

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	330.0	110.00	0.60
	Treatments	2	952.0	476.00	2.59
	Families/Rep/Treatment	169	55948.0	331.05	1.80
	Error	163	29936.0	183.65	
	Total	337	87166.0		
Generation III					
	Reps/Treatment	3	1747.0	582.33	2.76
	Treatments	2	3198.0	1599.00	7.59
	Families/Rep/Treatment	156	54503.0	349.40	1.60
	Error	254	53477.0	210.00	
	Total	415	112925.0		
Generation IV					
	Reps/Treatment	3	229.0	76.33	0.67
	Treatments	2	857.0	428.50	3.80
	Families/Rep/Treatment	134	25540.0	190.60	1.69
	Error	329	37117.0	112.82	
	Total	468	63743.0		
Generation V					
	Rep/Treatment	3	1667.0	555.67	4.73
	Treatments	2	1885.0	942.50	8.02
	Families/Rep/Treatment	183	38466.0	210.20	1.79
	Error	310	36509.0	117.45	
	Total	498	78427.0		
Generation VI					
	Rep/Treatment	3	254.0	84.67	0.91
	Treatments	2	1773.0	886.50	9.55
	Families/Rep/Treatment	177	32829.0	185.47	2.00
	Error	315	29250.0	92.86	
	Total	497	64106.0		

APPENDIX TABLE II. SHANK LENGTH - ANALYSIS OF VARIANCE IN QUAIL.

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	0.10	0.03	2.56
	Treatments	2	0.47	0.23	17.56
	Families/Rep/Treatment	169	2.86	0.02	1.27
	Error	163	2.17	0.01	
	Total	337	5.60		
Generation III					
	Reps/Treatment	3	0.09	0.03	3.98
	Treatments	2	0.46	0.23	29.14
	Families/Rep/Treatment	156	2.58	0.02	2.11
	Error	254	1.99	0.01	
	Total	415	5.13		
Generation IV					
	Reps/Treatment	3	0.25	0.08	11.99
	Treatments	2	0.28	0.14	19.96
	Families/Rep/Treatment	134	2.86	0.02	3.07
	Error	329	2.28		
	Total	468	5.67		
Generation V					
	Reps/Treatment	3	0.26	0.08	14.39
	Treatments	2	0.15	0.07	12.43
	Families/Rep/Treatment	183	3.55	0.02	3.25
	Error	310	1.85	0.01	
	Total	498	5.81		
Generation VI					
	Reps/Treatment	3	0.17	0.06	10.31
	Treatments	2	0.47	0.24	42.54
	Families/Rep/Treatment	177	2.92	0.02	2.97
	Error	315	1.75	0.01	
	Total	497	5.31		

APPENDIX TABLE III. SHANK WIDTH - ANALYSIS OF VARIANCE IN QUAIL.

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	0.000732	0.000244	0.423445
	Treatments	2	0.006561	0.003281	5.690048
	Families/Rep/Treatment	169	0.099060	0.000586	1.016644
	Error	163	0.093979	0.000577	
	Total	337	0.200333		
Generation III					
	Reps/Treatment	3	0.001556	0.000519	2.304162
	Treatments	2	0.001572	0.000786	3.490128
	Families/Rep/Treatment	156	0.051636	0.000331	1.470076
	Error	254	0.057190	0.000225	
	Total	415	0.111954		
Generation IV					
	Reps/Treatment	3	0.002319	0.000773	3.510811
	Treatments	2	0.001297	0.000648	2.944923
	Families/Rep/Treatment	134	0.044540	0.000332	1.509434
	Error	329	0.072449	0.000220	
	Total	468	0.120605		
Generation V					
	Reps/Treatment	3	0.002396	0.000799	5.698396
	Treatments	2	0.001709	0.000854	6.097647
	Families/Rep/Treatment	183	0.062210	0.000340	2.425849
	Error	310	0.043442	0.000140	
	Total	498	0.109756		
Generation VI					
	Reps/Treatment	3	0.001389	0.000463	2.709101
	Treatments	2	0.002991	0.001495	8.752481
	Families/Rep/Treatment	177	0.061340	0.000347	2.028419
	Error	315	0.053818	0.000171	
	Total	497	0.119537		

APPENDIX TABLE IV. TOTAL EGG WEIGHT - ANALYSIS OF VARIANCE IN QUAIL.

Source		D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	10592.00	3530.67	0.49
	Treatments	2	93600.00	46800.00	6.62
	Families/Rep/Treatment	169	1154368.00	6830.58	0.97
	Error	163	1152672.00	7071.61	
	Total	337	2411232.00		
Generation III					
	Reps/Treatment	3	22000.00	7333.33	1.05
	Treatments	2	160384.00	80192.00	11.47
	Families/Rep/Treatment	156	1417632.00	9087.39	1.30
	Error	254	1775920.00	6991.81	
	Total	415	3375936.00		
Generation IV					
	Reps/Treatment	3	39136.00	13045.33	2.20
	Treatments	2	52656.00	26328.00	4.44
	Families/Rep/Treatment	134	1158480.00	8645.37	1.46
	Error	329	1949456.00	5925.39	
	Total	468	3199728.00		
Generation V					
	Reps/Treatment	3	27216.00	9072.00	1.93
	Treatments	2	460032.00	230016.00	49.06
	Families/Rep/Treatment	183	1509776.00	8250.14	1.76
	Error	310	1453424.00	4688.46	
	Total	498	3450448.00		
Generation VI					
	Reps/Treatment	3	20944.00	6981.33	1.29
	Treatments	2	100512.00	50256.00	9.30
	Families/Rep/Treatment	177	1482784.00	8377.31	1.55
	Error	315	1701216.00	5400.68	
	Total	497	3305456.00		

APPENDIX TABLE V. TOTAL EGG NUMBER - ANALYSIS OF VARIANCE IN QUAIL

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	124.25	41.42	0.69
	Treatments	2	594.25	295.63	4.77
	Families/Rep/Treatment	169	10363.50	61.32	0.99
	Error	163	10094.81	61.93	
	Total	337	21173.81		
Generation III					
	Reps/Treatment	3	157.13	52.38	0.85
	Treatments	2	1230.44	615.22	10.02
	Families/Rep/Treatment	156	12969.31	83.14	1.35
	Error	254	15593.13	61.39	
	Total	415	29950.00		
Generation IV					
	Reps/Treatment	3	617.94	205.98	3.68
	Treatments	2	316.94	180.97	3.24
	Families/Rep/Treatment	134	10152.13	75.76	1.35
	Error	329	18398.69	55.92	
	Total	468	29530.69		
Generation V					
	Reps/Treatment	3	185.75	61.92	1.27
	Treatments	2	4184.19	2092.09	42.97
	Families/Rep/Treatment	183	14803.50	80.89	1.66
	Error	310	15091.75	48.63	
	Total	498	34265.19		
Generation VI					
	Reps/Treatment	3	311.19	103.73	2.09
	Treatments	2	597.06	298.53	6.03
	Families/Rep/Treatment	177	12663.12	71.54	1.45
	Error	315	15593.56	49.50	
	Total	497	29164.94		

APPENDIX TABLE VI. INDEX - ANALYSIS OF VARIANCE IN QUAIL

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	0.65	0.22	0.67
	Treatments	2	3.15	1.57	4.86
	Families/Rep/Treatment	169	49.08	0.29	0.89
	Error	163	52.74	0.32	
	Total	337	105.62		
Generation III					
	Reps/Treatment	3	1.46	0.49	1.48
	Treatments	2	4.52	2.26	6.88
	Families/Rep/Treatment	156	64.36	0.41	1.26
	Error	254	83.45	0.33	
	Total	415	153.79		
Generation IV					
	Reps/Treatment	3	2.66	0.89	2.73
	Treatments	2	1.74	0.87	2.68
	Families/Rep/Treatment	134	53.22	0.39	1.23
	Error	329	106.65	0.32	
	Total	468	164.27		
Generation V					
	Reps/Treatment	3	0.75	0.25	0.97
	Treatments	2	22.86	11.43	44.39
	Families/Rep/Treatment	183	81.75	0.45	1.74
	Error	310	79.81	0.26	
	Total	498	185.17		
Generation VI					
	Reps/Treatment	3	1.32	0.44	1.54
	Treatments	2	3.29	1.65	5.73
	Families/Rep/Treatment	177	80.96	0.46	1.59
	Error	315	90.38	0.29	
	Total	497	1275.95		

APPENDIX TABLE VII. AVERAGE EGG WEIGHT - ANALYSIS OF VARIANCE IN QUAIL.

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	3.95	1.32	2.45
	Treatments	2	5.87	2.94	5.45
	Families/Rep/Treatment	169	135.35	0.80	1.49
	Error	163	87.72	0.54	
	Total	337	232.89		
Generation III					
	Reps/Treatment	3	1.00	0.33	0.70
	Treatments	2	3.71	1.86	3.90
	Families/Rep/Treatment	156	192.35	1.23	2.60
	Error	254	120.96	0.48	
	Total	415	318.02		
Generation IV					
	Reps/Treatment	3	6.56	2.19	5.09
	Treatments	2	11.67	5.83	13.60
	Families/Rep/Treatment	134	129.61	0.97	2.26
	Error	329	141.09	0.43	
	Total	468	288.93		
Generation V					
	Reps/Treatment	3	3.73	1.24	2.64
	Treatments	2	11.14	5.57	11.81
	Families/Rep/Treatment	183	149.83	0.82	1.74
	Error	310	146.13	0.47	
	Total	498	310.82		
Generation VI					
	Reps/Treatment	3	4.32	1.44	2.16
	Treatments	2	12.14	6.07	9.09
	Families/Rep/Treatment	177	182.33	1.03	1.54
	Error	315	210.07	0.67	
	Total	497	408.85		

APPENDIX TABLE VIII. SHANK LENGTH X SHANK WIDTH - ANALYSIS OF VARIANCE IN QUAIL.

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation II					
	Reps/Treatment	3	0.01	0.00	0.32
	Treatments	2	0.21	0.11	12.38
	Families/Rep/Treatment	169	1.52	0.01	1.05
	Error	163	1.40	0.01	
	Total	337	3.13		
Generation III					
	Reps/Treatment	3	0.02	0.01	1.45
	Treatments	2	0.08	0.04	11.50
	Families/Rep/Treatment	156	0.91	0.01	1.64
	Error	254	0.90	0.00	
	Total	415	1.91		
Generation IV					
	Reps/Treatment	3	0.01	0.00	1.21
	Treatments	2	0.10	0.05	12.96
	Families/Rep/Treatment	134	0.80	0.01	1.68
	Error	329	1.17	0.00	
	Total	468	2.08		
Generation V					
	Reps/Treatment	3	0.05	0.02	7.01
	Treatments	2	0.07	0.03	15.39
	Families/Rep/Treatment	183	1.24	0.01	3.01
	Error	310	0.70	0.00	
	Total	498	2.06		
Generation VI					
	Reps/Treatment	3	0.01	0.00	1.58
	Treatments	2	0.17	0.08	29.94
	Families/Rep/Treatment	177	1.10	0.01	2.24
	Error	315	0.87	0.00	
	Total	497	2.15		

APPENDIX TABLE IX. ANALYSIS OF VARIANCE FOR CHICKEN DATA

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation I Bird Weight	Reps/Treatments	3	463104.00	154368.00	3.45
	Treatments	2	2887168.00	1443584.00	32.23
	Families/Rep/Treatment	88	13136128.00	149274.00	3.33
	Error	423	18945280.00	44787.00	
	Total	516	35431680.00		
Generation II Bird Weight	Reps/Treatments	3	26112.00	8704.00	0.22
	Treatments	2	12922624.00	6461312.00	161.64
	Families/Rep/Treatment	75	4218112.00	56241.50	1.41
	Error	316	12631808.00	39974.07	
	Total	396	29798656.00		
Generation I Shank Length	Reps/Treatments	3	8.38	0.13	0.81
	Treatments	2	4.73	2.37	15.15
	Families/Rep/Treatment	88	44.18	0.50	3.21
	Error	423	66.09	0.16	
	Total	516	115.38		
Generation II Shank Length	Reps/Treatments	3	1.32	0.44	3.30
	Treatments	2	13.43	6.72	50.49
	Families/Rep/Treatment	75	22.04	0.29	2.21
	Error	316	42.04	0.13	
	Total	396	78.42		
Generation I Shank Width	Reps/Treatments	3	0.03	0.01	3.28
	Treatments	2	0.05	0.02	8.31
	Families/Rep/Treatment	88	0.55	0.01	2.15
	Error	423	1.22	0.00	
	Total	516	1.84		
Generation II Shank Width	Reps/Treatments	3	0.02	0.01	2.54
	Treatments	2	0.11	0.10	23.28
	Families/Rep/Treatment	75	0.35	0.00	1.96
	Error	316	0.76	0.00	
	Total	396	1.24		

APPENDIX TABLE IX. (CONTINUED)

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation I					
Total Egg Weight	Reps/Treatments	3	10121216.00	3373738.00	1.13
	Treatments	2	311947264.00	155973632.00	52.47
	Families/Rep/Treatment	88	323993600.00	3681745.00	1.24
	Error	423	1257463808.00	2972727.00	
	Total	516	1903525888.00		
Generation II					
Total Egg Weight	Reps/Treatments	3	10096640.00	3365546.00	1.41
	Treatments	2	52977664.00	26488832.00	11.08
	Families/Rep/Treatment	75	199729152.00	2663055.00	1.11
	Error	316	755789824.00	2391739.00	
	Total	396	1018593280.00		
Generation I					
Total Egg Number	Reps/Treatments	3	3129.00	1043.00	1.08
	Treatments	2	64272.00	32136.00	33.14
	Families/Rep/Treatment	88	103654.00	1177.87	1.21
	Error	423	410215.00	969.78	
	Total	516	581270.00		
Generation II					
Total Egg Number	Reps/Treatments	3	4911.00	1637.00	2.06
	Treatments	2	14312.00	7156.00	9.02
	Families/Rep/Treatment	75	71943.00	959.24	1.21
	Error	316	250687.00	793.32	
	Total	396	341853.00		
Generation I					
Index	Reps/Treatments	3	10.21	3.40	3.09
	Treatments	2	182.49	91.24	82.86
	Families/Rep/Treatment	88	199.39	2.27	2.06
	Error	423	465.79	1.10	
	Total	516	857.88		
Generation II					
Index	Reps/Treatments	3	1.73	0.58	0.52
	Treatments	2	145.87	72.94	65.57
	Families/Rep/Treatment	75	109.71	1.46	1.32
	Error	316	351.48	1.11	
	Total	396	608.80		

APPENDIX TABLE IX. (CONTINUED)

	Source	D.F.	Sum of Squares	Mean Squares	F Test
Generation I					
Index	Reps/Treatments	3	36.00	12.00	0.99
	Treatments	2	791.00	395.50	32.64
	Families/Rep/Treatment	88	2644.00	30.05	2.48
	Error	423	5125.00	12.12	
	Total	516	8596.00		
Generation II					
Index	Rep/Treatments	3	95.00	31.67	1.82
	Treatments	2	97.00	48.50	2.78
	Families/Rep/Treatment	75	2995.00	39.93	2.29
	Error	316	5513.00	17.45	
	Total	396	8700.00		
Generation I					
Shank Length x	Rep/Treatments	3	4.70	1.57	3.05
Shank Width	Treatments	2	1.80	0.90	1.76
	Families/Rep/Treatment	88	143.82	1.63	3.18
	Error	423	217.23	0.51	
	Total	516	367.55		
Generation II					
Shank Length x	Rep/Treatments	3	5.20	1.73	3.43
Shank Width	Treatments	2	38.78	19.39	38.46
	Families/Rep/Treatment	75	79.55	1.06	2.10
	Error	316	159.31	0.50	
	Total	396	282.84		

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